WILD BEE COMMUNITY RESPONSES TO FARM MANAGEMENT PRACTICES, WILDFLOWER RESTORATIONS, AND LANDSCAPE COMPOSITION

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ABSTRACT

WILD BEE COMMUNITY RESPONSES TO FARM MANAGEMENT PRACTICES, WILDFLOWER RESTORATIONS, AND LANDSCAPE COMPOSITION

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Conservation strategies for wild bee pollinators require information on community and species-level responses to environmental resources and stressors, including bees' responses to habitat composition and agricultural practices at different scales. The objectives of this research were to 1) determine the direction and variability of wild bee community responses in blueberry fields to pest management practices and landscape composition by revisiting previously-sampled farms where pesticide use has increased over recent years; and 2) to determine which habitats in Michigan farm landscapes are most suitable for soil-nesting bees, and whether bees nest preferentially in wildflower plantings over nearby unrestored habitats. The abundance, richness, diversity, and community composition of wild bees exhibited strong negative responses to insecticide program risk at the field scale over five years of sampling in 15 blueberry fields. In general, solitary bee species had more negative responses to insecticide risk than social species. Bees responded most strongly to landscape composition at the smallest scale studied (300 m). Wild bee abundance declined with decreasing area of forest and the associated increase in settled areas, while bee richness and diversity declined primarily with insecticide risk. Using emergence traps, I found that wildflower plantings generally support a greater abundance of soil-nesting bees than other habitat types in the surrounding landscape. Bee nesting abundance was higher in mature wildflower restorations than newly-established plantings, indicating that wildflower restorations are an effective conservation tool for building bee populations over time through the provision of both floral and nesting resources.

Dedicated to
Neil R. Taylor, Jr.

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KEY TO ABBREVIATIONS

BEF: Biodiversity-ecosystem functioning

FDis: Functional dispersion (Laliberté *et al.*, 2010)

IPR: Insecticide program risk (Tuell & Isaacs, 2010)

perMANOVA: Permutational multivariate analysis of variance

NMDS: Non-metric multidimensional scaling

CHAPTER 1:

INTRODUCTION

Wild bees provide essential pollination services to pollinator-dependent crops and wild plant populations (Klein *et al*., 2007; Kremen *et al*., 2007; Winfree *et al*., 2007). However, there is increasing evidence that pollinator populations are threatened by a combination of stressors, including habitat loss, degradation, and fragmentation, as well as an interacting combination of pesticides, parasites, and disease (Biesmeijer *et al*., 2006; Potts *et al*., 2010; Cameron *et al*., 2011; Goulson *et al*., 2015). Bee species are likely to differ in their sensitivity to environmental disturbances based on life-history traits such as sociality, body size, and nesting substrate (Larsen *et al*., 2005; Winfree *et al*., 2009; Williams *et al*., 2010; Brittain & Potts, 2011). These differences in trait-mediated responses to disturbance may buffer communities against environmental change (Elmqvist *et al*., 2003; Loreau *et al*., 2003; Fontaine *et al*., 2006). Alternatively, environmental stressors may lead to non-random changes in the functional diversity of bee communities (Brittain & Potts, 2011; Forrest *et al*., 2015). Understanding the interplay of resources and stressors that structures bee populations and their distributions across landscapes, as well as how species' responses may be mediated by functional traits, will be helpful in developing effective conservation strategies for these unmanaged insects (Winfree, 2010; Roulston & Goodell, 2011).

Biodiversity – ecosystem functioning

Human alteration of the natural environment, including activities such as deforestation, agricultural intensification, and the movement of species among biomes, has led to rates of species extinction estimated at 100 to 1,000 times pre-human levels in a wide range of taxonomic groups (Pimm *et al*., 1995; Sala *et al*., 2000). This rapid species loss has generated intense interest in research characterizing the relationship between biodiversity and ecosystem functioning (BEF), which is the key element needed to predict the potential consequences of biodiversity loss for ecosystem function (Chapin III *et al*., 2000; Loreau *et al*., 2001, 2002; Hooper *et al*., 2005).

Interest in the nature or shape of the biodiversity-ecosystem functioning relationship dates back to early work suggesting a connection between the structural complexity and stability of ecosystems (MacArthur, 1955; Elton, 1958). The rich body of BEF research that emerged over the decades following MacArthur's original hypothesis was complicated by differing measures and definitions of biodiversity – or complexity – and ecosystem function or stability, which led to widely contradictory descriptions of the BEF relationship (May, 1973; Pimm, 1979, 1984; Naeem *et al*., 2009; Jax, 2010). Understanding the distinction between the different variables used as proxies for complexity (species richness, interaction strength, connectance, and species evenness) and stability (resilience, resistance, and variability) in different studies is essential to drawing conclusions across studies (Pimm, 1984). Biodiversity-ecosystem functioning assessments also require careful consideration of the specific ecosystem, reference conditions, and spatial and temporal scales of observation in each study (Loreau *et al*., 2001; Jax, 2010).

One area of biodiversity-ecosystem functioning research that has received increasing attention over the past 20 years is the relationship between the functional diversity of organisms – rather than diversity of taxonomic identities – and ecosystem stability or function. Functional diversity is governed by ecological niche breadth (specialization) and niche differentiation (complementarity), both of which interact to allow competing species to coexist given limited resources (Blüthgen & Klein, 2011). The redundancy of ecological niches or functions can also be important in protecting ecosystems against loss of function as species are lost (Naeem, 1998;

Rosenfeld, 2002; Winfree & Kremen, 2009). Assessing loss of biodiversity through the lens of species' functional traits and niches allows for a mechanistic understanding of how species loss may affect ecosystem function (Rosenfeld, 2002).

Importance of pollination in natural and managed systems

Pollination is one example of a crucial ecosystem process that may be affected by biodiversity loss (Kremen, 2005; Larsen *et al*., 2005; Tscharntke *et al*., 2005; Winfree & Kremen, 2009; Blüthgen & Klein, 2011). Pollination, or the transfer of pollen from the male to the female parts of a plant to facilitate reproduction, is a critically important process in both natural and managed systems. Without pollination, many plant species would not set seed or fruit, leaving them unable to reproduce or to provide food resources for humans and other consumers (McGregor, 1976; Free, 1993; Klein *et al*., 2007). While many animal-pollinated species have mixed mating systems that allow individuals to self-pollinate in the absence of pollinators, in the long term, these species also require outcrossing to maintain gene flow between members of the species.

Of the more than 350,000 species of angiosperms found worldwide, the majority are pollinated by insects and other animals, with a small minority receiving pollination via abiotic vectors such as wind and water (Ollerton *et al*., 2011). It has been estimated that over 80% of flowering plant species and 75% of the leading global food crops depend on animal pollinators, primarily bees (Klein *et al*., 2007; Ollerton *et al*., 2011). Globally, the managed European honey bee (*Apis mellifera* L.) is the dominant crop pollinator (Crane, 1990; Williams, 1994; Delaplane *et al*., 2000; Moritz *et al*., 2005). However, a recent meta-analysis determined that wild bee visitation is more strongly correlated with fruit set than honey bee visitation in many cultivated crops (Garibaldi *et al*., 2013), indicating that honey bees cannot fully substitute for diverse wild bee pollinators, nor do they maximize pollination service delivery in many systems. In addition, the cultivated area of pollinator-dependent crops has increased disproportionately relative to other agricultural crops over the past half-century, increasing demand for pollination services at a pace that well outstrips the rate of increase in the global stock of managed honey bees (Aizen *et al*., 2008a; Aizen & Harder, 2009). Wild bees and the pollination services they provide are therefore increasingly essential to the output and stability of global crop production; however, their populations are threatened by agricultural intensification and other environmental stressors (Kremen *et al*., 2002; Potts *et al.,* 2010; Goulson *et al*., 2015).

Overview of pollinator declines

Large-scale land use intensification over the past century has resulted in widespread declines in farmland biodiversity (Matson *et al*., 1997; Krebs *et al*., 1999; Tscharntke *et al*., 2005; Gonthier *et al*., 2014). Declines in global wild bee abundance and species richness associated with agricultural intensification may threaten the provision of pollination services to wild and domesticated plant species (Allen-Wardell *et al*., 1998; Kearns *et al*., 1998; Kremen *et al*., 2002; Biesmeijer *et al*., 2006; Potts *et al*., 2010). It is challenging to document declines in pollinator assemblages due to their high annual species turnover and the labor costs associated with intensive monitoring programs (Cane & Tepedino, 2001; Roubik, 2001; Williams *et al*., 2001; Winfree, 2010). However, historical collection records have provided evidence for widespread bee declines (pre- vs post-1980s) in the United Kingdom (Biesmeijer *et al.,* 2006), particularly bumble bees (*Bombus* spp.) (Goulson *et al*., 2008). Museum records have also been used to test for evidence of bumble bee declines in North America (Colla & Packer, 2008; Grixti *et al*., 2009; Cameron *et al*., 2011; Bartomeus *et al*., 2013). However, Bartomeus *et al*. (2013) found only weak declines in aggregate native bee richness for northeastern US species outside of the genus *Bombus*, with some species exhibiting significant declines in relative abundance over time but others exhibiting significant increases. Ecological traits associated with declining species included small dietary and phenological breadth and large body size (Bartomeus *et al*., 2013). There is also indirect evidence for declines from numerous studies indicating reduced bee abundance and diversity in intensive agricultural environments compared with natural or semi-natural areas (Kremen *et al*., 2002; Winfree *et al*., 2009; Potts *et al*., 2010).

Agricultural intensification occurs along a range of spatial scales: at the local scale, intensification leads to decreases in within-farm crop diversity and increases in chemical or other disturbance inputs, while at the landscape scale, intensification leads to increasingly homogenous cropped landscapes with reductions in natural and semi-natural habitat (Benton *et al*., 2003; Tscharntke *et al*., 2005; Kennedy *et al*., 2013). For bees, the result is both a local- and landscape-level loss of food and shelter resources and increasing exposure to stressors, including parasites, pathogens, diseases, and the use of pesticides, particularly insecticides, in agricultural and urban environments (Kearns *et al*., 1998; Steffan-Dewenter *et al*., 2002; Tscharntke *et al*., 2005; Carvell *et al*., 2006a; Hendrickx *et al*., 2007; Potts *et al*., 2010; Roulston & Goodell, 2011; Vanbergen & Insect Pollinators Initiative, 2013; Goulson *et al*., 2015). Many of these possible drivers of bee declines are interrelated and synergistic; for example, a bee with a weakened immune system due to sublethal pesticide exposure might be more susceptible to pathogen infection or its energetic consequences (Alaux *et al*., 2010a; Pettis *et al*., 2012; Goulson *et al*., 2015). More broadly, habitat loss and fragmentation concentrates bees on smaller resource patches, which may lead to higher rates of pathogen and disease transmission and greater chances of exposure to agricultural chemicals.

Bee communities and ecological diversity

The bees (Hymenoptera: Apoidea) are a large and diverse insect group, with an estimated 20,000 species worldwide, including more than 400 species in Michigan (Michener, 1979; Michener, 2000; JG, *unpublished*). Bees are functionally and ecologically diverse, with wide variation in life history traits such as sociality, body size, trophic specialization, and nesting location (Michener, 2000; Williams *et al*., 2010).

Wild bee communities are variable in space and time, with high species turnover across and within years (Williams *et al*., 2001; Petanidou *et al*., 2008; Mandelik *et al*., 2012; Sydenham *et al*., 2014). Communities are generally comprised of diverse local fauna, often with many rare species present, and only a small proportion of species remain from year to year (Williams *et al*., 2001). Within years, bee communities also move to track variation in resources across landscapes, so a locally species-rich community in early spring may have only a few species present in the same area in late summer (Mandelik *et al*., 2012; Sydenham *et al*., 2014).

Bee functional diversity and redundancy

Wild bee diversity is associated with increased fruit and seed set of insect-pollinated wild and domesticated plant species, particularly when measured in terms of functional diversity instead of species richness (Klein *et al*., 2003; Fontaine *et al*., 2006; Hoehn *et al*., 2008; Albrecht *et al*., 2012; Rogers *et al*., 2014). The functional diversity of pollinators – specifically, diversity in length of mouthparts - has been experimentally shown to increase the persistence of plant communities by increasing plant reproductive success (Fontaine *et al*., 2006). Conversely, the functional diversity of plant communities, such as complementary differences in flowering phenology or the nutritional content of nectar/pollen resources, is thought to increase the persistence of pollinator communities (Blüthgen & Klein, 2011).

In addition to diversity, functional redundancy in bee communities may buffer plant-pollinator networks, or the interaction networks between communities of plants and associated pollinators, against the consequences of species loss (Blüthgen & Klein, 2011). Plant-pollinator networks are generally highly nested, with specialist bee species visiting subsets of the plant species visited by generalist bees (Bascompte *et al*., 2003; Pawar, 2014; Rohr *et al*., 2014). Put another way, specialization in plant-pollinator networks is highly asymmetric; oligolectic bees, or bees with narrow diet breadth, are much more likely to visit generalist plants that are visited by many species of bees than plant species visited by only a few species (Vázquez & Aizen, 2004). This asymmetrical specialization and associated nestedness leads to redundancy in pollination function for the plant species visited by both specialist and generalist bees, creating stability in the network that allows rarer species of both plants and bees to persist (Bascompte *et al*., 2003; Pawar, 2014; Rohr *et al*., 2014). Theoretical work has shown that nestedness can increase the robustness and persistence of plant-pollinator networks to environmental disturbance (Memmott *et al*., 2004), with the caveat that there may be ecological “tipping points” after which nested communities exhibit sudden collapse (Lever *et al*., 2014).

The consequences of bee species loss for plant-pollinator networks and crop pollination also depend on the order of species loss, which is a function of the susceptibility of different bee species to extinction pressures and their relative functional contributions (Larsen *et al*., 2005). If the most functionally important bees are also the most at risk of extinction, plant-pollinator networks would be expected to lose function rapidly as species are lost. Larsen et al. (2005) hypothesized that the order of species loss – and associated loss of function – in bee communities will be highly non-random. Large-bodied bees, often with higher pollination efficiencies (e.g. *Bombus* spp.), are more susceptible to extinction pressures (Larsen *et al*., 2005). If this hypothesis is supported, loss of species may be quickly devastating for ecosystem function. However, the high annual and seasonal species turnover and variation in species interactions in plant-pollinator networks, as well the opportunistic nature of many plant-pollinator interactions, may mean that these networks are less susceptible to disturbance than these dire estimates would suggest (Petanidou *et al*., 2008).

Factors structuring wild bee communities: Resources

The major factors governing the organization of bee community assemblages across spatiotemporal scales are the availability of floral and nesting resources and the nature and strength of environmental stressors (Potts *et al*., 2003, 2005; Williams & Kremen, 2007; Roulston & Goodell, 2011). Bees feed their offspring with a mixture of pollen, nectar, and (rarely) plant oils (Michener, 2000). The quantity and quality of floral resources are generally accepted as the main drivers of bee community structure, abundance and richness (Potts *et al*., 2003; Hines & Hendrix, 2005), and their distribution can affect bees' reproductive outputs (Williams & Kremen, 2007). In the absence of sufficiently abundant and diverse floral resources, poor nutrition can lead to reduced larval development, colony growth, and stress resistance, as well as reduced fecundity, immunocompetence, and longevity in adult bees (Haydak, 1970; Hoover *et al*., 2006; Alaux *et al*., 2010b; Brodschneider & Crailsheim, 2010; Huang, 2012; DiPasquale *et al*., 2013). In considering the relationship between floral resource availability and bee community structure, abundance, and diversity, it is important to note that bee communities are affected by the availability of floral resources at multiple time points during their life cycle, and that the availability of resources during the period of offspring production in one year may be unconnected to the resources available for the emerging adults the following year (Tepedino & Stanton, 1981).

Nesting resources also play an important role in organizing bee communities, though there are limited data on bees' preferences for specific substrate characteristics (Potts *et al.*, 2003, 2005; *but see* Cane, 1991). Approximately two-thirds of bees nest in the soil, with the remaining third nesting above ground, generally in pre-existing cavities in dead wood or in pithy stems or canes (Cane, 1991; Michener, 2000). Potts *et al.* (2003) found that floral characteristics were the most important predictors of bee community structure in a Mediterranean habitat, but the diversity of nesting habitats explained only 5-10% of the community structure. A later study in the same Mediterranean environment found that the availability of nesting resources explained 40-60% of the variation in species-abundance pattern, in particular the availability of bare ground and suitable nesting cavities (Potts *et al.*, 2005). There remain significant knowledge gaps in understanding nest site preferences, particularly for soil-nesting bees. Only a few studies have examined the nesting requirements and preferences of bees, and for a small number of species (Michener *et al.*, 1958; Osgood, 1972; Cane, 1991; Potts & Willmer, 1997; Svensson *et al.*, 2000; Potts *et al.*, 2005; Kim *et al.*, 2006; Sardiñas & Kremen, 2014). These gaps in our understanding also undermine the predictive capacity of landscape models of pollinator abundance, which could be important tools for developing landscape-scale pollinator conservation strategies (*e.g.* Lonsdorf *et al.*, 2009).

Factors structuring wild bee communities: Environmental stressors

Along with resource distributions, there are several interacting environmental stressors that may act as filters on local and regional species pools (Keddy, 1992; Kraft *et al*., 2014; Sydenham *et al*., 2014). Environmental "filters" are local or regional environmental conditions that place restrictions on the ability of species to persist in those environments based on different species' traits, which thus determine the species - and trait - composition of communities living in those environments (Keddy, 1992). In one example of how environmental filtering might determine community assembly, a wetland-adapted plant species is unlikely to persist in dry site conditions, even if the species exists within dispersal range of the dry site. With enough information on species' functional traits and environmental conditions, an environmental filtering framework could be used to predict the species composition of different sites based on a given set of environmental conditions and the range of species' trait values for the functional traits that determine species' responses to those environmental conditions (Keddy, 1992).

Environmental stressors potentially affecting wild bees include exposure to pesticides (Desneux *et al*., 2007; Brittain *et al*., 2010b; Tuell & Isaacs, 2010a); infection with diseases, pathogens, and parasites (Colla *et al*., 2006; Otterstatter & Thomson, 2008; Singh *et al*., 2010; Cameron *et al*., 2011); as well as the possible effects of climate change (Hegland *et al*., 2009; Schweiger *et al*., 2010; Bartomeus *et al*., 2011), invasion of alien plant species (Cox & Elmqvist, 2000; Aizen *et al*., 2008b; Kleijn & Raemakers, 2008; Stout & Morales, 2009), and competition with managed bees (Goulson, 2003a). These stressors may also interact with the distribution of resources at different scales across the landscape to determine community assembly at the local scale (Sydenham *et al*., 2014). Individual bee species are able to persist in local environments only if their functional traits are compatible with the local conditions; that is, if local resources are sufficiently available and accessible, and if species are not "filtered out" by the set of local environmental stressors.

Bees can be exposed to a diverse array of pesticides across the landscape (Chauzat *et al.*, 2006; Johnson *et al.*, 2010; Mullin *et al.*, 2010; Wu *et al.*, 2011; Krupke *et al.*, 2012). Pesticide risk to bees is a function of the route and length of exposure and the toxicity of the chemical. Exposure to a pesticide, whether by contact or ingestion, can be through direct contact from an application or indirect through contact with foliar residues or spray drift, or via ingestion of systemic compounds expressed in nectar or pollen, etc. (Thompson, 2001; Desneux *et al.*, 2007; Krupke *et al.*, 2012). Chronic exposure can also affect bees, for example if developing brood are fed contaminated pollen or nectar, or if foraging bees are routinely exposed to low levels of residues or spray drift across the landscape. All of these types of exposure can have deleterious effects on managed and wild bees.

Pesticide toxicity to bees is most commonly measured as the contact LD_{50} for honey bees, or the dose that kills 50% of a given population of adults upon external contact exposure, which is required for the registration of a pesticide by the US Environmental Protection Agency. However, honey bee responses to different chemicals may not always be representative of the risk to other bee species (Arena & Sgolastra, 2014), and only a handful of chemicals have been tested for their toxicity to other bee species, particularly solitary species (Helson *et al.*, 1994; Thompson, 2001; Morandin *et al.*, 2005; Scott-Dupree *et al.*, 2009; Cresswell *et al.*, 2012; Biddinger *et al.*, 2013).

Bees exhibit a wide range of physiological and behavioral responses to pesticides, which can differ significantly among different taxonomic groups based on life history and ecological traits (Thompson, 2001, 2003; Desneux *et al.*, 2007; Brittain & Potts, 2011). For example, small-bodied bees may be more susceptible to insecticide exposure, since their higher surface area to volume ratio may increase contact absorption relative to larger bodied bees (Brittain & Potts, 2011). Other life-history traits, such as sociality, can be less straightforward in their effects on susceptibility to pesticides, but these types of trait-based responses to pesticide exposure could lead to non-random changes in bee community structure due to disturbance by pesticides (Brittain & Potts, 2011). A few studies have found community-level effects of pesticides on wild bees in agricultural landscapes, with declines in wild bee species richness reported in two blueberry systems and one diversified European agricultural landscape (Kevan, 1977; Brittain *et al*., 2010b; Tuell & Isaacs, 2010a).

In many agricultural systems, it is common to apply a variety of insecticides through the season to control different insect pests, as well as fungicides to control diseases; often these are applied as tank mixes of insecticides and fungicides. While fungicides have generally been considered safe to bees, several studies have shown that some fungicides can exhibit synergistic toxicity with certain insecticides (Pilling & Jepson, 1993; Thompson & Wilkins, 2003; Iwasa *et al*., 2004; Biddinger *et al*., 2013). For example, ergosterol biosynthesis inhibiting (EBI) fungicides have been found to synergize the toxicity of the pyrethroid class and some members of the neonicotinoid class of insecticides by interfering with the cytochrome P450 detoxification pathway in honey bees (Pilling & Jepson, 1993; Thompson & Wilkins, 2003; Iwasa *et al*., 2004). Synergistic interactions may also occur with varroacides applied for in-hive mite treatments for honey bees, or with certain combinations of insecticides that bees may be exposed to while foraging across a diverse landscape (Brittain *et al*., 2010b; Johnson *et al*., 2010; Gill *et al*., 2012; Goulson *et al*., 2015). However, few studies have measured synergistic interactions of chemicals at field-realistic levels, particularly for wild bee species (Gill *et al*., 2012; Biddinger *et al*., 2013).

Many diseases, pathogens, and parasites can be spread within and between populations of wild and managed bees (Colla *et al*., 2006; Otterstatter & Thomson, 2008; Singh *et al*., 2010; Cameron *et al*., 2011). The spillover of pathogens from commercially managed bumble bees to wild populations has been implicated in the disappearance of a western North American bumble bee species (*Bombus franklini*) and the decline of several other species in the same subgenus (Colla *et al*., 2006; Otterstatter & Thomson, 2008; Colla & Ratti, 2010; Cameron *et al*., 2011; Szabo *et al*., 2012). Cameron *et al*. (2011) found that declining populations of *Bombus* have significantly higher infection levels of the microsporidian pathogen *Nosema bombi*, which can reduce individual fitness and longevity as well as colony growth (Otti & Schmid-Hempel, 2007, 2008). While honey bee pathogens have been fairly well-studied over the last 50 years, the scope of transmission of viruses and parasites between managed honey bees and wild bees has only begun to be recognized (Fürst *et al*., 2014; Ravoet *et al*., 2014). Many diseases previously thought to be restricted to honey bees, such as deformed wing virus and the *Varroa*-transmitted Macula-like virus, have now been discovered in populations of wild bees, including several species of solitary bees (Fürst *et al*., 2014; Ravoet *et al*., 2014). These new findings suggest that the movement of managed honey bee colonies for commercial pollination may spread pathogens to wild bee populations, which may in turn act as reservoirs of honey bee pathogens (Ravoet *et al*., 2014).

Climate change is an additional factor that may lead to extinctions of bee species if they or their host plants are unable to shift their ranges to accommodate their thermal tolerance, or if range shifts cause temporal or spatial mismatches in plant-pollinator interactions (Hegland *et al*., 2009; Schweiger *et al*., 2010; Winfree, 2010). Using historical collection data from northeastern North America, Bartomeus *et al*. (2011) showed that plant and pollinator phenological advances have occurred at similar rates in response to long-term temperature increases for ten common generalist bee species. Similar analytical methods using museum data are not possible for rare specialist species, for whom phenological mismatches with host plants may be more devastating (Bartomeus *et al*., 2011). Diversity of bee communities may help to buffer plant-pollinator networks against shifts in flowering phenology (Bartomeus *et al*., 2013). However, increasing temperatures and more frequent droughts may reduce flower production and nectar volume in flowering plants, leading to nutritional stress for pollinators regardless of range or phenology (Carroll *et al*., 2001; Fang *et al*., 2010; Minckley *et al*., 2013). In addition, the climate is predicted to become more variable, with more erratic rainfall and larger fluctuations in weather conditions on a short time scale (Francis & Vavrus, 2012; Thornton *et al*., 2014). This increase in variability could be more problematic for bees and spring-flowering crops than gradual changes in mean climate conditions, with greater chance of floods, drought, and variable spring weather during key foraging periods for early spring bees (Katz & Brown, 1992; Tuell & Isaacs, 2010b; Francis & Vavrus, 2012).

None of these stressors act in isolation, and the combined effects of multiple stressors are likely to be more harmful than any single source of environmental stress (Goulson *et al*., 2015). Complex causes of pollinator declines mean that strategies for conservation and restoration of bee communities need to address these complexities.

Importance of pollination for Michigan highbush blueberry

The highbush blueberry (*Vaccinium corymbosum* L.) agroecosystem in southwest Michigan is an ideal system in which to examine the complex interacting stressors that bees face in agricultural environments. The landscape is a heterogeneous mix of agriculture, forest, settled areas, and some fallow and ruderal areas, but is chiefly dominated by commercial fruit production, with the associated characteristics of agricultural intensification: pesticide use and relatively scarce floral resources when the crop is not in bloom. In addition, the main crop is dependent on pollinators for marketable yields, creating an incentive for growers to be interested in the conservation of wild bees.

Michigan is the nation's leading producer of cultivated blueberries, with 114 million pounds of blueberries valued at $121 million dollars, produced on 19,000 acres in 2013 (NASS, 2014). Highbush blueberry, the main blueberry species grown in Michigan, is dependent on insect-mediated pollination for economically viable yields (Merrill, 1936; Schaub & Baver, 1942; Meader & Darrow, 1947; Free, 1993). At least 80% of flowers must set fruit to achieve a commercial-scale blueberry crop (Merrill, 1936). Though cultivated varieties of *V. corymbosum* exhibit varying degrees of self-compatibility, cross-pollination generally produces earlier ripening berries, increased berry size, and higher seed and fruit set (Schaub & Baver, 1942; Meader & Darrow, 1947; Dorr & Martin, 1966; Brewer *et al.*, 1969; Krebs & Hancock, 1990; Lang & Danka, 1991; VanderKloet, 1991; Hokanson & Hancock, 2000; Chavez & Lyrene, 2009; MacKenzie, 2009).

Blueberry growers typically rent commercial honey bee hives to fulfill pollination needs (Brewer *et al.*, 1969; Isaacs & Kirk, 2010). Isaacs and Kirk (2010) estimated that honey bees (*Apis mellifera* L.) provide 88% of the yield increase due to pollination in the Michigan highbush blueberry system, with wild bees providing the remaining 12%. However, wild bees are the dominant pollinators in small, isolated fields, providing a level of pollination comparable to what stocked honey bees provide in large commercial fields. Over 100 wild bee species have been recorded in Michigan highbush blueberry fields during bloom, including at least 10 species exhibiting high abundance and/or fidelity to blueberry flowers (Tuell *et al.*, 2009).

Diverse wild bee communities, with their diversity of ecological and life-history traits, may ensure the stability of pollination service delivery to highbush blueberry (Rogers *et al.*, 2014). Many wild bees, particularly those species capable of vibratile pollination (hereafter "buzz pollination"), exhibit high pollination efficiencies on *Vaccinium* flowers (Buchmann, 1983; Cane & Payne, 1993; Sampson & Cane, 2000; Stubbs & Drummond, 2001; Javorek *et al.*, 2002; Dedej & Delaplane, 2003; Desjardins & De Oliveira, 2006; Rogers *et al.*, 2013). In the closely related lowbush blueberry (*Vaccinium angustifolium* Aiton), *Bombus* spp. queens and *Andrena* spp. were found to pollinate 3-6x more flowers than honey bees in the same amount of time, and deposit 4x the amount of pollen in a single visit (Javorek et al. 2002). In British Columbia, blueberry weight in six highbush blueberry fields was correlated with the abundance of bumble bees (*Bombus* spp.), but not the abundance of honey bees or other wild bees (Ratti *et al.*, 2012). Furthermore, large-bodied wild bees, such as *Bombus* spp., are capable of foraging in the suboptimal weather conditions typical of spring blueberry bloom (Heinrich, 2004; Tuell & Isaacs, 2010b). Rogers et al. (2014) found that while honey bees were three times less abundant in blueberry fields in inclement weather, overall wild bee density did not differ between inclement and optimal weather conditions due to the stable abundances of large-bodied bee genera such as *Bombus, Habropoda,* and *Xylocopa*. The biodiversity insurance that these wild bee communities provide may help buffer the blueberry agroecosystem against fluctuations in honey bee pollination supply (Winfree *et al.*, 2007; Rogers *et al.*, 2014).

Pest management in highbush blueberry

Though blueberry is highly dependent on bees for pollination during bloom, many fields are managed intensively to control pests and diseases throughout the growing season, with potential negative consequences for the wild bees living in and around fields after bloom. While short-lived bees that are tightly linked with blueberry bloom are unlikely to be affected by post-bloom insecticides, the sprays may have fitness consequences for bees with longer life cycles, including bumble bees (*Bombus* spp.). A 3-year pan trapping study found that wild bee abundance and species richness in blueberry fields declined with increasing insecticide use in 2 of 3 years, suggesting that season-long pest management program intensity can affect the bee community emerging during bloom the following year (Tuell & Isaacs, 2010a). Similarly, Kevan *et al*. (1997) found that the diversity and abundance of wild bees in lowbush blueberry fields fitted a log-normal model in fields unaffected by pesticide applications to the surrounding forests, but departed from the model in fields subject to pesticide stress.

For the past ten years, blueberry production in Michigan has trended toward greater adoption of integrated pest management (IPM) strategies, including reductions in the quantity and toxicity of insecticides applied per season (NASS, 1991-2011). The use of broad-spectrum insecticides, such as azinphos-methyl, malathion, and carbaryl, declined strongly from 2001-2011 in favor of reduced-risk insecticides such as acetamiprid and methoxyfenozide. However, the recent arrival of spotted-wing drosophila (*Drosophila suzukii* Matsumura, Diptera: Drosophilidae), an invasive pest that can cause major economic damage to stone and small fruits, threatens the continued viability of IPM strategies in blueberry and other susceptible fruit crops (Bolda *et al*., 2010; Hauser, 2011; Lee *et al*., 2011; Walsh *et al*., 2011). Estimates for Michigan indicate 2012 losses due to *D. suzukii* at nearly $27 million (R. Isaacs, *unpublished*), and the eFly

SWD Working Group has estimated $207 million losses from SWD in the eastern US alone (eFly, 2012). This invasive pest, with its short generation time, high dispersal ability, and lack of natural enemies, has led to Michigan blueberry growers applying broad-spectrum insecticides in a prophylactic manner to control this insect prior to harvest, a trend that may be highly deleterious to the bees and natural enemies active in and around crop fields after bloom.

Conservation strategies for wild bees

Given the importance of wild bees for pollination of wild and cultivated plants and the growing indications of declining wild bee populations, conservation strategies are needed to support, restore, and enhance diverse and abundant wild bee populations, particularly in intensified agricultural landscapes where resources are scarce and pollination services are most needed (Kremen *et al*., 2002; Winfree, 2010). Multiscale conservation strategies for bees can include species-targeted approaches, such as listing individual species as threatened or endangered to receive federal protections, or habitat-targeted approaches, such as preserving natural areas or restoring lost, degraded, or fragmented habitats (Edwards, 1996; Murray *et al*., 2009c; Winfree, 2010; Gonthier *et al*., 2014). Cane (2001) defines habitat for bees as “minimally consist[ing] of rewarding patches of floral resources plus suitable nesting sites, all within flight range of each other.” The scale of the necessary habitat patchwork varies based on the nutritional requirements and flight radius of different bee species. Successful habitat restoration for bee conservation, therefore, will incorporate provision of both floral and nesting resources at multiple spatial scales to support diverse bee communities and the pollination services they provide (Potts *et al*., 2005).

There is considerable evidence to show that restoring diverse floral resources to resource-poor environments can increase local bee abundance and diversity (Kells *et al.*, 2001; Carvell *et al.*, 2007; Pywell *et al.*, 2007; Blaauw & Isaacs, 2014a, 2014b). There are many possible strategies for introducing additional floral resources into landscapes, including the planting of flowering cover crops, sequentially blooming agricultural crops, spring-flowering shrubs and trees, and/or annual or perennial forb mixes. Of these, the easiest to incorporate in the marginal areas around perennial fruit plantings is likely to be perennial forb mixes, which can be tailored to fit site conditions and can provide floral resources for years following the initial planting, but do not necessarily represent a permanent investment of land (as flowering trees and shrubs might).

These perennial wildflower plantings can provide diverse, season-long nectar and pollen resources for adult bees and their developing larvae (Carreck & Williams, 2002; Carvell *et al.*, 2006b; Pywell *et al.*, 2007; Blaauw & Isaacs, 2014b; Williams *et al.*, 2015). Perennial plantings may also supply nesting and hibernation sites for ground-nesting and stem-nesting bees (Carvell *et al.*, 2007). Using molecular markers, Wood *et al.* (2015) found that floral restorations significantly increased the nest density of four bumble bee species (*Bombus* spp.) on farms in the UK. However, most bee species are solitary and their nest density cannot be assessed with molecular tests based on relatedness of collected specimens. One technique that has shown promise for evaluating nest density of these species is soil emergence traps, which can be used to capture emerging bees over several days or over the course of a growing season (Sardiñas & Kremen, 2014). Stem and cavity-nesting species can be relatively easily monitored in different landscapes with installations of wood blocks, cardboard tubes, or natural reeds (Krombein, 1967; Tscharntke *et al.*, 1998a; Buschini, 2006; Cane *et al.*, 2007). These aboveground-nesting species may be more nest site limited than soil-nesting species in highly simplified agricultural landscapes (Williams *et al*., 2010), so conservation schemes may also need to incorporate provision of additional nesting resources for these bees.

Establishing forb-rich wildflower patches, strips, or meadows near pollinator-dependent crops, such as blueberry, can result in net economic benefits for growers by increasing pollination and yield in those crops (Carvalheiro *et al*., 2012; Blaauw & Isaacs, 2014b). Using crop yield scenarios estimated from berry weight data, Blaauw and Isaacs (2014b) found that the increased pollination service spillover from wildflower plantings sown on marginal land adjacent to blueberry could generate a yield benefit exceeding the costs of planting establishment and maintenance within five years. These ecosystem service benefits, along with financial incentive programs that support beneficial insect conservation, can help to encourage grower adoption of these conservation practices (Kennedy *et al*., 2013; Blaauw & Isaacs, 2014b).

Thesis overview

The main goal of my research is to determine the most effective strategies for conserving and enhancing wild bee populations in the Michigan blueberry agroecosystem. Within this, my specific research objectives were:

1) to determine how pest management at the field scale and landscape composition at a broader scale have affected wild bee communities in highbush blueberry fields before and after the arrival of *D. suzukii*.
2) to determine which habitats in Michigan farm landscapes are most suitable for soil-nesting bees, and whether bees nest preferentially in wildflower plantings compared with nearby unrestored habitats.

CHAPTER 2:

WILD BEE COMMUNITY RESPONSES TO PEST MANAGEMENT AND LOCAL LANDSCAPE COMPOSITION IN MICHIGAN HIGHBUSH BLUEBERRY

Introduction

An estimated 80% of wild plant species and 75% of the leading global food crops depend on animal pollinators, primarily bees (Klein *et al*., 2007). Declines in global wild bee abundance and richness, especially in intensively managed agricultural areas, may be threatening the provision of pollination services to wild and domesticated plant species (Allen-Wardell *et al*., 1998; Kremen *et al*., 2002; Biesmeijer *et al*., 2006; Potts *et al*., 2010). A number of possible causes for these declines have been hypothesized, including habitat loss, fragmentation, and degradation; interacting effects of parasites, pathogens, and diseases; and the use of pesticides, particularly insecticides, in agricultural and urban environments (Kearns *et al*., 1998; Tscharntke *et al*., 2005; Roulston & Goodell, 2011; Goulson *et al*., 2015). Understanding how these factors interact with resource availability and landscape composition to determine bee community assembly will be important in developing effective wild bee conservation strategies, particularly in agricultural areas that require robust wild bee populations to support pollination of fruits and vegetables. In this study, I investigated the interactive effects of landscape composition and insecticide use on wild bee communities in the intensively managed highbush blueberry agroecosystem of southwest Michigan.

Highbush blueberry (*Vaccinium corymbosum* L.) requires insect pollination for economically viable yields (Merrill, 1936; Schaub & Baver, 1942; Meader & Darrow, 1947; Free, 1993; Isaacs & Kirk, 2010). While most Michigan blueberry growers rely on rented honey bee (*Apis mellifera* L.) colonies for pollination, the high winter losses of managed honey bee colonies across North America over the last 20 years, combined with the rising costs of hive management, have increased hive rental prices and weakened remaining colonies (Rucker *et al*., 2012). The rising costs and lower returns associated with honey bee rental underscore the importance of supporting wild pollinator populations to ensure the resilience of pollination services and crop yields (Allen-Wardell *et al*., 1998; Winfree *et al*., 2007).

Over 100 wild bee species have been recorded in Michigan highbush blueberry (*Vaccinium corymbosum* L.) fields during bloom, including at least 10 species exhibiting high abundance and/or fidelity to blueberry flowers (Tuell *et al*., 2009). However, management of insect pests following bloom often necessitates several insecticide applications per season. While short-lived bee species that are temporally linked with blueberry bloom may not be affected by post-bloom insecticides, these sprays may have fitness consequences for bees with longer life cycles. Several bumble bee species (*Bombus* spp.), for example, are efficient blueberry pollinators that emerge prior to bloom and continue to forage and reproduce throughout the growing season, potentially placing them at risk of exposure to the insecticide use during berry ripening and harvest. Within this system, season-long pest management program intensity has been negatively correlated with wild bee abundance and species richness (Tuell & Isaacs, 2010).

For the past 10 years, blueberry producers in Michigan have increasingly adopted integrated pest management (IPM) strategies, including reductions in the quantity and toxicity of insecticides applied (Figure 2.1; NASS 2001-2011; Isaacs *et al*., 2009). The use of broad-spectrum insecticides, such as azinphos-methyl, malathion, and carbaryl, declined from 2001-2011, in favor of reduced-risk insecticides such as acetamiprid and methoxyfenozide. However, the recent arrival of spotted wing drosophila (*Drosophila suzukii* Matsumura), an invasive fruit fly that can cause economic damage to stone and small fruits (Lee *et al*., 2011), threatens the continued viability of IPM strategies in many fruit crops, particularly berry and cherry (*Prunus* spp.) crops. In 2012, there were an estimated $207 million in losses from *D. suzukii* in the eastern United States alone (eFly 2012). To prevent these losses, blueberry growers have switched to repeated use of broad-spectrum insecticides applied on a calendar schedule, generally every 7 days during the harvest period, to prevent infestation by *D. suzukii* (Van Timmeren & Isaacs, 2013), a trend that may be highly deleterious to the bee species active in and around crop fields after bloom.

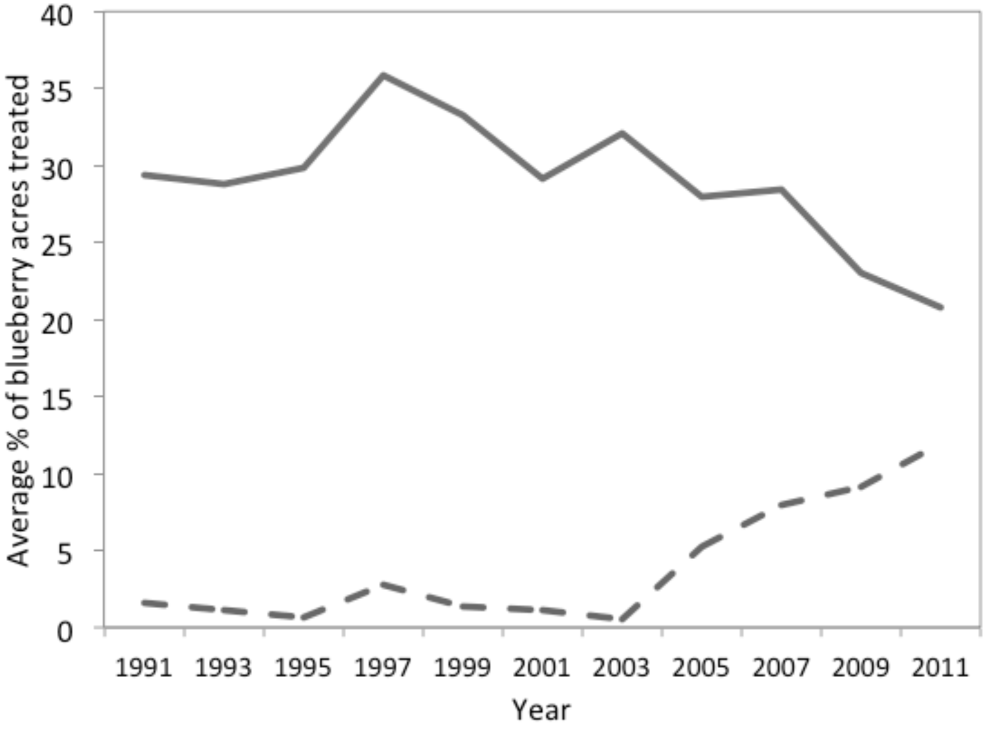

Figure 2.1. Average percentage of bearing Michigan blueberry acres treated with each of the eight conventional insecticides (solid line) and eight reduced-risk insecticides (dashed line) reported by the National Agricultural Statistics Service (NASS 1991-2011). Conventional insecticides included organophosphates, carbamates, and pyrethroids; reduced-risk insecticides included biological insecticides, insect growth regulators, and neonicotinoids.

Community-level studies of wild bees have found that bees respond to resources and stressors at multiple scales, with different species exhibiting differential responses to landscape and other factors based on life-history traits such as body size, sociality, and nesting substrate (Kleijn & van Langevelde, 2006; Brosi *et al*., 2007; Brittain *et al*., 2010a; Williams *et al*., 2010; Watson *et al*., 2011; Sydenham *et al*., 2014). Crop flower visitation by bees declines with increasing distance from natural and semi-natural habitats in a variety of agricultural systems (Kremen *et al*., 2002; Hendrickx *et al*., 2007; Ricketts *et al*., 2008), but the scale at which bees exhibit this response to habitat can differ based on individual species' foraging ranges and diet requirements (Cresswell *et al*., 2000; Steffan-Dewenter & Kuhn, 2003; Westphal *et al*., 2006). Bee community responses to insecticide exposure may be similarly mediated by functional traits; for example, smaller bees may have higher contact absorption of pesticides than larger bees due to their higher surface area to volume ratio (Johansen, 1977; Brittain & Potts, 2011). Differences in species-specific responses to insecticides based on functional or life-history traits could lead to non-random changes in bee community composition in intensively managed landscapes (Brittain & Potts, 2011). However, few studies have examined community-level responses of wild bees to insecticides (*but see* Kevan *et al*., 1997; Brittain *et al*., 2010b; Tuell & Isaacs, 2010). Understanding trait-based responses of bee communities to landscape composition and insecticides will allow better prediction of the effects of land use change and agricultural intensification on the pollination of crops and wild plants (Williams *et al*., 2010; Brittain & Potts, 2011; Bartomeus *et al*., 2013).

Finally, in order to accurately estimate the effects of management practices and conservation efforts at the local and landscape scales on pollination, it is necessary to identify the main 'ecosystem service providers' and isolate their responses to these factors (Kremen, 2005;

Luck *et al*., 2009). Not all of the bee species captured by Tuell *et al*. (2009) in the Michigan highbush agroecosystem provide pollination services to blueberry. Cleptoparasitic species, for example, do not collect pollen because they are able to co-opt the pollen resources of their host (Wcislo & Cane, 1996; Bogusch, 2003); while cleptoparasites have been found nectaring on blueberry, they are unlikely to provide measurable pollination services. Isolating the responses of service-providing bees to local and landscape factors will allow for better quantification of the potential tradeoffs and cost/benefit analysis of different management practices and conservation strategies for blueberry pollination (Luck *et al*., 2009).

In this study, I examined the major factors influencing wild bee abundance, richness, and community composition in Michigan highbush blueberry fields during crop bloom in 3 years prior to the arrival of *D. suzukii* (2004-2006) and 2 years following its arrival (2013-2014). My objectives were (1) to determine whether insecticide use at the field scale and habitat composition at the broader landscape scale are major drivers of wild bee abundance, richness, diversity, and community composition in highbush blueberry fields, and (2) to determine whether bee functional traits contribute to their responses to these factors. This study has broad implications for the conservation of wild bee species for ecosystem service provision and biodiversity in agricultural landscapes.

Materials and Methods

Study sites

The study was conducted in 15 highbush blueberry fields previously sampled by Tuell *et al*. (2009), located in Allegan, Van Buren, and Ottawa counties in southwest Michigan (Figure 2.2). The lakeshore counties on the west coast of Michigan's Lower Peninsula are characterized by sandy, acidic soils and a lake-moderated microclimate that allows for a longer growing season than other regions at the same latitude. This diverse and productive agricultural zone, sometimes termed Michigan's "Fruit Belt," leads the nation in the production of highbush blueberries (NASS 2011). The 15 sampled fields span a gradient of management intensity from unmanaged fields to fields sprayed every 5-7 days for insect and disease control. Sites were located at least 3 km apart.

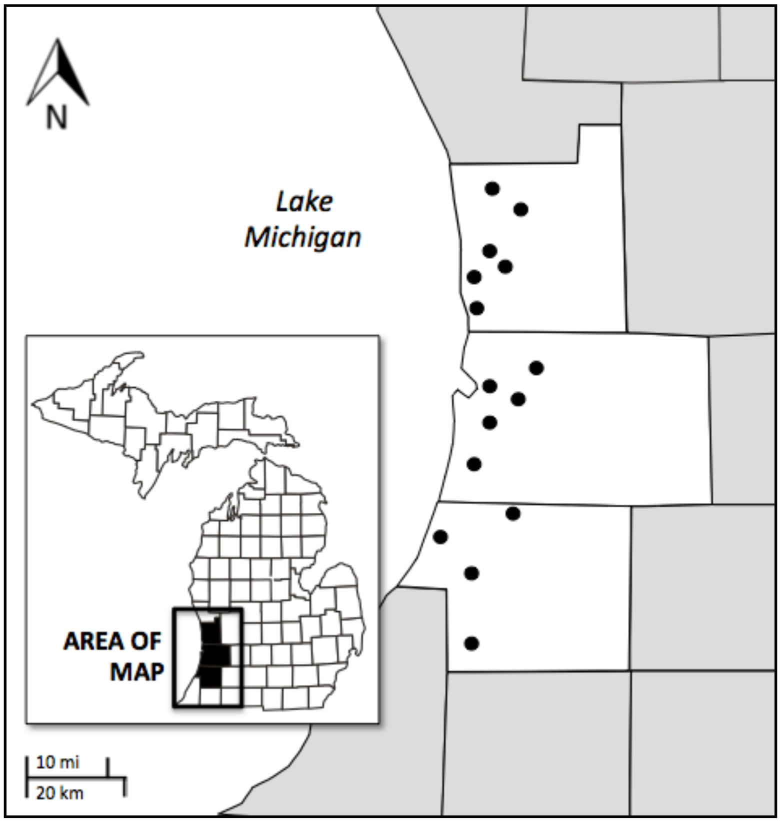

Figure 2.2. Map of the study area showing the location of highbush blueberry sites sampled in 2004-2006 (Tuell *et al*. 2009; Tuell & Isaacs 2010) and in 2013 and 2014 (this study).

Bee collections

To measure the abundance, richness, and community composition of wild bee communities in the Michigan highbush blueberry agroecosystem, I used pan traps to collect bees during blueberry bloom in 2013 and 2014 at the 15 sites previously sampled in 2004, 2005, and 2006 (reported in Tuell *et al*. 2009; Tuell & Isaacs 2010). In all years, bees were collected using five pairs of pan traps (355 ml white and yellow plastic bowls; Amscan, Inc., Elmsford, NY) placed 5 m apart along one transect at the field edge and a second transect 25 m into the field. The twenty traps were half filled with a 2% soap solution (Dawn Ultra dish soap, Proctor & Gamble, Cincinnati, OH) and mounted on 1.2 m PVC poles stabilized with rebar (Tuell & Isaacs, 2009). Traps were placed in the morning and collected after a minimum 6 h trapping period, 2-3 times during the bloom period depending on the duration of suitable weather conditions. Specimens were placed in the freezer, then washed and dried as described in Tuell *et al.* (2009). In addition, because pan trapping is likely to collect a biased subset of the total bee community (Cane *et al.*, 2001), wild bees were also hand netted from blueberry flowers for 10 minutes along a transect from the field edge to 25m into the field interior at each site on the same day or the day following pan trap collections.

Bee specimens (Hymenoptera: Apoidea) were identified to genus and species using dichotomous keys (Mitchell, 1960, 1962; LaBerge, 1980; Michener *et al*., 1994; Gibbs, 2011; Rehan & Sheffield, 2011) and the online keys available through www.discoverlife.org. Specimens were compared with voucher specimens from Tuell *et al*. (2009) for verification. Specimens from Tuell *et al*. (2009) in the *Ceratina calcarata/dupla* species complex were reclassified according to Rehan and Sheffield (2011). *Lasioglossum* (subgenus *Dialictus*) and *Andrena* species were identified by Dr. Jason Gibbs (Department of Entomology, Michigan State

University). Voucher specimens from this study were deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University.

Insecticide program risk

Growers provided spray records for the years 2003-2005 and 2012-2013 for 13 of 15 sites. Two sites provided records for four out of the five years. Prior-year insecticide applications were used to calculate the per-site insecticide program risk (IPR) for each year, a metric used to estimate the risk of insecticide use to bees described in Tuell and Isaacs (2010) (Equation 2.1). Pesticide records from the year before bee collections were used because most insecticides are applied after petal fall in blueberry, so effects of insecticides on the bee communities present during bloom are likely to be seen the following season (Tuell & Isaacs, 2010). Fungicide applications were not considered in this metric of insecticide risk.

(Equation 2.1)

$$\textit{insecticide program risk}\ (\mathit{IPR}) = \sum \frac{\textit{amount of active ingredient (kg)/Ha}}{\textit{contact } \mathit{LD}_{50} \textit{ for honeybees}}$$

Landscape characterization

Tuell (2007) digitized the landscape within a 1.5 km radius around the central pair of pan traps in each field in ArcGIS (ArcMap 9.2, ESRI, Redlands, CA) using 2005 orthoimagery at the 1:2000 scale (National Agriculture Imagery Program (NAIP), accessed via the NRCS Geospatial Data Gateway). These maps were updated using 2014 NAIP orthoimagery at the same scale in ArcMap 10.1 (ESRI, Redlands, CA). Habitat types were classified into categories (Table 2.1) and ground-truthed during site inspections in 2014 and using Google$^{\mathrm{TM}}$ Street View. Concentric circles with radii of 300, 500, 1000, and 1500 m were overlaid on the digitized landscape from

2005 and 2014 in order to calculate the proportion of habitat types surrounding each site at different scales in the two years.

Table 2.1. Categories of habitat types used in landscape characterization (from Tuell, 2007).

Habitat type	**Description**
Blueberry plantations	commercial and semi-abandoned highbush blueberry
Perennial crops	other perennial crops, including vineyards and nurseries
Annual crops	field and vegetable crops
Pastures	grazing pastures
Open uncultivated	meadows, scrubland, fallow and other ruderal areas
Ditches and treelines	running along or bisecting agricultural land
Other field margins	margins along agricultural land other than ditches and tree lines
Forest/woodland margin	<10 m from forest edge
Forest/woodland interior	>10 m from forest edge
Settlement	suburban development including golf courses and a landfill
Road	paved or dirt
Railroad tracks	abandoned or still in use
Utility	areas cleared for powerlines
Shoreline	vegetation along Lake Michigan
Wetlands	vegetation on periodically flooded land
Riparian areas	vegetation along inland bodies of water such as ponds and lakes
Open water	open bodies of water including lakes, ponds, and river

Functional traits

A database of species functional traits for the collected specimens, including sociality, nesting substrate, diet specialization, and intertegular distance, was compiled primarily from Wolf & Ascher (2008) and the supplementary materials in Bartomeus *et al*. (2013), with additional floral records to determine diet breadth for several *Lasioglossum* species from Gibbs (2011) (Appendix B). These ‘response traits’ were selected for their likely association with bees’ responses to environmental factors such as resource distributions (Lavorel & Garnier, 2002). Body size (as measured by intertegular distance) and sociality affect how far bees can travel in search of food resources (Gathmann & Tscharntke, 2002), and thus determine at what scale individuals interact with the surrounding landscape. Additionally, these two traits are likely to affect how bees respond to pesticide exposure (Brittain *et al.*, 2011). Nesting substrate and diet specialization describe two resource requirements that also affect how bees interact with landscape composition, as certain nesting substrates or floral hosts may be limited in different environments (Roulston & Goodell, 2011). Bees that nest in wood, for example, may have difficulty locating nest sites in highly simplified landscapes with little forest cover (Williams *et al.*, 2010). While some of these traits may also affect whether and how much different bee species contribute to crop pollination – for example, larger-bodied bees tend to be more efficient pollinators (Larsen *et al.*, 2005) – I was not explicitly considering the effect that these functional traits might have on pollination services.

To examine how the diversity of functional traits in bee communities might be affected by landscape composition and insecticide risk, I calculated an index of functional dispersion for the collected bee communities in each site in each year using four response traits: sociality, nesting location, diet specialization, and body size (Table 2.2; Laliberté *et al.*, 2010). Functional dispersion is calculated from the mean distance in multidimensional trait space of individual species to the centroid of all species, weighted by relative species abundances (function *dbFD* in R package *FD*; Laliberté *et al.*, 2010). I used the *cailliez* correction for the non-Euclidean distances in the trait distance matrix generated by inclusion of categorical traits (Cailliez, 1983). To quantify the impact of individual traits on the response of functional dispersion to predictor variables, I recalculated trait diversity with each of the traits excluded in turn and ran the analyses with each iteration.

Table 2.2. Traits used to calculate dispersion of functional traits of bees in the samples collected in blueberry fields. Body size was condensed into a categorical variable, using inter-tegular (IT) distance where available (Bartomeus *et al.*, 2013).

Trait	**Categories**
Sociality	Solitary
	Eusocial
	Facultatively eusocial
	Cleptoparasite
Body size	Small (IT <1.5 mm)
	Medium (IT 1.5-2.5 mm)
	Large (IT >2.5 mm)
Lecty (diet breadth)	Oligolectic
	Polylectic
	Cleptoparasite
Nest location	Soil (excavate)
	Soil (rent)
	Pithy stem
	Cavity
	Wood
	Cleptoparasite

Service providing bees

Not all of the species collected in pan traps are likely to provide pollination services to highbush blueberry. To isolate the response of service-providing bees to the studied factors, I compiled a list of the subset of collected species that have been recorded foraging on *Vaccinium corymbosum* L. and close relatives (lowbush blueberry, *Vaccinium angustifolium* Aiton and deerberry, *Vaccinium stamineum* L.) in the eastern United States and Canada (Cane *et al.*, 1985; Stubbs *et al.*, 1992; MacKenzie & Eickwort, 1996; Stubbs & Drummond, 1997; Javorek *et al.*, 2002; Sheffield *et al.*, 2003; Tuell *et al.*, 2009; Adamson, 2011; Benjamin *et al.*, 2014; Moisan-Deserres *et al.*, 2014). I excluded cleptoparasitic bees from this list; although some species of *Nomada* and *Sphecodes* have been recorded nectaring on *Vaccinium* spp., these species do not actively collect pollen and thus are unlikely to provide effective pollination. Because only a few of the blueberry pollination studies identified all observed *Lasioglossum* (Dialictus) and *Andrena* to species, this list of 80 out of the 150+ species collected may be a conservative estimate of the total number of species that can provide pollination services to *Vaccinium* in Michigan (Appendix B).

Data analysis

All data analysis was performed in R version 3.0.2 (R Core Team, 2013). Species accumulation curves were used to determine whether the sampling effort was sufficient to estimate the community of bees likely to be captured in pan traps and nets in this habitat (Gotelli & Colwell, 2001; Tuell *et al*., 2009). Netting and pan trapped collections were pooled, and all observations were then averaged by site by year to avoid pseudoreplication and to correct for uneven numbers of sampling rounds in different years. Average bee species richness was characterized for each site in each year using the Chao1 richness estimator, which estimates unseen species based on the rarity of sampled species (function *estimateR* in R package *vegan*; Chao, 1987; Oksanen *et al*., 2013). Bias-corrected Shannon's diversity indices using the Chao-Shen estimator for unseen species were also calculated for each site in each year (function *entropy.ChaoShen* in R package *entropy*; Chao & Shen, 2003).

Spatial autocorrelation was assessed using Mantel tests to compare pairwise bee community similarity indices (Morisita-Horn index) with pairwise geographic distances between each of the fifteen blueberry farms in each year (function *mantel* in R package *vegan,* 1000 permutations). No spatial autocorrelation among sites was detected in any year (all $p > 0.29$).

Non-metric multidimensional scaling (NMDS) ordination was used to visualize differences in species composition of the wild bee communities among sites and across years (function *metaMDS* in R package *vegan*; Oksanen *et al*., 2013). Species abundance data were square root transformed and then submitted to Wisconsin double standardization prior to calculating Bray-Curtis dissimilarities in order to improve the quality of ordination (functions *wisc* and *vegdist* in R package *vegan*; Oksanen, 2006). Because of the large number of zeroes in the site-by-species matrix, Bray-Curtis dissimilarities were zero-adjusted using a dummy species with a value of 1 for all sites (Clarke *et al*., 2006). NMDS ordination was used to show the trajectory of bee communities at individual sites over time (function *ordiarrows* in R package *vegan*; Figure 2.6). I also fitted vectors of species loadings on the NMDS axes for the most abundant species across all five years to examine possible trends related to functional traits (function *envfit* in R package *vegan*), as well as 95% confidence ellipses around the group centroids for different groups of species functional traits (function *ordiellipse* in R package *vegan*).

Insecticide program risk (IPR) was not normally distributed, so I compared IPR across years using a non-parametric Kruskal-Wallis test with post-hoc Dunn's test with Bonferroni correction. Two sites did not provide spray records in one of the five years; however, the Dunn's test for the median difference between groups is also appropriate for unbalanced designs.

Permutational analysis of variance (perMANOVA), a nonparametric equivalent of multivariate analysis of variance that generates *p*-values using permutations and therefore does not require the data to meet assumptions of normality, was used to compare bee community composition across years (function *adonis* in R package *vegan*). Multivariate homogeneity of variances was confirmed prior to perMANOVA analysis (function *betadisper* in R package *vegan*). Similarity percentage (SIMPER) analysis was used to determine which species made the largest contributions to the contrasts between years (function *simper* in R package *vegan*).

Principal components analysis (PCA), an ordination technique that creates orthogonal vectors to explain major axes of variation in multivariate data sets, was used to reduce the dimensionality of the landscape variables in 2005 and 2014 (function *prcomp* in R package *stats*; R Core Team, 2013). Typically only a small number of principal components are needed to explain the majority of the variation in complex data sets (Gotelli & Ellison, 2004). Because these axes are orthogonal to each other – and thus wholly uncorrelated – the use of principal components instead of raw landscape variables avoids potential problems with multicollinearity in regression analyses.

I conducted separate principal components analyses (PCAs) for each of the four landscape radii (300, 500, 1000, and 1500 m) for the 2005 and 2014 landscape data. I then examined each PCA individually to determine a) how many landscape components to extract for analysis and b) what major axes of variation were explained by the extracted components. I used a combination of visual examination of scree plots (function *fviz_screeplot* in R package *factoextra;* Kassambara, 2015) and the broken stick model (function *evplot*; Borcard *et al.*, 2011) to determine, for each model, which components retained valuable landscape information (Jackson, 1993). These methods indicated consistent support for extracting at least the first two principal components for all PCA models, with some support for extraction of one or two additional axes depending on the landscape radius and year.

Bee species respond to habitat at different spatial scales based on life-history traits such as diet breadth and body size, which determine resource requirements as well as maximum flight radius and therefore which resources they can access in the landscape (Kreyer *et al.*, 2004; Greenleaf *et al.*, 2007; Osborne *et al.*, 2008; Jha & Kremen, 2013a; Wright *et al.*, 2015). To identify the scale at which surrounding landscape composition had the most explanatory power, I used linear regressions of average bee abundance and estimated species richness against the first two principal components for landscape variables at radii of 300, 500, 1000, and 1500 m, and compared the resulting R^2 values (Table 2.3; Steffan-Dewenter *et al*., 2002; Holland *et al*., 2004). These regressions were conducted separately for abundance and richness pooled from 2004-2006 samples and 2013-2014 samples on the landscape data from 2005 and 2014, respectively. R^2 values peaked at the 300 m radius for abundance in 2005 and 2014 and for richness in 2005 (Table 2.3), so only the 300 m scale landscape components were retained for use in subsequent analyses.

Table 2.3. Linear regressions of pooled average bee abundance and estimated richness from 2004-2006 and 2013-2014 on the first two principal components from 2005 and 2014 landscape data at 300m, 500m, 1000m, and 1500m radii around sampled sites.

Landscape	**Abundance**			**Richness**		
radius	R^2	F	p	R^2	F	p
2005						
300m	0.29	2.48	0.13	0.44	4.62	0.03*
500m	0.20	1.53	0.26	0.11	0.73	0.50
1000m	0.07	0.46	0.64	0.01	0.05	0.95
1500m	0.04	0.26	0.78	0.03	0.17	0.84
2014						
300m	0.37	3.46	0.06	0.02	0.14	0.87
500m	0.28	2.33	0.14	0.07	0.44	0.66
1000m	0.23	1.76	0.21	0.05	0.32	0.74
1500m	0.18	1.34	0.3	0.02	0.12	0.88

* significant at $p = 0.05$

Examination of the biplots and factor loadings for the first two principal components for landscape composition at the 300 m scale indicated that the major axes of variation explained by these components were the same for 2005 and 2014 (Figures 2.9 and 2.10; Table 2.4). Linear regressions of the first two PCA components from the 2005 and 2014 landscape analyses showed strong positive correlations for both PC1 and PC2 (both $R^2 > 0.88$ and $p < 0.0001$). The first two components from the 2005 and 2014 landscape PCAs were therefore combined for repeated measures analysis, with the 2005 component values assigned to sites for the years 2004-2006 and the 2014 component values assigned to sites in 2013-2014.

To examine variability in responses to insecticide program risk by year, I ran simple linear regressions of wild bee abundance and Chao1 estimated species richness on prior-year IPR for each year of bee collections (2004, 2005, 2006, 2013, and 2014). Bee abundance was log-transformed prior to analysis to meet the assumption of normality. Only 14 sites were included in the 2013 and 2014 analyses due to missing spray records from one site in each of those years. To determine if bee responses to insecticide risk differed by collection period as well as over all five years of collections, I performed separate repeated measures analyses of bee abundance and richness on prior-year IPR for the 2004-2006 and 2013-2014 collections, as well as for all five years of collections (function *lme* in R package *nlme*; Laird & Ware, 1982; Pinheiro *et al*., 2014). Because of the non-continuous time series for bee collections (*e.g*. the five-year gap between the 2006 and 2013 collections), the repeated measures analyses were conducted with a variance-covariance matrix using a linear spatial correlation structure to account for the distance between collection years (function *corLin* in R package *nlme*: Pinheiro *et al*., 2014). In addition, variances were modeled explicitly for each year to account for heterogeneous variances for the response variables in different years (function *varIdent* in R package *nlme;* Galecki & Burzykowski, 2013).

Following these analyses of IPR in different years and collection periods, repeated measures linear mixed models were used to determine the combined effect of IPR and landscape factors on the abundance, richness, diversity, and functional dispersion of bees across all five years of collections (function *lme* in R package *nlme*; Laird & Ware, 1982; Pinheiro *et al*., 2014). The two sites with only four years of insecticide records were removed prior to repeated measures analyses, which require a balanced variance-covariance matrix. These analyses were conducted with an unstructured variance-covariance matrix with heterogeneous variances by year. Variance components were estimated using maximum likelihood. Bee abundance data were log-transformed prior to analysis to meet the assumption of normality.

Automated model selection for each response variable was performed using the *dredge* function in R package *MuMIn*, which calculates Akaike's information criterion (AIC) values for models using all possible combinations of predictor variables and ranks them based on AIC (Barton, 2014). The relative importance of each predictor variable was then calculated from the sum of AIC weights for all models with delta AIC (ΔAIC) ≤ 2 containing the variable (function *importance* in R package *MuMIn*). Delta AIC is a measure of each model relative to the model with the lowest AIC value (the 'best' model in terms of goodness of model fit with a minimum number of model parameters); according to a rule of thumb provided by Burnham & Anderson (2002), there remains substantial evidence for models within 2 AIC values of the 'best' model, while ΔAIC > 10 indicates that the model is very unlikely.

I ran the five-year repeated measures analyses again with only the subset of wild bees that could potentially provide pollination services in blueberry (Appendix B). I also compared the responses of social bee and solitary bee abundance and estimated richness in separate regression models to determine whether sociality affects the response of bee species to the predictor variables. Abundances of social and solitary species were log(x + 1) transformed prior to analysis to meet the assumption of normality. Following this analysis, I ran separate analyses for the 2004-2006 and 2013-2014 collection periods to rule out the possibility that the patterns were related to extreme weather between the two periods.

Following mixed model analyses, I fitted vectors of significant landscape variables and insecticide program risk from the mixed models onto the NMDS ordination of bee communities among sites using a multivariate correlation analysis that partitions the linear component of each predictor on the NMDS axes (function *envfit* in R package *vegan*; Williams & Winfree, 2013). When ordination stress is low, this approach can be used to test the effect of predictor variables on community composition.

Results

Bee collections

In 2013, I collected 793 bees during three bloom samples at each of the 15 sites, representing at least 81 species, 17 genera, and 5 families. These samples included 372 honey bees (*Apis mellifera* L.) and 421 wild bees (Appendix B). In 2014, I collected 1,829 bees representing at least 90 species, 17 genera, and 5 families, including 1,055 *A. mellifera*. Tuell *et al*. (2009) collected a total of 3,228 non-*Apis* bees at these sites from 2004-2006 over seven bloom samples (2-3 samples per year per site), representing at least 112 species, 20 genera and 5 families (Tuell *et al*. 2009). The species accumulation curve calculated across all five years of sampling, with one sample round per site (20 pan traps and 10 minutes of net collecting) as the base sampling unit, indicated that the number of species collected begins to level off after the equivalent of one year's worth of sampling at 15 sites (n = 45 samples) (Figure 2.3). Species accumulation curves for individual years showed differences in total asymptotic richness collected in different years, with lower asymptotic richness in 2013 and 2014 than in the 2004-2006 samples (Figure 2.4).

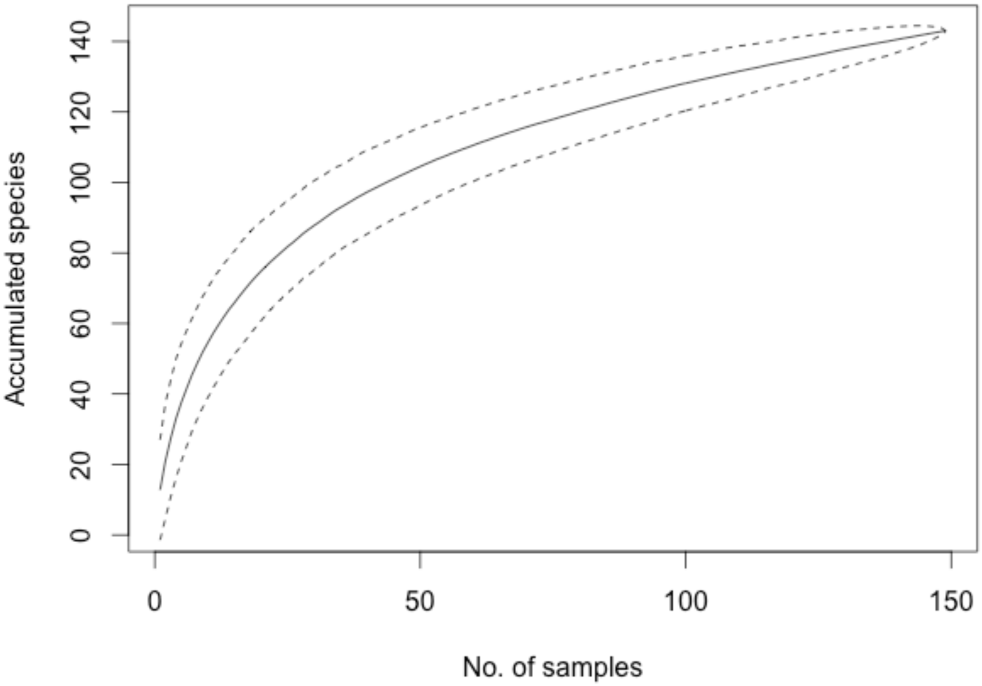

Figure 2.3. Species accumulation curve generated from bee community samples during bloom in 2004-2006 and 2013-2014 at 15 blueberry farms. One sample represents the community of bees collected in one day at one site (20 pan traps and 10 minutes of hand netting). Dashed line represents the 95% confidence interval around the mean.

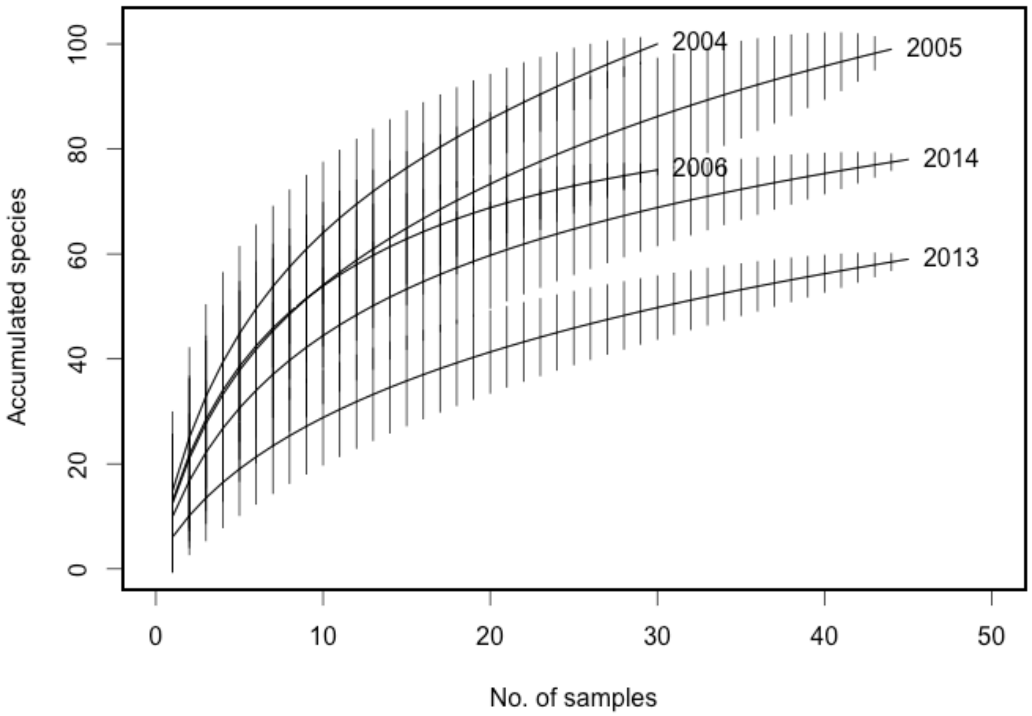

Figure 2.4. Species accumulation curves for each year of sampling. One sample represents the community of bees collected in one day at one of the 15 sites (20 pan traps and 10 minutes of hand netting). At each site, there were two sampling rounds during bloom in 2004 and 2006 (30 samples) and three sampling rounds in 2005, 2013, and 2014 (45 samples). Error bars represent 95% confidence around the mean line for each additional sample.

The most abundant bee captured in pan traps in all years (2004-06, 2013-14) was *A. mellifera,* the managed European honey bee. While the *Vaccinium* specialist *Andrena carolina* Viereck represented 16% of all wild bee abundance in the 2004-2006 collections by Tuell *et al*. (2009), only 8 specimens of *A. carolina* were captured in 2013 and 16 specimens in 2014, representing 1.9% and 2.1% of wild bee abundance, respectively. The most abundant non-*Apis* bees in 2013 and 2014 were several social or semisocial halictid and apid species, including *Lasioglossum pilosum* (Smith), *Lasioglossum coriaceum* (Smith), *Bombus impatiens* Cresson, *Augochlorella aurata* (Smith), *Lasioglossum cressonii* (Robertson), and *Lasioglossum imitatum* (Smith).

Nonmetric multidimensional scaling (NMDS) ordination of Bray-Curtis dissimilarities between bee communities at each site in each year suggested that the communities in the first three years of sampling were more similar to each other than to the communities collected in 2013 and 2014 (k =2, stress = 0.25; Figure 2.5). Total community composition across sites differed significantly among years ($F = 3.32$, $df = 4, 70$, $p = 0.001$). Individual sites had high species turnover from year to year, resulting in dissimilar communities from year to year in ordination space (Figure 2.6).

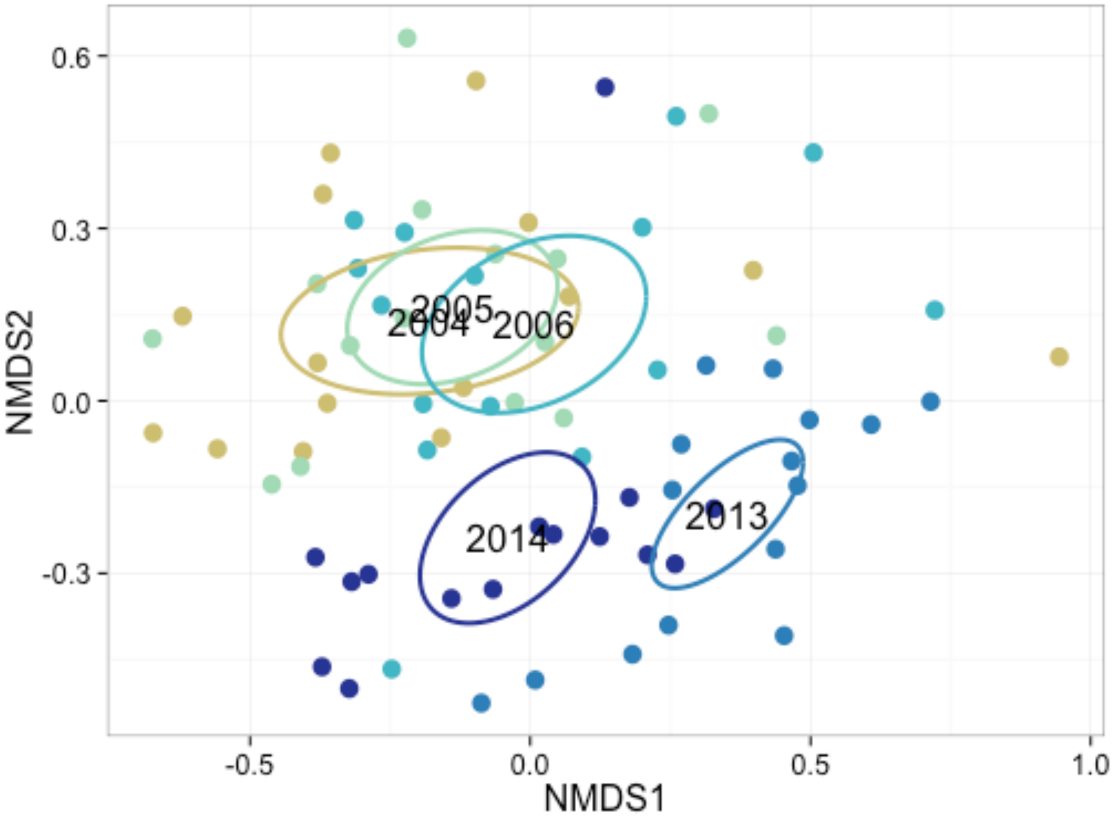

Figure 2.5. Nonmetric multidimensional scaling ordination of bee communities collected in pan traps and nets in 15 blueberry fields from 2004-2006 and 2013-2014. Each point represents one site in one year, with different colors for each of the five years. Ellipses represent 95% confidence ellipses around the group mean for each year.

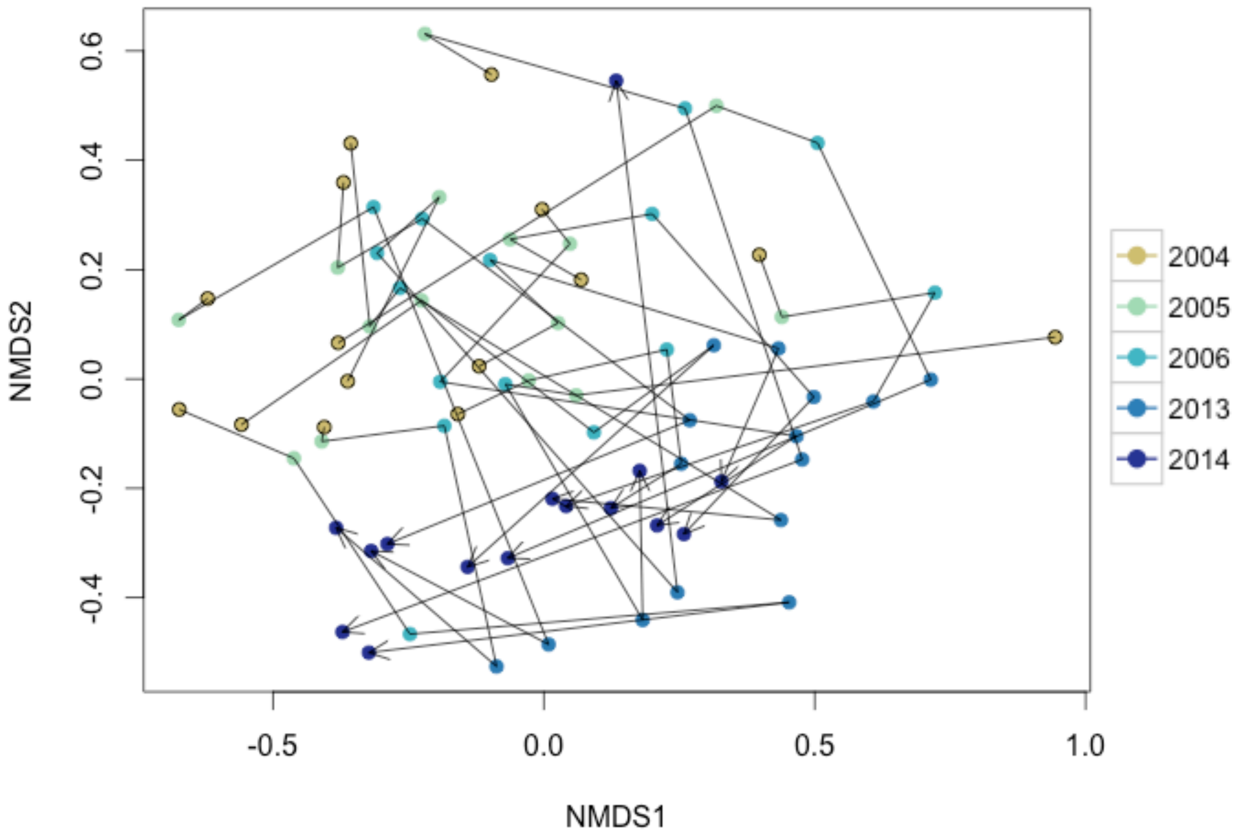

Figure 2.6. Nonmetric multidimensional scaling ordination of bee communities collected in pan traps and nets in 15 blueberry fields from 2004-2006 and 2013-2014. Each point represents one site in one year. Black arrows show the trajectory of one site beginning in 2004 (circled points) and ending in 2014.

Insecticide program risk

The 15 farms varied in both the types and rates of insecticides used in all years, resulting in a wide range of insecticide program risk (IPR) scores within and across years (Figure 2.7). The median IPR score differed across years ($\chi^2 = 12.8$, $df = 4$, $p = 0.01$), increasing from 2005 to 2012 with additional increase in 2013. Most growers did not apply insecticides during the bloom period, but began spraying more intensively during the berry sizing and pre-harvest periods to control for blueberry maggot (Diptera: Tephritidae; *Rhagoletis mendax* Curran), Japanese beetle (Coleoptera: Scarabaeidae; *Popillia japonica* Newman), and *D. suzukii*, according to grower records (Figure 2.8).

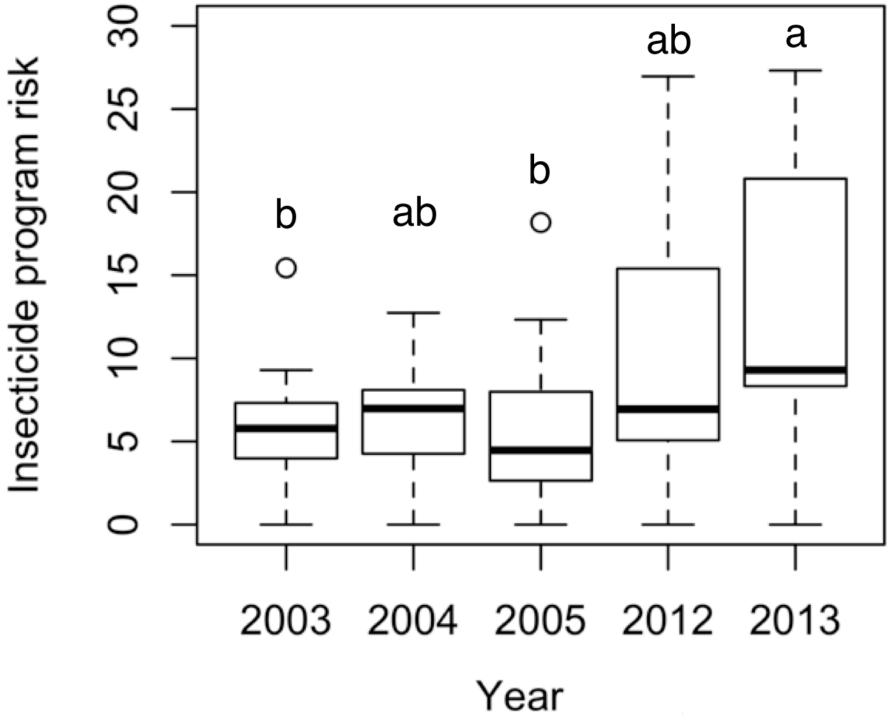

Figure 2.7. Boxplot of insecticide program risk across 15 blueberry farms in each of the five years prior to bee collections.

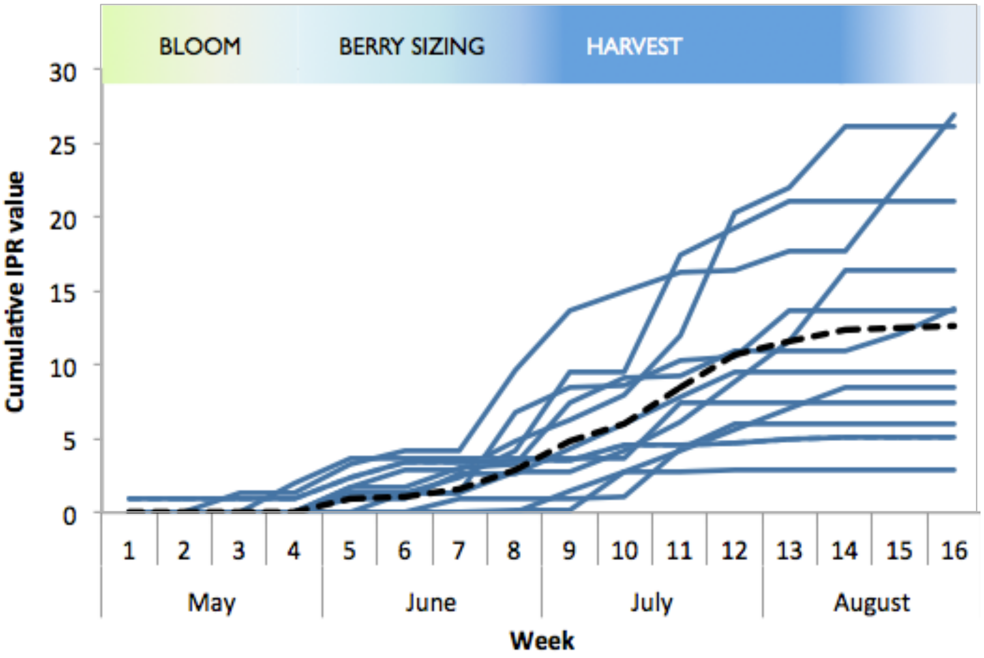

Figure 2.8. Increase in cumulative insecticide program risk (IPR) value over the 2012 growing season at the 13 conventionally managed blueberry fields. The average cumulative IPR is represented by the black dashed line.

Landscape characterization

Sites varied in the proportion of each land-use type in the surrounding landscape, but experienced relatively little land use change from 2005 to 2014. Blueberry plantings were the dominant land cover category within a 300 m radius of the sampled fields, comprising approximately 29-30% of the area within 300 m. This proportion stayed constant from 2005 to 2014 when averaged across sites. Individual sites had larger changes at this scale; two farms cleared several acres of forest to plant additional blueberry, while another farm removed older stands of blueberry and replaced them with row crops. Forest interiors, which represented around 24% of land cover in 2005, decreased by only about 1% over all sites from 2005-2014, with around 16 acres of forest cleared for agricultural and development purposes. However, forest margins (the first 10 m edge of forest patches) increased from 6 to 8% of total land area as these larger forest patches were cleared. Settled areas, which represented around 10% of land cover in 2005, increased by 14 acres, or around 2%. Row crops represented 4% of land cover at the 300 m scale in 2005, increasing by 11.5 acres to 5% of land cover in 2014.

The first two principal components in the PCA of landscape at the 300 m scale around the sample sites represented tradeoffs in four of the dominant categories of land cover directly surrounding sampled fields: blueberry plantings, forest patches, row crops, and settled areas (Figures 2.9 and 2.10; Table 2.4). The first principal component for landscape at 300 m was strongly associated with the proportion of blueberry plantings in the surrounding landscape (Table 2.4). Several of the sampled fields were part of large commercial blueberry farms that included many acres of blueberry within a 300 m radius. In addition, the area of forest interior (more than 10 m into forest patches) and row crops, which consisted primarily of corn and soybean fields, loaded negatively on this first component. This axis (PC1) represents the main axis of variation in the landscape directly surrounding the sampled fields: as the amount of blueberry in the landscape increases, large forest patches and other agricultural crops decrease.

The second principal component for landscape at 300 m was also strongly negatively associated with forest interior (Table 2.4); however, unlike the first principal component, blueberry plantings also loaded negatively on this axis. Settled areas – comprised primarily of houses, farm buildings, mowed lawns, and driveways – had a strong positive loading on this component. PC2 therefore represents the second dominant axis of variation in the landscape directly surrounding blueberry fields: as the amount of developed land increased, the area of forested patches and blueberry plantings decreased.

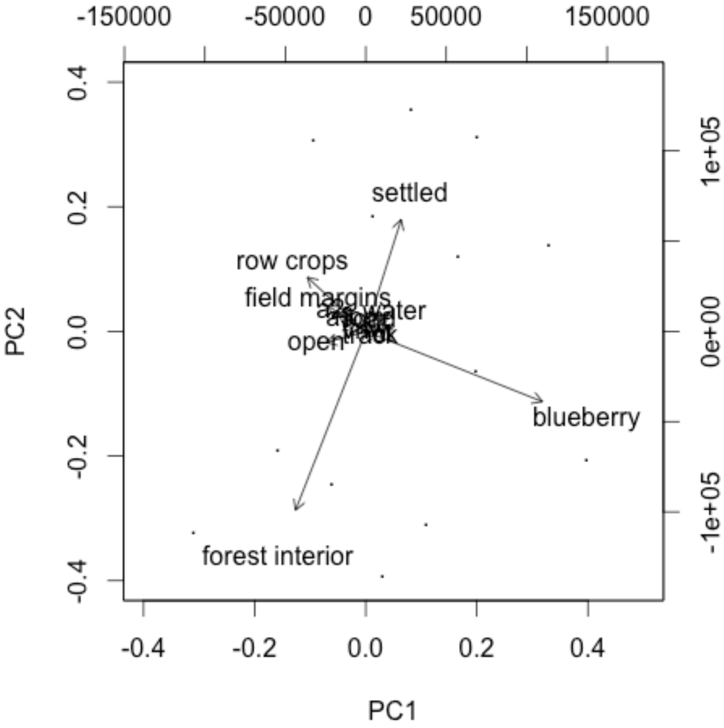

Figure 2.9. Biplot of first two principal components for landscapes surrounding blueberry field locations sampled for bees at the 300 m scale in 2005.

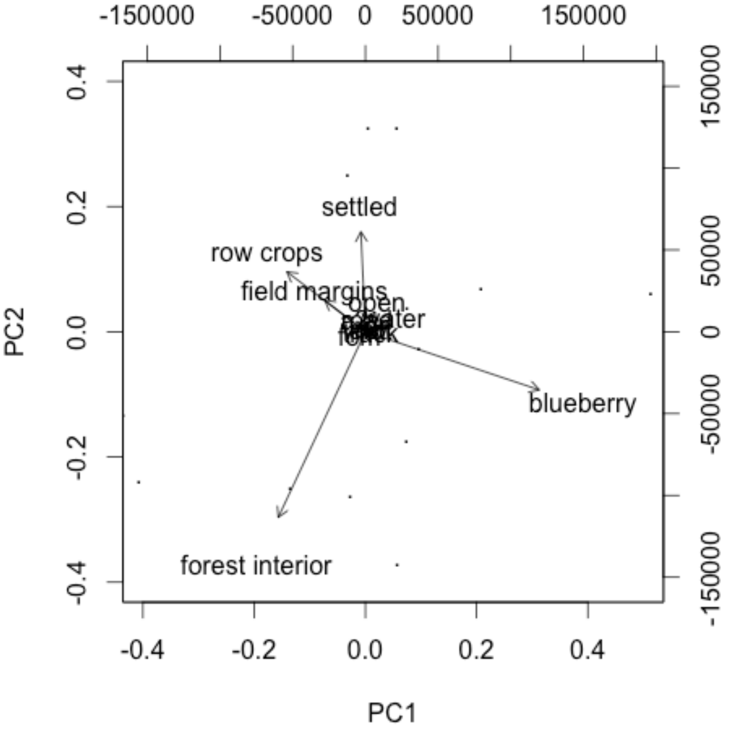

Figure 2.10. Biplot of first two principal components for landscapes surrounding blueberry field locations sampled for bees at the 300 m scale in 2014.

Table 2.4. Factor loadings for the first two principal components for landscape in 2005 and 2014. Loadings > 0.4 are shown in bold.

Land use	**2005**		**2014**	
	PC1	**PC2**	**PC1**	**PC2**
Blueberry	**0.83**	-0.30	**0.81**	-0.25
Other perennial crops	-0.13	0.08	-0.04	0.05
Pasture	-0.09	0.05	0.00	0.01
Row crops	-0.27	0.23	-0.36	0.26
Open uncultivated	-0.18	-0.05	0.04	0.09
Ditches	0.06	0.00	0.06	0.01
Field margins	-0.18	0.11	-0.19	0.14
Forest interior	-0.33	**-0.77**	**-0.40**	**-0.80**
Forest margins	-0.01	0.05	-0.02	-0.01
Road	0.02	0.05	0.01	0.04
Settled	0.17	**0.48**	-0.02	**0.43**
Railroad track	0.02	-0.01	0.02	0.00
Riparian areas	0.00	0.00	0.00	0.00
Water	0.11	0.07	0.10	0.05

Bee responses to pest management and landscape

Simple linear regressions of log-transformed wild bee abundance on IPR found significant negative relationships between abundance and prior-year IPR for the 2004 and 2014 collections (Table 2.5). Relationships in the other three years were more variable, including a positive trend between IPR and abundance in 2006 (Figure 2.11). Linear regressions of Chao1 estimated species richness of wild bees on prior-year IPR for each year of collections found a marginally significant negative correlation in 2004 and a significant negative correlation in 2013 (Table 2.5). The relationship trended negative in 2005 and 2014 and – like abundance – showed a positive trend in 2006 though this had a weak correlation (Figure 2.12).

When abundance and richness were analyzed against prior-year IPR separately for the two collection periods (2004-2006 and 2013-2014) and then for all five years of sampling, only the five year repeated measures analyses found significant negative relationships with IPR (Table

2.6). The slope of the relationship between bee abundance and IPR was positive for the 2004-2006 collection period and negative for the 2013-2014 collections (Table 2.6), though neither were significant. Wild bee richness had a marginally significant negative correlation with prior-year IPR for the 2004-2006 period ($F = 3.57$, $df = 1{,}29$, $p = 0.07$; Table 2.6), but was less correlated with IPR in 2013-2014 ($F = 2.48$, $df = 1{,}12$, $p = 0.14$). However, this relationship was highly significant when analyzed across all five years ($F = 13.6$, $df = 1{,}51$, $p = 0.0005$).

Log-transformed bee abundance across all five years was significantly negatively correlated with IPR and the second principal component for landscape at 300 m, which was associated with increasing settlement and decreasing forest cover (Tables 2.7 and 2.8; Figures 2.13 and 2.14). Bee richness (Chao1) was also significantly negatively correlated with IPR (Tables 2.9 and 2.10; Figure 2.15). The competing models for bee richness included one or both landscape components, both of which were negatively correlated with bee richness (Table 2.9).

Bias-corrected Shannon's diversity of wild bees had a significant negative relationship with insecticide program risk, though the null model also had substantial support according to ΔAIC (Tables 2.11 and 2.12; Figure 2.16). However, functional dispersion (FDis) was not explained well by any of the predictor variables (Table 2.13). Akaike weights indicated little confidence in any model of functional dispersion (all models <22% confidence; Table 2.13). No combination of functional traits (sociality, body size, lecty, or nest location) substantially improved the model fit for FDis; the null model was either the best model or within 0.34 ΔAIC for all combinations of FDis.

Table 2.5. Slopes (β ± SE), coefficients of determination (R^2), and *p*-values for simple linear regressions of log-transformed wild bee abundance and Chao1 estimated species richness on prior-year insecticide program risk for each year of collections at 13 blueberry farms.

Collection year	**Log-transformed abundance**			**Chao1 estimated species richness**		
	β ± SE	R^2	***p***	**β ± SE**	R^2	***p***
2004	-0.18 ± 0.05	0.5	0.003**	-0.81 ± 0.43	0.21	0.09
2005	-0.08 ± 0.05	0.16	0.15	-0.69 ± 0.43	0.17	0.13
2006	0.05 ± 0.04	0.09	0.28	0.36 ± 0.57	0.03	0.54
2013	0.001 ± 0.02	0.0001	0.97	-0.34 ± 0.12	0.41	0.01*
2014	-0.04 ± 0.02	0.33	0.03*	-0.33 ± 0.26	0.12	0.23

*significant at *p*=0.05; ***p*=0.01

Table 2.6. Slopes (β ± SE), degrees of freedom (*df*), and *p*-values for repeated measures regressions of log-transformed wild bee abundance and Chao1 estimated species richness on prior-year insecticide program risk for 2004-2006 collections, 2013-2014 collections, and all five years of collections at 13 blueberry farms.

Collection period	**Log-transformed abundance**			**Chao1 estimated species richness**		
	β ± SE	***df***	***p***	**β ± SE**	***df***	***p***
2004-2006	0.02 ± 0.02	29	0.41	-0.58 ± 0.31	29	0.07
2013-2014	-0.02 ± 0.02	12	0.22	-0.26 ± 0.17	12	0.14
All years	-0.03 ± 0.01	51	0.046*	-0.46 ± 0.12	51	0.0005***

*significant at *p*=0.05; ***p*=0.01; ****p*=0.001

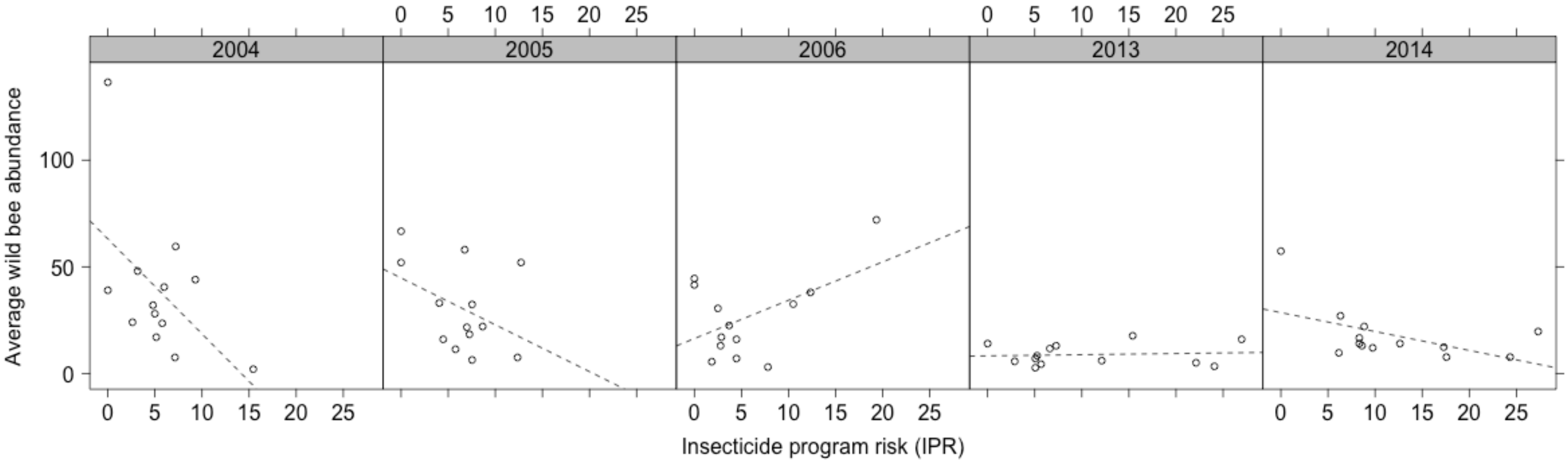

Figure 2.11. Simple linear regressions of log-transformed abundance of wild bees on prior-year insecticide program risk (IPR) at the 13 blueberry farms that provided 5 years of application records. Dashed lines represent regression trend lines.

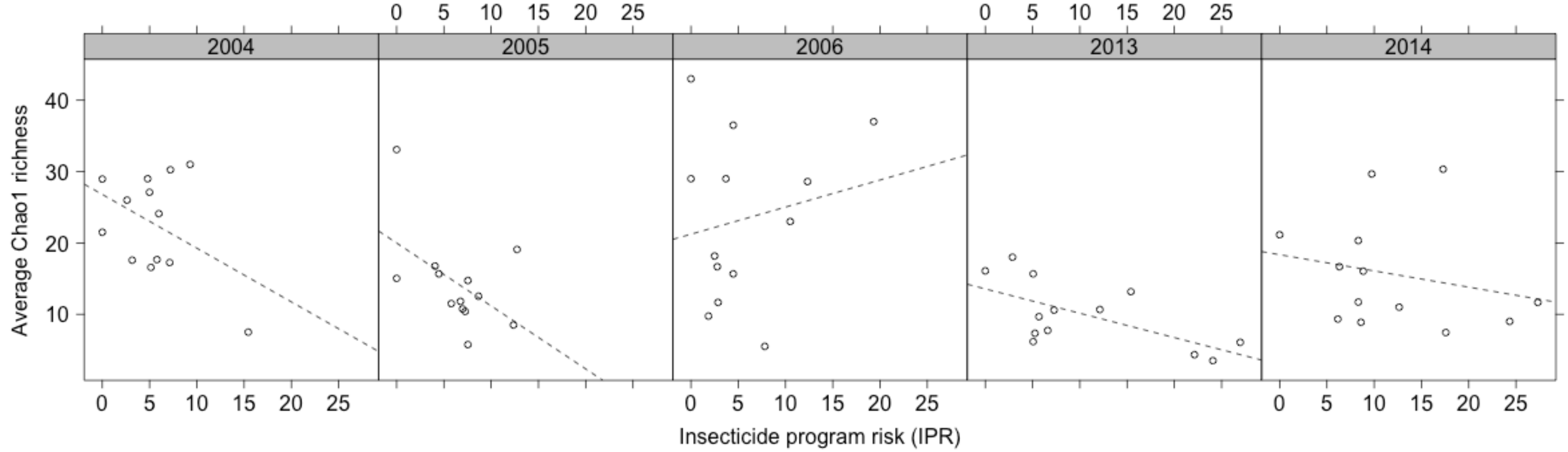

Figure 2.12. Simple linear regressions of Chao1 estimated species richness of wild bees on prior-year insecticide program risk (IPR) at the 13 blueberry farms that provided 5 years of application records. Dashed lines represent regression trend lines.

Table 2.7. Model selection table for log-transformed wild bee abundance based on repeated measures analysis on all combinations of insecticide program risk (IPR) and the two first principal components for landscape composition (300 m radius). Models are ranked according to Akaike's information criterion (AIC), with the regression slopes, AIC, ΔAIC, AIC weight, and relative variable importance based on Akaike weights shown for the best competing models (ΔAIC ≤ 2) only.

Model rank	**Model components**			***k***	**Akaike's information criterion (AIC)**	**ΔAIC**	**AIC weight**
	IPR	**PC1**	**PC2**				
1	-0.03*	n.i.	-5.0x10^{-6}*	2	154.7	0	0.455
2	n.i.	n.i.	-5.7x10^{-6}*	1	155.5	0.84	0.299
3	-0.03*	-3.8x10^{-6}	-5.5x10^{-6}*	3	155.9	1.43	0.198
Importance	0.70	0.25	1.00				

n.i. = not included in model.
*significant at $p = 0.05$.

Table 2.8. Best model for log-transformed wild bee abundance across five years of sampling (2004-2006 and 2013-2014) at 13 blueberry farms.

Parameter	**Model coefficient ± SEM**	***df***	***t*-value**	***p*-value**
IPR	-0.03 ± 0.01	50	-2.02	0.048*
PC2	-0.00001 ± 0.00	50	-2.29	0.03*

*significant at $p = 0.05$.

Table 2.9. Model selection table for Chao1 estimated richness for wild bees based on repeated measures analysis on all combinations of insecticide program risk (IPR) and the two first principal components for landscape composition (300 m radius). Models are ranked according to Akaike's information criterion (AIC), with the regression slopes for model components, AIC, ΔAIC, AIC weight, and relative variable importance based on Akaike weights shown for the best competing models (ΔAIC ≤ 2) only.

Model rank	**Model components**			***k***	**Akaike's information criterion (AIC)**	**ΔAIC**	**AIC weight**
	IPR	**PC1**	**PC2**				
1	-0.46***	n.i.	n.i.	1	470.6	0	0.451
2	-0.48***	-3.5x10^{-5}	n.i.	2	471.4	0.78	0.305
3	-0.43**	n.i.	-1.7x10^{-5}	2	471.8	1.22	0.245
Importance	1.00	0.30	0.24				

n.i. = not included in model.
*significant at $p = 0.05$; **$p = 0.01$; *** $p = 0.001$.

Table 2.10. Best model for Chao1 estimated wild bee richness across five years of sampling (2004-2006 and 2013-2014) at 13 blueberry farms.

Parameter	**Model coefficient ± SEM**	***df***	***t*-value**	***p*-value**
IPR	-0.46 ± 0.12	51	-3.69	0.0005***

***significant at $p = 0.001$.

Table 2.11. Model selection table for bias-corrected Shannon's diversity of wild bees based on repeated measures analysis on all combinations of insecticide program risk (IPR) and the two first principal components for landscape composition (300 m radius). Models are ranked according to Akaike's information criterion (AIC), with the regression slopes for model components, AIC, ΔAIC, AIC weight, and relative variable importance based on Akaike weights shown for the best competing models (ΔAIC ≤ 2) only.

Model rank	**Model components**			***k***	**Akaike's information criterion (AIC)**	**ΔAIC**	**AIC weight**
	IPR	**PC1**	**PC2**				
1	-0.01**	n.i.	n.i.	1	13.9	0	0.397
2	-0.01***	$9.7\text{x}10^{-7}$	n.i.	2	14.7	0.82	0.263
3	n.i.	n.i.	n.i.	0	15.3	1.43	0.194
4	-0.01**	n.i.	$2.6\text{x}10^{-8}$	2	15.9	2.00	0.146
Importance	0.81	0.26	0.15				

n.i. = not included in model.
*significant at $p = 0.05$; **$p = 0.01$; *** $p = 0.001$.

Table 2.12. Best model for bias-corrected Shannon's diversity of wild bees collected across five years of sampling (2004-2006 and 2013-2014) at 13 blueberry farms.

Parameter	**Model coefficient ± SEM**	***df***	***t*-value**	***p*-value**
IPR	-0.009 ± 0.003	51	-3.05	0.004**

**significant at $p = 0.01$.

Table 2.13. Model selection table for functional dispersion (FDis) of wild bees based on repeated measures analysis on all combinations of insecticide program risk (IPR) and the two principal components for landscape composition (300 m radius). Models are ranked according to Akaike's information criterion (AIC), with the regression slopes for model components, AIC, ΔAIC, AIC weight, and relative variable importance based on Akaike weights shown for the best competing models (ΔAIC ≤ 2) only.

Model rank	**Model components**			***k***	**Akaike's information criterion (AIC)**	**ΔAIC**	**AIC weight**
	IPR	**PC1**	**PC2**				
1	n.i.	$-4.7x10^{-7}$	n.i.	1	-171.7	0	0.216
2	n.i.	n.i.	n.i.	0	-171.3	0.31	0.185
3	0.001	$-4.4x10^{-7}$	n.i.	2	-171.3	0.36	0.180
4	0.002	n.i.	n.i.	1	-171.1	0.52	0.167
5	n.i.	$-4.6x10^{-7}$	$-7.8x10^{-8}$	2	-169.8	1.81	0.087
6	0.002	$-4.3x10^{-7}$	$-1.2x10^{-7}$	3	-169.8	1.90	0.083
7	0.002	-	$-1.4x10^{-7}$	1	-169.7	1.96	0.081
Importance	0.51	0.57	0.25				

n.i. = not included in model.

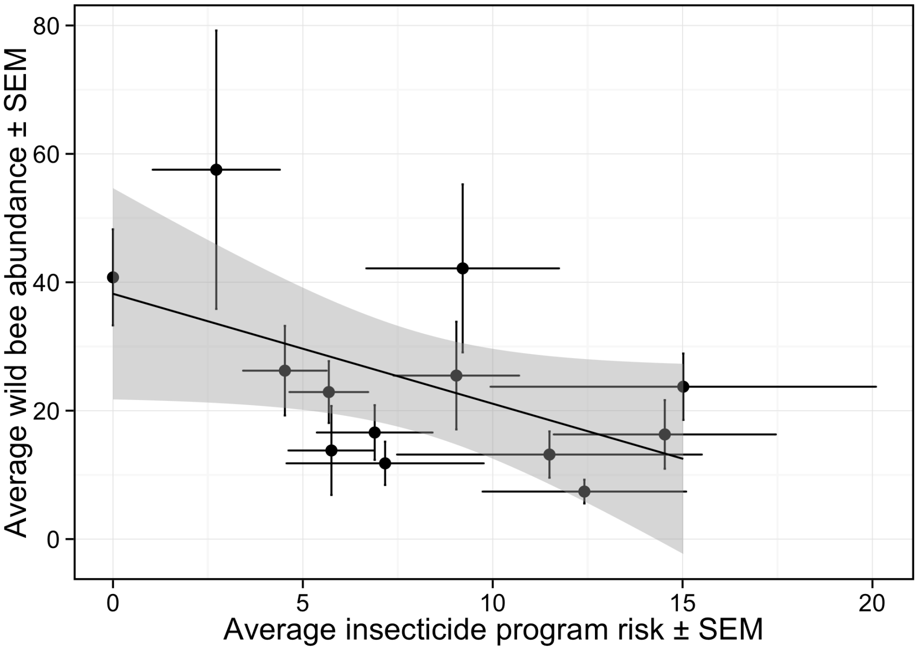

Figure 2.13. Average untransformed abundance of wild bees per site captured over five years of sampling during bloom at 13 blueberry farms, plotted against the average prior-year insecticide program risk at those farms. Gray area represents 95% confidence around the regression line. Two farms that did not provide all five years of spray records were not included in the regression analysis and are not shown here.

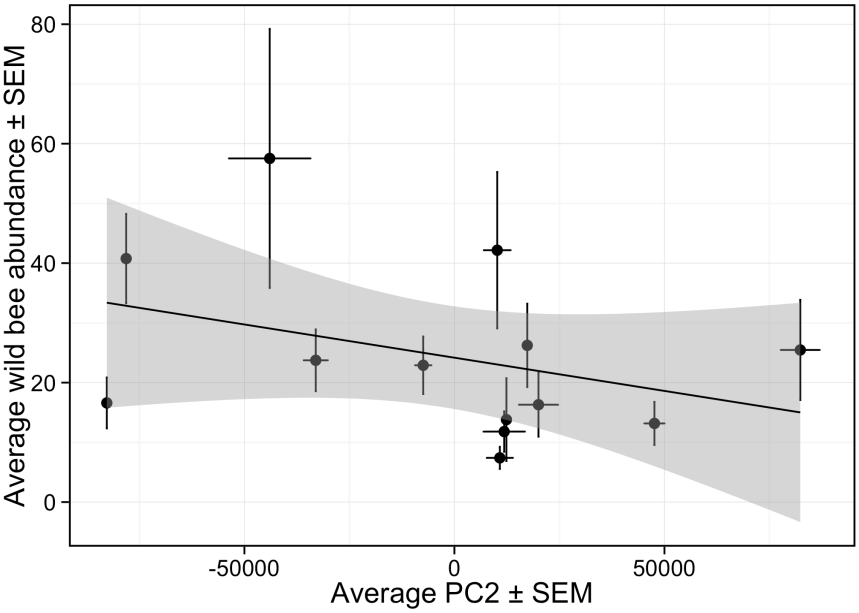

Figure 2.14. Average untransformed abundance of wild bees per site captured over five years of sampling during bloom at 13 blueberry farms, plotted against the second principal component for landscape at 300 m (PC2) at those farms. Increasing PC2 is associated with decreasing forest cover and increasing area of settlement (farm buildings, houses, lawns, driveways, etc.). Grey area represents 95% confidence around the regression line. Two farms that did not provide all five years of spray records were not included in the regression analysis and are not shown here.

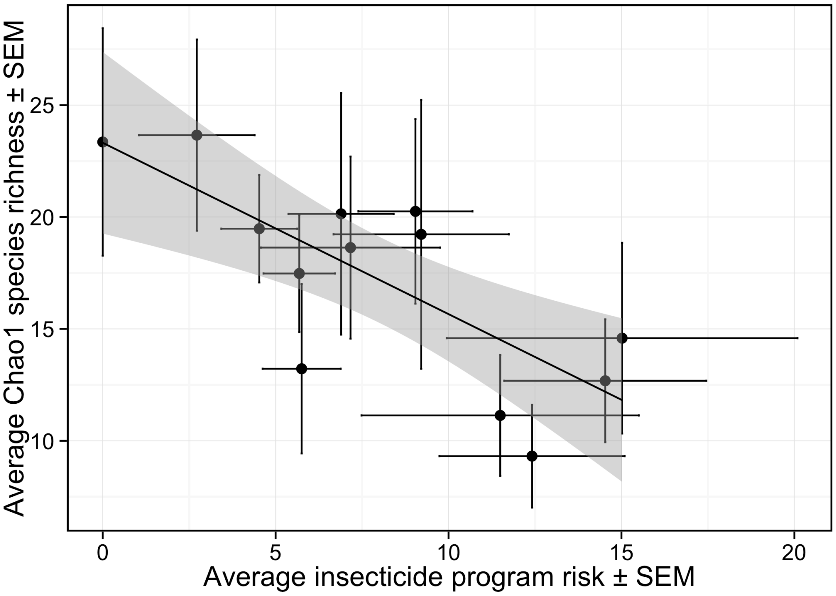

Figure 2.15. Repeated measures regression of prior-year insecticide program risk on Chao1 estimated species richness of the wild bees captured over 5 years of sampling during bloom at 13 blueberry farms. Grey area represents 95% confidence around the regression line. Two farms that did not provide all five years of spray records were not included in the regression analysis and are not shown here.

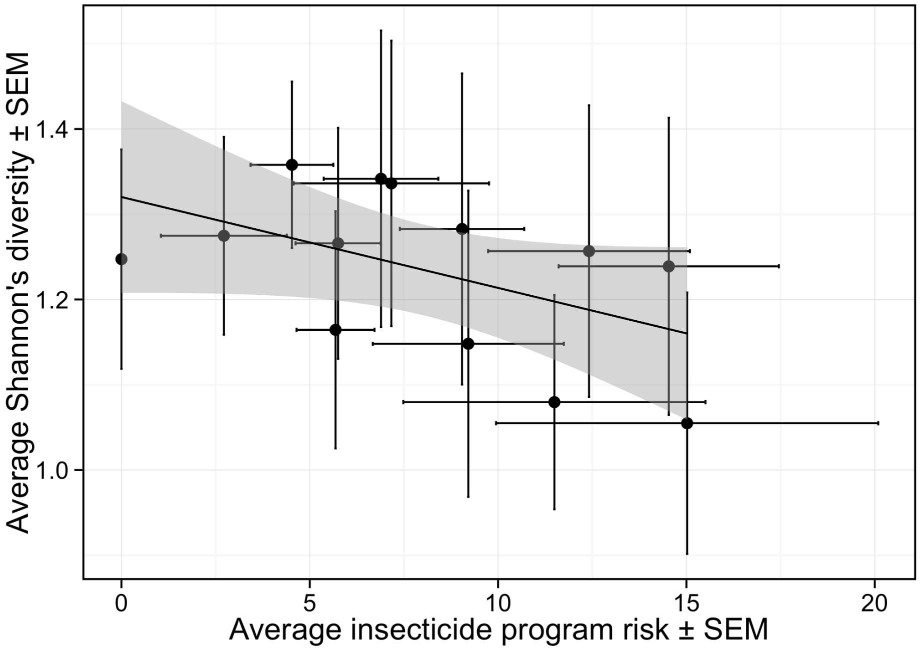

Figure 2.16. Average bias-corrected Shannon's diversity of the wild bees captured over five years of sampling during bloom at 13 blueberry farms, plotted against the average prior-year insecticide program risk at those farms. Two farms that did not provide all five years of spray records were not included in the regression analysis and are not shown here.

When vectors of insecticide program risk and the two landscape components were fitted onto the NMDS ordination of bee communities, both IPR and PC1, or increasing area of blueberry in the landscape, showed significant correlation with community composition (Figure 2.17; Table 2.14). The second principal component for landscape, which represented increasing settlement and decreasing forest cover, was not significantly correlated with community composition (Table 2.14).

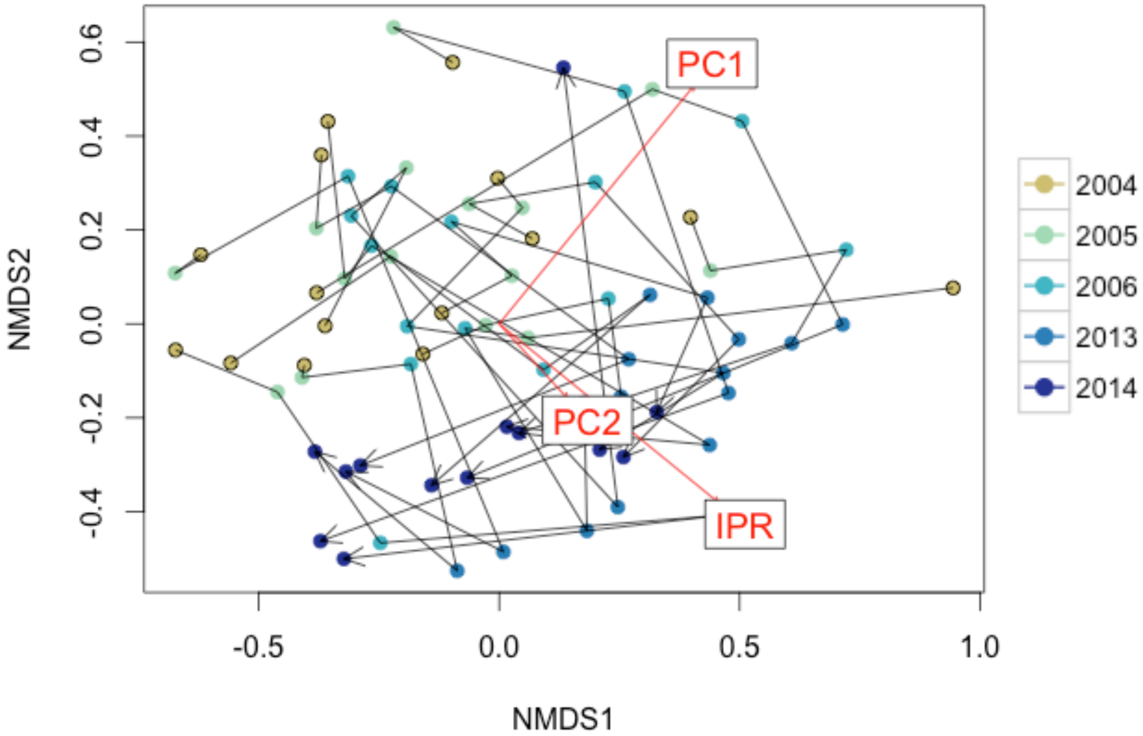

Figure 2.17. Nonmetric multidimensional scaling ordination of bee communities collected in pan traps and nets in 15 blueberry fields from 2004-2006 and 2013-2014. Each point represents one site in one year. Black arrows show the trajectory of one site beginning in 2004 (circled points) and ending in 2014. Red arrows show the projected vectors of insecticide program risk (IPR) and the two first principal components for landscape at the 300 m scale. Arrow lengths for IPR, PC1, and PC2 are scaled based on correlation with the ordination configuration.

Table 2.14. Direction cosines and correlations of the three predictor variables with the two-dimensional NMDS ordination of bee community composition.

Predictor variable	**Direction cosines**		r^2	*p*-value
	NMDS1	NMDS2		
IPR	0.77	-0.64	0.20	**0.002**
PC1	0.97	0.26	0.02	0.45
PC2	0.55	0.84	0.26	**0.001**

Comparison of social and solitary species

Visual examination of the NMDS ordination with fitted vectors of species loadings for the most abundant wild bee species collected across all years suggested that the most abundant solitary species (*Andrena* spp. and *Lasioglossum leucozonium* (Schrank)) were more associated with the first three years of collection, while the most abundant social, subsocial, and facultatively social species were more associated with the 2013 and 2014 collections (*Lasioglossum* (Dialictus) spp., *B. impatiens, Ceratina calcarata* Robertson, *Augochlora pura* (Say), and *Augochlorella aurata* (Smith)) (Figure 2.18). Across all collected species, solitary and social species grouped separately in ordination space (Figure 2.19).

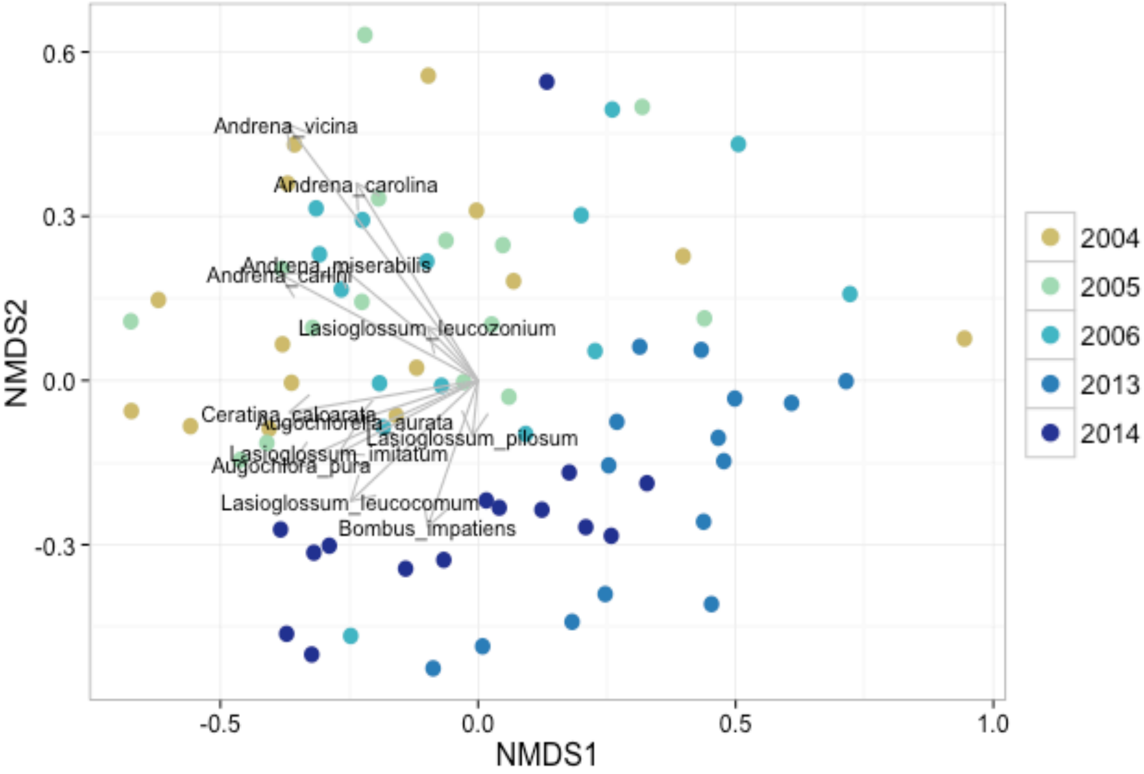

Figure 2.18. Biplot of NMDS ordination of bee communities collected from 2004-2006 and 2013-2014, showing the projection of fitted vectors for the most abundant species across all five years. Each colored dot represents one site in one year. *Andrena imitatrix* and *Lasioglossum cressonii,* which overlapped strongly with *A. miserabilis* and *L. leucococum*, respectively, are not shown.

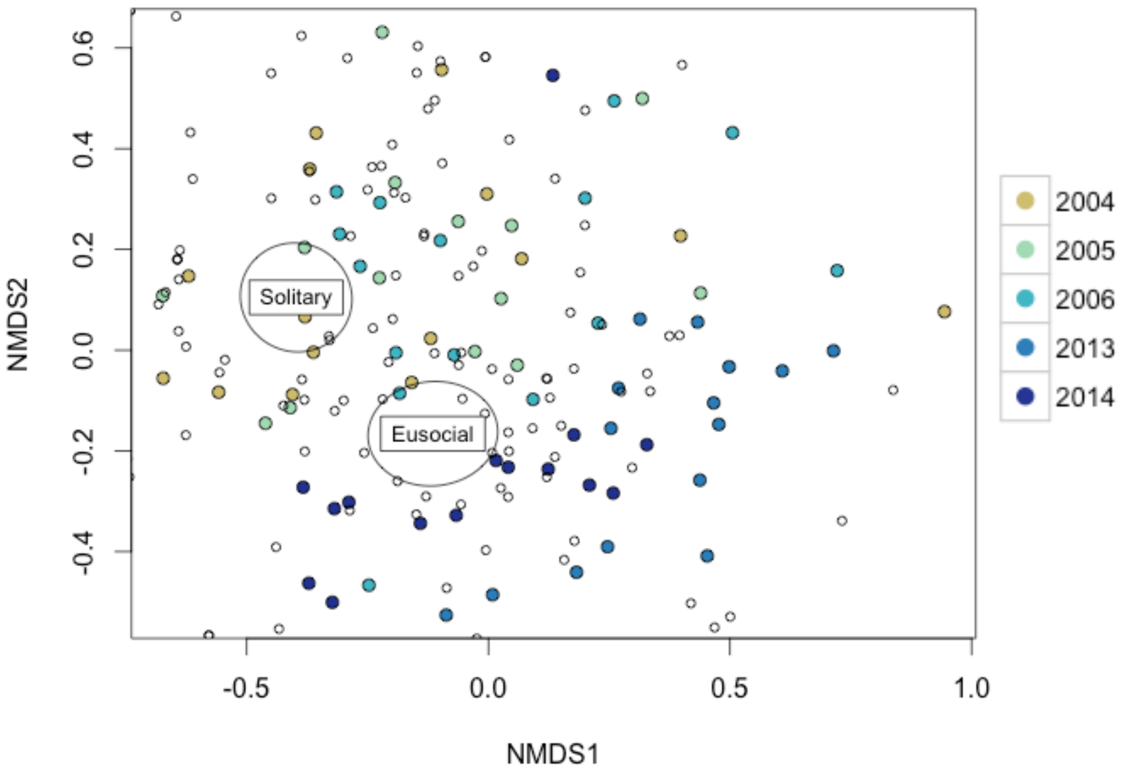

Figure 2.19. Nonmetric multidimensional scaling ordination of bee communities collected in pan traps and nets in 15 blueberry fields from 2004-2006 and 2013-2014. Each colored dot represents one site in one year. Open black circles represent a single species across all five years. Ellipses represent 95% confidence ellipses around the group mean for solitary and social (including social, subsocial, and facultatively social) bee species.

Social (including eusocial, facultatively social, and subsocial) and solitary bee species varied in their responses to IPR and landscape variables. Log-transformed abundance of solitary species had a significant negative correlation with PC1 ($F = 7.41$, $df = 1{,}49$, $p = 0.009$) and a marginally significant negative relationship with IPR ($F = 2.75$, $df = 1{,}49$, $p = 0.09$). However, while log abundance of social species was also negatively correlated with PC1 ($F = 4.90$, $df = 1{,}49$, $p = 0.03$), it showed no correlation with IPR ($F = 0.13$, $df = 1{,}49$, $p = 0.72$). Species richness of solitary species was strongly negatively correlated with IPR (Figure 2.19; $F = 12.43$, $df = 1{,}49$, $p = 0.0009$) and PC2 ($F = 6.72$, $df = 1{,}49$, $p = 0.01$). Social bee species richness was also significantly negatively correlated with IPR (Figure 2.19; *F* = 5.16, *df* = 1,49, *p* = 0.03), and had a marginally significant negative correlation with PC1 (*F*= 3.01, *df* = 1,49, *p* = 0.08).

When analyzed separately, the 2004-2006 collections showed slightly different patterns than the analyses across all years. Log abundance of solitary bees was significantly negatively correlated with IPR (*F* = 10.92, *df* = 1,29, *p* = 0.003), and had a marginally significant negative correlation with PC2 (*F* = 4.67, *df* = 1,12, *p* =0.052). Social bee abundance was marginally negatively correlated with PC1 (*F* = 3.64, *df* = 1,12, *p* = 0.08), but not IPR or PC2. Solitary richness was significantly negatively correlated with PC2 (*F* = 8.31, *df* = 1,12, *p* = 0.01), but was not significantly correlated with IPR (*F* = 2.57, *df* = 1,29, *p* = 0.12) or PC1 (*F* = 3.09, *df* = 1,12, *p* = 0.10). Social bee richness was negatively correlated with PC1 (*F* = 7.17, *df* = 1,12, *p* = 0.02) and positively correlated with PC2 (*F* = 6.47, *df* = 1,12, *p* = 0.03), but was not correlated with IPR (*F* = 1.99, *df* = 1,29, *p* = 0.17).

The 2013-2014 collections also showed different patterns than all five years together. Log abundance of solitary bees had a significant negative correlation with PC1 (*F* = 5.40, *df* =1,10, *p* = 0.04) and a marginally significant negative correlation with IPR (*F* = 4.56, *df* = 1,12, *p* = 0.054). Similar to the 2004-2006 collection years, log abundance of social species had a marginally significant negative correlation with PC1 (*F* = 4.82, *df* = 1,10, *p* = 0.053), but was not correlated with IPR or PC2. Solitary richness was significantly negatively associated with IPR (*F* = 6.43, *df* = 1,12, *p* = 0.03), but was not associated with either landscape variable. Species richness of the 2013-2014 social species was not associated with any of the measured variables.

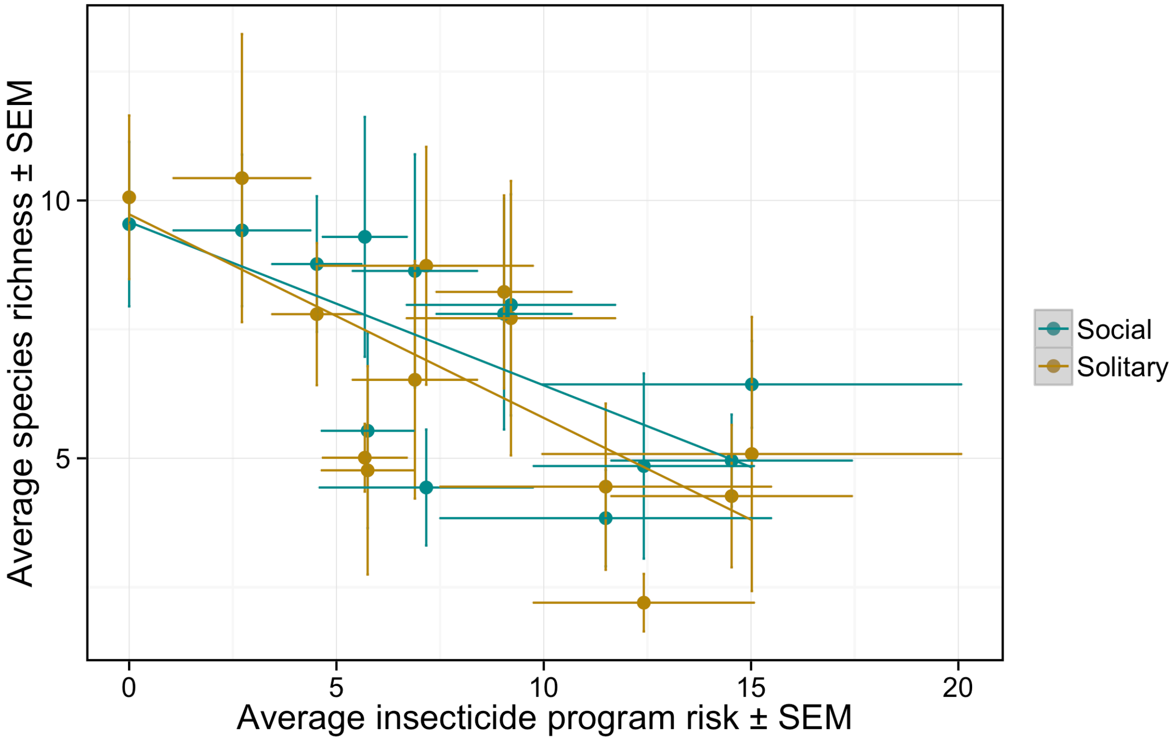

Figure 2.20. Repeated measures regressions of the average species richness of social (blue line) and solitary (yellow line) wild bee species on the prior-year insecticide program risk at 13 blueberry farms over five years of collections.

Service providing bees

Overall community responses to pest management and landscape composition were similar for the subset of 80 wild bee species that have been recorded foraging on blueberry. Log-transformed abundance for these bees was significantly negatively correlated with the first principal component for landscape ($F = 7.95$, $df = 1,49$, $p = 0.007$), and had a marginally significant negative correlation with IPR ($F = 3.36$, $df = 1,49$, $p = 0.07$). Chao1 estimated species richness of service-providing bees was significantly negatively correlated with IPR ($F = 5.89$, $df = 1,49$, $p = 0.02$), but not either landscape variable. Bias-corrected Shannon's diversity for the service-providing bees had a marginally significant negative correlation with PC2 ($F = 2.94$, $df = 1,49$, $p = 0.09$), but was not correlated with IPR or PC1.

Discussion

The agricultural matrix of the Michigan highbush blueberry agroecosystem consists largely of intensively managed crop fields surrounded by other blueberry fields, strips of grass, and patches of forest. Despite this relatively resource-poor environment for wild bees, blueberry fields consistently receive between 10 and 50% of their pollination from the wild bees living in this matrix (Isaacs & Kirk, 2010). This study shows that the diverse communities of wild bee visiting blueberry fields during bloom, including the subset of species that provide pollination services to blueberry, respond strongly to local-scale factors, including insecticide program risk and local landscape composition. In particular, the intensity of insecticide use at the field scale has a strong negative effect on the abundance, richness, and diversity of wild bee communities foraging in blueberry fields during bloom. Landscape composition around blueberry fields is also associated with environmental stress on wild bee communities; wild bee abundance declined with decreasing area of forest and the associated increase in nonagricultural developed areas.

This work builds directly on that of Tuell (2007), Tuell *et al.* (2009), and Tuell & Isaacs (2010), by providing a longer-term evaluation of the community-level and species-specific responses of wild bees to landscape composition and insecticide risk. Tuell & Isaacs (2010) found that bee responses to insecticide risk differed both at the community and species levels from year to year. High annual variability in the abundance, richness, and community composition of bee communities mean that the results of short-term ecological studies of these communities may not be representative of long-term trends (Roubik, 2001; Williams *et al.*, 2001). Using repeated measures analyses of bee communities at these sites, I was able to determine that wild bee communities were more consistent in their responses to insecticide risk over the sampled period than to landscape variables, although there was less change in land cover than in insecticide use in this time frame. I was also able to establish that the total wild bee community and the subset of species that provide pollination services to blueberry show similar responses to insecticide risk and landscape; therefore, conservation strategies that benefit the bees that provide pollination services to blueberry are also likely to support the overall biodiversity of bees in this landscape, and vice versa.

Wild bee communities responded most strongly to the major axes of landscape composition variation at the smallest scale studied (300 m). Bee foraging ranges vary based on body size, sociality, and resource distributions in the landscape, with larger social bees, such as some *Bombus* spp., traveling a kilometer or more in search of floral resources (Walther-Hellwig & Frankl, 2000; Gathmann & Tscharntke, 2002; Greenleaf *et al*., 2007; Jha & Kremen, 2013a). However, many solitary species have more restricted foraging ranges (Gathmann & Tscharntke, 2002; Greenleaf *et al*., 2007; Zurbuchen *et al*., 2010a, 2010b). Zurbuchen *et al*. (2010b) found that while some small *Hylaeus* could travel a maximum distance of approximately 1 kilometer in search of food, half of the studied females did not forage at distances longer than 100-300m. Long foraging distances may impose greater costs on solitary species, which must return to their nests several times a day to provision offspring, while social species can spread the energetic costs of foraging flights across a greater number of individuals (Zurbuchen *et al*., 2010a, 2010b). Over half of the bee species in this study were small solitary species likely to nest and forage close to the capture site, which may explain why the community as a whole responded most strongly to the smallest landscape scale encompassing all species' foraging ranges.

Wild bee communities showed clear negative responses to prior-year insecticide program risk (IPR) at the field scale across the five years of collections. While it is widely known –

primarily from laboratory studies – that many chemicals used for agricultural pest management are toxic to bees at individual and colony levels (Helson *et al*., 1994; Thompson, 2003; Morandin *et al*., 2005; Desneux *et al*., 2007; Mullin *et al*., 2010; Brittain & Potts, 2011; Gill *et al*., 2012; Biddinger *et al*., 2013; Arena & Sgolastra, 2014), few studies have examined wild bee community responses to pesticides (*but see* Kevan, 1975; Kevan *et al*., 1997; Dormann *et al*., 2007; Brittain *et al*., 2010; Tuell & Isaacs, 2010). This study found that wild bees are less abundant, species-rich, and diverse on farms with more intensive insecticide use, providing support for the assertion of Goulson *et al*. (2015) that pesticides are an important contributing factor to the declines in bee populations observed in various agricultural systems.

Bee abundance also increased with increasing forest cover and declined with increasing settlement at the 300 m scale, as represented by PC2. These results align well with Watson *et al*. (2011), who found that the abundance and richness of wild bees in Wisconsin apple orchards during bloom were positively correlated with the proportion of forest cover and negatively correlated with the proportion of nonagricultural developed land in the surrounding landscape. Early spring bees, such as the mining bees (*Andrena* spp.) that are active pollinators of blueberry and apple, may be associated with forested areas, which provide floral resources in the form of flowering trees and shrubs at this time of year (Giles & Ascher, 2006; Westwood, 2006; Grundel *et al*., 2010). Many wild bee species collect pollen from flowering trees, including those commonly found in forest understories, such as those in the genera *Salix, Crataegus, Cornus, Acer,* and *Prunus* (Batra, 1985; Stubbs *et al*., 1992; Giles & Ascher, 2006). In a season-long survey of bees in different habitats in northwest Indiana, Grundel *et al*. (2010) found wild bees were relatively abundant in forests in early to mid May, before the canopy filled in, but were not abundant in these habitats later in the season. Following blueberry bloom, therefore, wild bee communities may exhibit different relationships with land cover that reflect seasonal changes in resource distributions.

Increasing area of nonagricultural developed land, including houses, driveways, farm buildings, and mowed lawns around those built spaces, may be correlated with reductions in the availability of floral resources or nesting sites for wild bees (Westrich, 1996; Kearns & Inouye, 1997). Conversion of land from natural habitat to built spaces may also lead to fragmentation of plant communities and create barriers to pollinator movement (Westrich, 1996; Kearns & Inouye, 1997; Steffan-Dewenter & Tscharntke, 1999; Hernandez *et al*., 2009). Bates *et al*. (2011) found that wild bee abundance and richness along an urban to rural gradient declined with the percentage of built space in the surrounding landscape. Ground-nesting bees respond negatively to an increasing proportion of impervious surfaces in the surrounding environment (Ahrné *et al*., 2009; Jha & Kremen, 2013a). Jha & Kremen (2013a, 2013b) found that nest density and gene flow of bumble bees (*Bombus* spp.), which nest in the soil, decrease with an increasing proportion of impervious surface in the landscape. Reductions in forest cover in favor of increasing development may therefore have non-random effects on bee communities based on life-history traits such as nesting substrate.

Functional trait diversity, as measured by functional dispersion (Laliberté *et al*., 2010), remained stable along gradients of landscape composition and insecticide risk in this study. However, sociality appears to mediate wild bee responses to these environmental factors, with solitary species showing slightly more negative responses to insecticide risk than social species. Abundance of solitary species, but not social species, was negatively correlated with IPR for both the 2004-2006 and 2013-2014 collections, as well as for the bees from all five years analyzed together. Both social and solitary bee richness were significantly negatively correlated with IPR when analyzed across all years of the study, with solitary richness showing a stronger correlation and steeper negative slope than social richness. However, neither social nor solitary bee richness for the 2004-2006 bees were correlated with IPR, though both had significant correlations with at least one landscape variable during this time period. Solitary bee richness, but not social bee richness, was significantly negatively correlated with IPR in the 2013-2014 collections. The differences in species richness responses between these time periods may indicate that the major environmental filter for these communities has shifted from the resource distribution in the landscape (2004-2006) to the distribution of environmental stress (2013-2014).

The observed pattern of greater effect of insecticide risk on solitary species abundance and richness was somewhat unexpected, as Tuell & Isaacs (2010) suggested that social bees might be more affected by typical blueberry pest management programs because colonies remain active during the periods of more intensive insecticide use for pest control following crop bloom. However, only one of three studied social species in Tuell & Isaacs (2010) supported this expectation. Two previous meta-analyses of wild bee species' responses to environmental disturbance (Winfree *et al*., 2009; Williams *et al*., 2010) found that social species exhibited significantly more negative responses to pesticide use than solitary species. However, none of the agricultural crops included in the Williams *et al*. (2010) meta-analysis (pumpkin, squash, watermelon, and olives) are comparable to highbush blueberry in terms of growth habits, seasonality, or pest management needs. Additionally, the Winfree *et al*. (2009) meta-analysis includes the same pumpkin and squash paper as Williams *et al*. (2010) (Shuler *et al*., 2005), as well as a study of the effects of aerial applications of an organophosphate on exposure-caged bees (Plowright & Rodd, 1980). The types of chemicals, seasonality, and routes of exposure to those chemicals may differ for wild bees in the highbush blueberry system, leading to differences in species' responses.

Solitary species may be more likely to be negatively affected than social species when exposed to insecticides because a solitary female bee is the sole provider for her nest and all of her reproductive potential is therefore lost if she is killed or otherwise impaired prior to mating or laying eggs (Brittain & Potts, 2011). In contrast, social species can rely on multiple foragers to provide resources; if one nestmate is killed while foraging in a treated field, there may be others foraging elsewhere in the landscape that are not affected and can continue to provide pollen and nectar resources to the colony (Brittain & Potts, 2011). Additionally, in some socially polymorphic species, such as *Halictus ligatus* Say, female workers can mate and lay fertilized eggs, even in queenright nests; if the nest-founding queen is killed, she can be replaced by a recently eclosed worker (Richards *et al*., 1995; Rehan *et al*., 2013). This flexibility in foraging and egg-laying may afford social species an advantage in intensively managed agricultural areas. In a study of the effects of different agricultural practices and landscape structure on bee communities, Le Féon *et al*. (2010) found that *Bombus* spp. were relatively more abundant at sites with high inputs of insecticides and nitrogen fertilizers, while solitary species were less abundant at those sites. More work is needed to characterize the timing and identity of insecticide applications that may be particularly deleterious to solitary or social bees in this and other crop systems.

The observed difference between social and solitary bee species responses to IPR might also be related to the scale at which those species respond to the landscape; social species may be responding to insecticide risk at a larger scale than the immediate field scale. Both abundance and richness of social species were negatively associated with the first principal component for landscape, which represented increasing area of blueberry in the surrounding landscape. As the area of managed blueberry increases in the landscape, the potential for exposure to insecticides for bees foraging in that landscape also increases. Because social species, on average, travel longer distances than solitary species to forage for nectar and pollen resources (Zurbuchen *et al.*, 2010), they may respond more strongly to exposure risk at the landscape rather than the field scale.

These results are suggestive of wild bee declines related to intensive insecticide use in this cropping system. However, wild bee communities, including those studied here, are characterized by large annual variation in bee abundance, richness, and composition (Cane & Tepedino, 2001; Roubik, 2001; Williams *et al.*, 2001), and thorough collections at multiple time points and multiple sites within each year are needed over a long period before declines (if present) could be detected (Roubik, 2001; Williams *et al.*, 2001; Lebuhn *et al.*, 2013). In 2013, only 421 wild bees were collected over 3 days of pan trapping at the 15 sites, fewer than half the average number of wild bees captured each year during bloom in 2004-2006 by Tuell *et al.* (2009). Had similar numbers of bees been collected in 2014, declines might have been suspected. However, nearly double the 2013 captures were collected in 2014, indicating that low captures in 2013 may have been a single-year fluctuation in bee abundance in response to an unusually warm spring in 2012, which was followed by frost damage to spring-blooming plants and a severe midsummer drought.

The record-breaking heat and drought of 2011 and 2012, including July 2012, the hottest month in the instrumental record (Karl *et al.*, 2012), may have led to a short-term reduction in wild bee abundance by reducing the quantity and quality of nectar and pollen resources available in the landscape (Alarcón *et al.*, 2008; Minckley *et al.*, 2013), by disrupting physiological development or reproductive processes (Bale & Hayward, 2010; Sgolastra *et al.*, 2011), and/or by desiccating developing larvae and prepupae in uninsulated environments, such as nests located aboveground or belowground nests close to the soil surface (Cane & Neff, 2011). Adult females foraging for pollen and nectar in summer 2012 may have had to visit more flowers and travel longer distances to collect sufficient pollen and nectar for their developing brood; this increase in energy expenditure during foraging is likely to reduce the number of offspring produced by individual females (Williams & Kremen, 2007).

Fluctuations in bee populations due to these types of climatic perturbations and other variables can make detection of overall declines challenging. Roubik (2001) reported annual variability of bee abundance in a tropical bee community of up to 300%, or fourfold changes in bee abundance from year to year, and annual changes in bee richness of up to 14-fold. Long-term collections by a single researcher in the E.S. George Reserve in Michigan over several decades corrected for differences in sampling intensity also showed wide variation in bee abundance among years, with five times as many bees collected in each of two years in the 1970s than in any other year (Williams *et al.*, 2001). In addition, the sites in my study included only one unmanaged site. To separate natural variation from an environmental impact of interest – for example, intensive insecticide use in this system – any future sampling should include additional unmanaged sites to account for natural community variability removed from specific disturbance factors (Williams *et al.*, 2001).

The diversity of individual species' responses to environmental stressors may be an important stabilizing mechanism for species-rich communities and, by extension, the ecosystem services that these communities provide (Elmqvist *et al.*, 2003; Hooper *et al.*, 2005; Winfree & Kremen, 2009; Winfree, 2013). Species-specific responses to insecticide risk and landscape composition in this study differed widely, with some species, such as the *Vaccinium* oligolege *Andrena carolina,* exhibiting strong negative responses to insecticide risk, while others, such as the social halictid *Lasioglossum pilosum*, being positively correlated with insecticide risk. These responses may be mediated by life-history traits, such as sociality. Maintaining a broad diversity of species and associated functional traits may help to buffer these communities and the plants they pollinate against environmental stressors, including intensive agricultural practices, conversion of land for development, and changing plant phenologies due to climate change (Winfree *et al*., 2007; Winfree & Kremen, 2009; Bartomeus *et al*., 2011; Blüthgen & Klein, 2011; Albrecht *et al*., 2012). Management strategies for the enhancement of pollination service delivery in highbush blueberry should therefore place a priority on conserving functional diversity as well as species diversity in order to improve the annual stability of these vernal pollinator communities, as well as their resilience to current and future environmental disturbances.

Not all of the bees captured in pan traps and nets provide pollination services to blueberry, and their responses to farm management practices and landscape may be of less interest to growers intending to conserve bees solely for their value as pollinators of blueberry. However, the subset of bees providing pollination services in blueberry responded no differently to pest management than the community as a whole. My analysis did not weight individual species by their pollination efficiency on blueberry (Javorek *et al*., 2002), which might provide a more accurate picture of how pollination services may be affected by species-specific responses to environmental stress. However, continued intensive pest management is likely to have long-term deleterious effects on the wild bee communities living in and around blueberry fields, as well as the pollination they provide. If growers want to increase pollination service delivery by wild bee species, they will likely need to adopt approaches to pest management that minimize risk to bees, such as spraying at night, minimizing spray drift, and selecting the least toxic insecticide options to control target pests.

CHAPTER 3:

PERENNIAL WILDFLOWER PLANTINGS SUPPORT INCREASED NESTING BY SOIL-NESTING BEES

Introduction

Bees (Hymenoptera: Apoidea) provide essential pollination services to wild angiosperms and many cultivated agricultural crops (Klein *et al.*, 2007; Winfree *et al.*, 2007; Ollerton *et al.*, 2011; Garibaldi *et al.*, 2013). However, they face complex challenges in agricultural environments, including loss, fragmentation, and degradation of suitable habitats; exposure to agricultural chemicals; and infection with pathogens and diseases (Kremen *et al.*, 2002; Potts *et al.*, 2010; Kennedy *et al.*, 2013; Goulson *et al.*, 2015). Of these, the decline in foraging and nesting resources associated with agricultural intensification may be the most fundamental cause of observed declines in wild bee populations in managed ecosystems (Kremen *et al.*, 2002; Tscharntke *et al.*, 2005; Biesmeijer *et al.*, 2006; Goulson *et al.*, 2008, 2015; Kleijn & Raemakers, 2008; Grixti *et al.*, 2009; Naug, 2009; Potts *et al.*, 2010; Winfree, 2010). There is a critical need to conserve and enhance wild bee populations, particularly in agricultural landscapes with pollination service demands (Allen-Wardell *et al.*, 1998; Klein *et al.*, 2007; Winfree, 2010), but this requires knowledge of to what extent potential conservation strategies support bee populations in these settings.

Strategies for conserving wild bees in agricultural landscapes have focused on mitigating habitat loss, primarily through floral restorations such as hedgerows, wildflower strips, and meadows (Winfree, 2010). Government subsidy programs that were developed to remove arable land from production, such as the set aside programs under the Common Agricultural Policy of the European Union and the USDA Conservation Reserve Program in the United States, now include incentives for restoration projects aimed at conserving farmland biodiversity (Goulson, 2003b; Winfree, 2010). The response of bee populations to these biodiversity restorations can be mixed (Kleijn *et al.*, 2006; Carvell *et al.*, 2007); however, more targeted restorations that include the establishment of bee-attractive flowering plants to provide pollen and nectar resources throughout the growing season have consistently been found to increase wild bee abundance and richness over time (Marshall *et al*., 2006; Carvell *et al*., 2007; Pywell *et al*., 2011; Carvalheiro *et al*., 2012; Morandin & Kremen, 2013; Blaauw & Isaacs, 2014b; Jönsson *et al*., 2015).

Management strategies to support bees are only as good as our knowledge of bees' resource requirements and our ability to match those requirements with the components of the conservation strategy. Due to the nutritional needs of both adult and immature bees, floral resources are an important part of these requirements, and wildflower mixes are designed with increasingly detailed consideration of bee nutritional requirements and foraging preferences (Pywell *et al*., 2005; Smith *et al*., 2008; Tuell *et al*., 2008; Williams *et al*., 2015). However, nesting resources may also be a limiting factor in disturbed landscapes. While the nesting requirements and preferences of aboveground nesting bees, such as mason and leafcutter bees, are relatively well studied (Medler, 1966; Krombein, 1967; Hubbell & Johnson, 1977; Frankie *et al*., 1993; Vandenberg, 1995; Cane *et al*., 2007; Vickruck & Richards, 2012), little is known about the nesting requirements and substrate preferences of most bees that nest in the soil (Murray *et al*., 2009b; Winfree, 2010; *but see* Michener *et al*., 1958; Cane, 1991; Potts *et al*., 2005; Cane & Neff, 2011; Sardiñas & Kremen, 2014). This paucity of nesting information persists despite the fact that the soil-nesting guild of bees comprises around two-thirds of all known bee species (Michener, 2000), perhaps because of the challenges in detecting the inconspicuous nest entrances and excavating subterranean nests (Cane, 1997; Waters *et al*., 2011; O'Connor *et al*., 2012).

Bees have evolved diverse adaptations for nesting in soil and other substrates, and different species are likely to exhibit different ranges of tolerance for edaphic and microclimate conditions (Eickwort *et al*., 1981; Cane, 1991; Potts & Willmer, 1997; Cane & Neff, 2011). Soil-dwelling sphecoid wasps, the ancestors of bees, generally do not line their nests with glandular secretions (Michener, 1964). However, many ground-nesting bees have adaptations of this nature, such as female cellophane bees (Hymenoptera: Colletidae), which line their nests with a waterproof secretion from the Dufour's gland, allowing them to live in a wide range of moisture conditions (Michener, 1964; Hefetz, 1987; Cane, 1991). Many bees in the Halictidae and Andrenidae families also line their nests with different combinations of water-repellent lipids from the Dufour's gland (Hefetz, 1987; Cane, 1991). Bees in the genus *Megachile* (Hymenoptera: Megachilidae) have diverse nesting strategies, with some members of the genus nesting in pre-existing cavities aboveground and others excavating shallow soil nests (Eickwort *et al*., 1981). All megachilids, however, share the behavioral adaptation of using weather-resistant foreign materials, such as leaves, resin, or mud, to partition and line the cells of their nests as an alternative to the glandular secretions used by other guilds (Eickwort *et al*., 1981).

Different tolerances or preferences for edaphic and climatic conditions mean that nest-founding females may search for specific microhabitat characteristics in choosing a nest site (Potts & Willmer, 1997). Bumble bees (Hymenoptera: Apidae; *Bombus* spp.) search for large pre-existing cavities, such as abandoned rodent burrows, to found their nests. Many other bees also tend to reuse pre-existing cavities rather than excavate new nests (Cane, 1991). In an observational study of roadside banks, Michener *et al*. (1958) found that the distribution of bee nests in the banks was influenced by large-scale microhabitat characteristics, such as slope, aspect, and soil type, but not by finer-scale characteristics such as the particle size, pH, or soil color within a soil type. Several studies have also suggested that bees prefer to nest in areas with exposed bare ground (Potts *et al*., 2005; Hopwood, 2008; Sardiñas & Kremen, 2014). It is unclear, however, how limiting the distribution of preferred microhabitat characteristics in human-altered landscapes may be for bee species with different ranges of edaphic and climatic tolerances, and whether these characteristics can be used to accurately predict bee nesting in different habitat types.

Because bees are central-place foragers that return to their nest after each foraging bout, nest location is an essential piece of information needed to predict the distribution of bees and their associated pollination services across the landscape (Lonsdorf *et al*., 2009; Sardiñas & Kremen, 2014). Lonsdorf *et al*. (2009) developed a spatial model of native bee abundance in agricultural landscapes based on nesting resource availability and the forage resources within their flight range, which can be used for predicting wild bee contributions to crop pollination across the landscape and developing landscape-scale conservation strategies (Lonsdorf *et al*., 2009, 2011; Kennedy *et al.,* 2013). However, the dearth of empirical information on bee nesting preferences has necessitated the use of expert opinion surveys to determine the nesting suitability of different land use/land cover classes, a key model parameter (Lonsdorf *et al*., 2009; Chapin, 2014). These expert opinions can differ widely among people, leading to high uncertainty for the nesting parameter within the models (Murray *et al*., 2009a; Chapin, 2014). This uncertainty increases the model prediction error and decreases the correlation with observed patterns of bee abundance, particularly as the Lonsdorf *et al*. (2009) model has been found to be sensitive to altering the parameters for soil-nesting bees (Chapin, 2014). Better information about the nesting suitability of different habitats and the mechanisms underlying bee nesting preferences is needed to improve the ability to use these models to inform bee conservation and management decisions.

For this study, I chose to focus on the pollination-dependent blueberry agroecosystem of southwest Michigan. Highbush blueberry (*Vaccinium corymbosum* L.), the main blueberry species grown in the state, is highly dependent on insect-mediated pollination for economically viable yields (Merrill, 1936; Schaub & Baver, 1942; Meader & Darrow, 1947; Free, 1993), and at least 80% of flowers must set fruit to achieve a commercial-scale blueberry crop (Merrill, 1936). Wild bees are important contributors to pollination of this crop, supplying approximately 12% of the yield increase due to pollination in large commercial fields and nearly all of the pollination (88%) in smaller, more isolated fields that are not stocked with managed honey bee (*Apis mellifera* L.) hives for pollination (Isaacs & Kirk, 2010). The cost associated with renting hives, and the concerns about future health and availability of this managed species, has led to considerable interest in on-farm strategies to increase wild bee contributions to pollination. Current approaches include planting wildflowers in fallow areas or field margins and providing nesting materials such as wood blocks or cardboard tubes for mason bees; however, little is known about the preferred nesting resources of most soil-nesting bee species, which comprise most of the wild species that supply pollination in this region (Tuell *et al*., 2009). Understanding where bees choose to nest in this farm landscape could help to determine which areas are most suitable for soil-nesting bees, and how to best mitigate risk to nesting bees from management practices such as tillage or pesticide use.

The main objectives of this study were 1) to evaluate the nesting suitability of different land use types and associated microhabitat characteristics for soil-nesting bees on blueberry farms, and 2) to determine whether perennial wildflower restorations enhance nesting by soil-nesting bees, and 3) to determine whether restoration age affects the abundance of nesting bees. For the first objective, I sampled soil-nesting bees in four different land use types on blueberry farms that included established perennial wildflower plantings next to managed crop fields. For the second and third objectives, I compared the abundance and diversity of soil-nesting bees nesting in three newly-established wildflower plantings, three mature plantings, and unrestored areas in the same landscapes.

Materials and Methods

Nesting suitability of blueberry farm habitats

Study sites

This study was conducted at four blueberry farms located in Allegan, Berrien, and Van Buren counties in southwest Michigan with mature wildflower plantings sown with a diverse mix of native forbs and grasses in 2008 or 2009 (Figure 3.1). These wildflower plantings ranged in size from 0.3 to 3 acres. At each farm, mesh emergence traps (60cm^2; MegaView Science, Taiwan) were used to sample soil-nesting bees in four different habitat types: the blueberry crop field, an adjacent grassy field margin, a wooded area, and the wildflower planting. The crop field, field margin, and wooded areas selected for trapping were located at least 100m from the wildflower planting at each site to reduce potential spillover from the plantings (Figure 3.2). These habitats represent the dominant land use types in the Michigan highbush blueberry agroecosystem, and were present at all sites.

Emergence trapping

To sample soil-nesting bees, ten traps were placed at 5m intervals along a haphazardly-placed 50m transect in each of the four habitats - the crop field, field margin, wooded area, and the wildflower planting - for a total of 40 traps per site per sample round. Traps were placed at midday (between 0900 and 1500 hours) and left for 2-3 days prior to collection. Bees emerging from under a trap were captured in a jar containing 2% soap solution at the apex of the trap

(Dawn Ultra Original Scent, Procter & Gamble Co., Cincinnati, OH). Specimens were strained into ziplock bags and frozen before being washed, dried, and identified. This process was repeated three times per farm from late June to early September in 2013 and 2014, for a total of six sampling events per farm. Pesticide applications in the crop field interfered with trap placement in several sample rounds, resulting in uneven sampling in the crop field relative to the three other habitats, with an average of 3.2 sample rounds per site in the crop field over the two years of sampling.

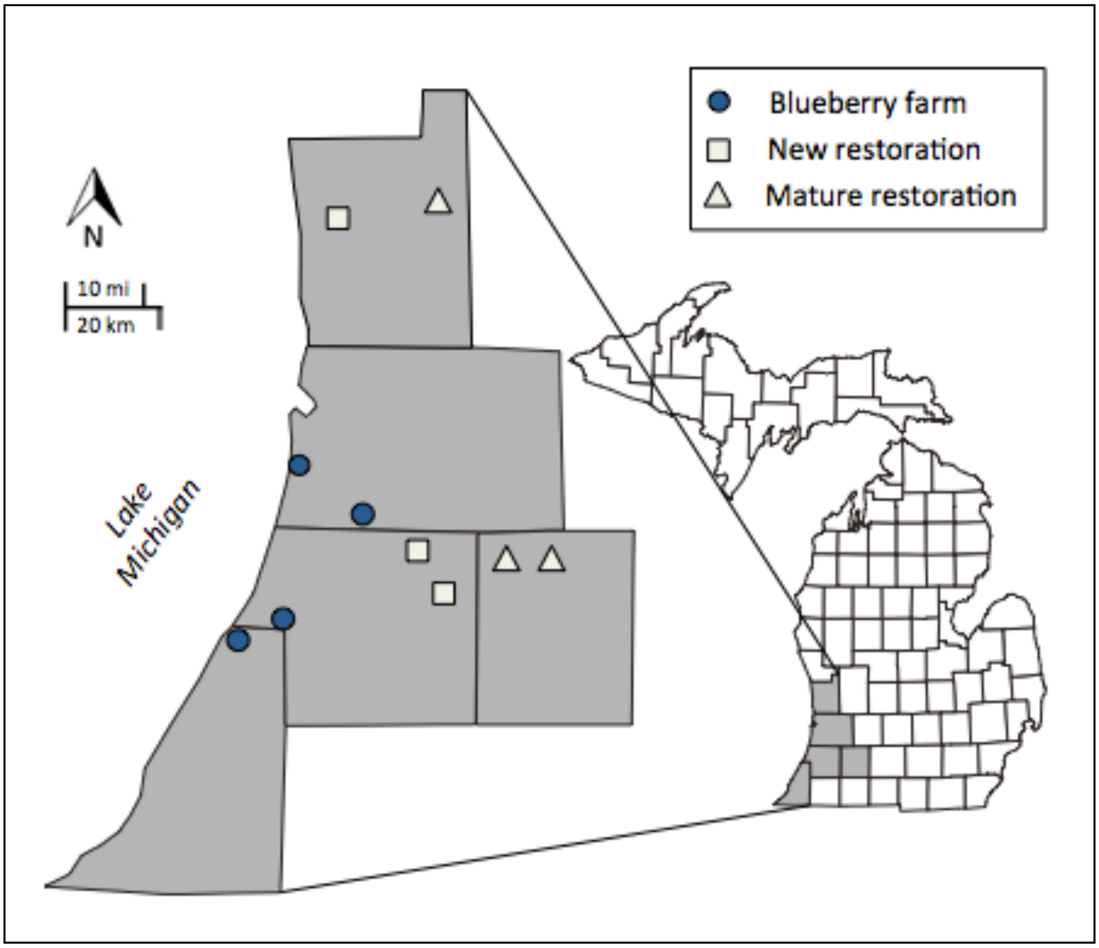

Figure 3.1. Map of study sites sampled for soil nesting bees. Dark circles represent the approximate locations of four blueberry farms sampled using emergence traps in four different habitat types per farm in 2013 and 2014. Light rectangles represent newly-established wildflower restorations sampled in 2014. Light triangles represent mature wildflower plantings sampled in 2014. Each restoration site had a paired unrestored control site within 400 m (not marked).

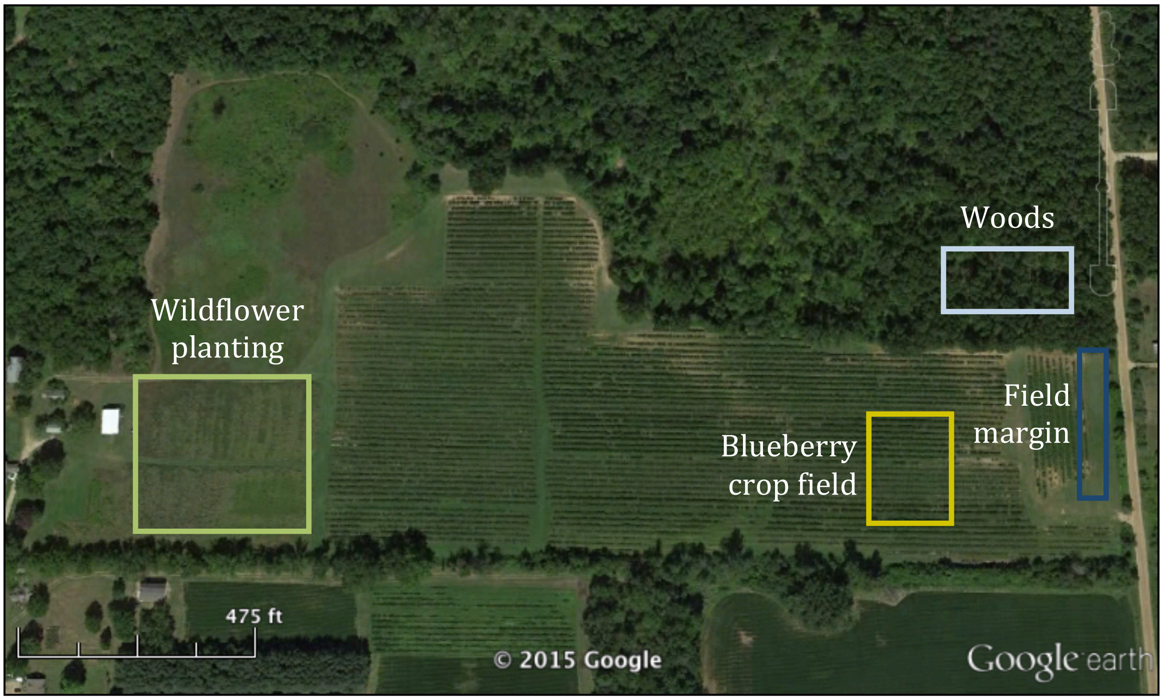

Figure 3.2. Representative distribution of habitat types and sampling locations at one of four blueberry sites sampled using emergence traps and netting in 2013 and 2014. Imagery © 2015 Google^{TM}.

Bee species richness was characterized for emergence trapped bees pooled by habitat by farm using the Chao1 abundance-based richness estimator in the *estimateR* function of R package *vegan*, which corrects for undetected species (R version 3.0.2, R Core Team, 2013; Chao, 1987; Oksanen *et al*., 2013). Non-parametric Kruskal-Wallis tests were used to determine whether bee abundance, richness, or Simpson's (1/D) diversity in the emergence traps differed among the four habitats, as these data violated the assumption of normality for analysis of variance. The abundance variable included all trapping events (n=838), while Chao1 estimated richness and Simpson's (1/D) diversity were calculated by habitat by farm (n=16). Means separation for abundance of bees in different habitats was carried out using a post-hoc Dunn's test with Bonferroni correction for *p*-values for the multiple comparisons among habitat types, which as a test for median difference is an appropriate multiple comparisons method for unbalanced designs (Dunn, 1961, 1964).

Microhabitat characteristics

Prior to placing a trap, I recorded microhabitat characteristics in the 60cm^2 sampling quadrat according to the methods of Potts *et al.* (2005) and Sardiñas and Kremen (2014) (Table 3.1). Percent cover attributes did not always sum to 100%, as all surface-level categories (bare ground, leaf litter/thatch, rocks, and wood) were counted as a percentage of the quadrat area regardless of tall vegetation. Surface cracks were measured as a percentage of the quadrat area, but were nested within bare ground. Surface soil strength (kg/cm^2) was measured in three locations in each quadrat using a pocket soil penetrometer (Forestry Supplies, Inc., Jackson, MS). Following measurement of microhabitat characteristics but prior to trap placement, surface vegetation was cut back to a height of 4-6 inches using manual hedge shears and the area was examined thoroughly to ensure no bees were visible above the surface.

Table 3.1. Microhabitat characteristics measured in each emergence trap quadrat in four habitat types on blueberry farms in 2013 and 2014.

Microhabitat characteristic	Unit of measurement
Vegetation	% cover (to nearest 1%)
Bare ground	% quadrat area (to nearest 1%)
Leaf litter/thatch	% quadrat area (to nearest 1%)
Rocks	% quadrat area (to nearest 1%)
Wood (including sticks)	% quadrat area (to nearest 1%)
Surface cracks	% quadrat area (to nearest 1%)
Cavities	# of cavities of <2 cm or >2 cm diameter
Ant nests	# of ant nests
Shade	Full, partial, or none
Slope	To nearest 1%
Aspect	N, NW, W, SW, S, SE, E, NE
Soil surface compaction	Three penetrometer readings

Microhabitat measurements were assessed for collinearity using a Spearman's rank correlation matrix (Table 3.4). To address the issue of multicollinearity in these data, I used principal components analysis to reduce the dimensionality of the microhabitat variables (function *prcomp* in R package *stats*; R Core Team, 2013). Visual examination of the scree plot supported the extraction of the first two principal components for use as predictor variables in a model with bee abundance in emergence traps as the response variable (Figure 3.3; Table 3.5).

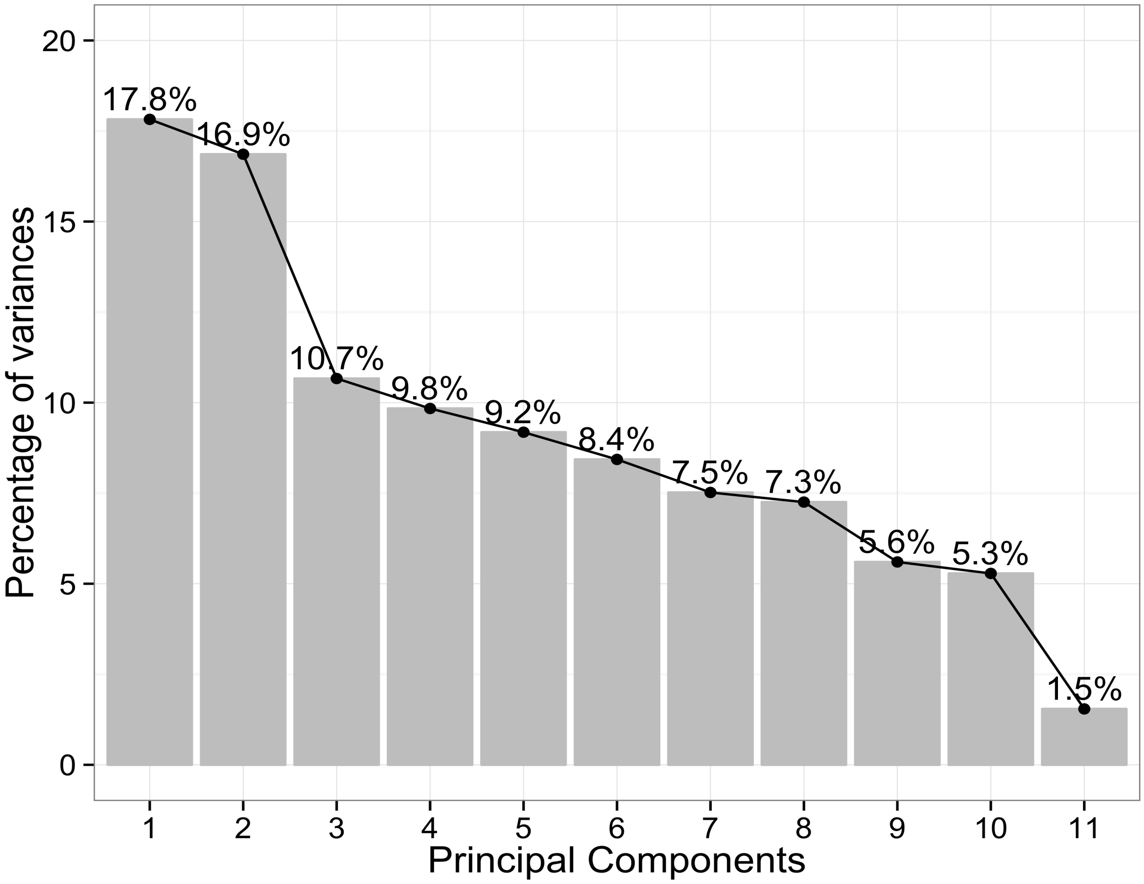

Figure 3.3. Scree plot of the percentage of variation explained by the principal components generated from 11 microhabitat characteristics measured in emergence traps in four different habitat types on blueberry farms in 2013 and 2014 (n=645 traps).

Because the bee capture data included many zeros, the data were modeled using a zero-inflated regression model with Poisson distribution (function *zeroinfl* in R package *pscl*; Zeileis *et al*., 2008), which includes a point mass at zero and is typically better suited for modeling over-dispersed count data than a generalized linear model (GLM) with Poisson distribution. Model selection for the two principal components was conducted using backward stepwise elimination based on Akaike's information criterion (AIC) values (function *step* in R package *stats;* R Core Team, 2013). To ensure optimal model fit, I compared the zero-inflated Poisson model with a zero-inflated negative binomial regression model using AIC values, and with a GLM with Poisson distribution using Vuong's likelihood ratio test (function *vuong* in R package *pscl*; Vuong, 1989). The zero-inflated regression model with Poisson distribution exhibited the best fit of the competing models.

Visual examination of the relationship between the first two principal components and habitat type suggested that the microhabitat characteristics vary non-independently from habitat type (Figure 3.6). For example, on average, crop fields had more bare ground than other habitats, which is expected given that most fields were treated with herbicides for weed control under the blueberry bushes. Analysis of variance (ANOVA) was used to determine whether the principal components for microhabitat differed significantly by habitat type. The second principal component was log(x+5) transformed prior to analysis to improve normality. Means separation by habitat was performed using Tukey's HSD ($\alpha = 0.05$).

Following the analysis of the first two principal components, I used logistic regression to explicitly examine the relationship between presence and absence of bees in traps and the microhabitat variables with factor loadings greater than 0.4 (Table 3.5). Logistic regression allows for the direct derivation of the change in probability of encountering a bee in a trap given a unit increase in a predictor variable. Because percent bare ground and number of small cavities were positively correlated (Table 3.4), each variable was first analyzed in separate logit models of bee presence in traps. These individual models were then compared with the combined model using AIC values (Table 3.5). The model coefficients (β) remained stable in the combined model, indicating that the positive correlation between the two predictor variables did not lead to problems with collinearity in the combined model. Wald's χ^2 tests were used to determine the significance of the individual model coefficients (Table 3.6).

Soil characteristics

To measure the compaction and texture of the topsoil, I took 10 replicate soil samples per habitat per farm in July 2013 using a manual drop hammer soil core sampler to a depth of 7.5 cm (331.3 cm^3 core volume). In order to calculate soil moisture and bulk density, fresh soil samples were placed in #5 paper bags and weighed, then oven dried at 105°C for 24 hours. Dried samples were set aside to cool for 15 minutes prior to measuring dry weights. Soil mass was determined by subtracting the mean weight of ten empty oven-dried #5 bags from the dried sample weights. Samples from each habitat were then processed through a 2mm mesh sieve before being aggregated and sub-sampled for texture. Bulk density was calculated as follows (Robertson *et al*., 1999):

$$\textit{Bulk density } (g/cm^3) = \textit{Dry soil weight } (g) \,/\, \textit{Soil volume } (cm^3)$$

Particle size analysis for soil texture determination was conducted using a hydrometer method adapted from Day (1965). From each habitat, 40 g +/- 0.05 g of sieved soil was weighed into a 150mL shaker bottle, to which 100mL of a 5% sodium hexametaphosphate dispersing solution was added. Bottles were capped and placed on a reciprocating horizontal shaker at 150 rpm for two hours. After two hours, the suspension was transferred to a 1.0 L sedimentation cylinder, and deionized water was added to bring a 1.0 L final volume. The suspension was allowed to equilibrate to room temperature for two hours before being mixed thoroughly with a plunger. After 30 seconds, a hydrometer (ASTM No. 1. 152H-Type with Bouyoucos scale in g L^{-1}) was lowered into the suspension, and at 40 seconds a reading was taken to the nearest 0.5 g L^{-1} (reading “Rsand”). This process was repeated with a blank solution (reading “RC1”). The soil suspensions were left for six hours, after which the temperature of the suspension was recorded. A second hydrometer reading was taken at the settling time for clay, as determined by the temperature of the suspension (reading “RClay” or “RC2” for the blank solution). Oven dry soil moisture was determined on a separate 40 g sample of soil from each habitat. Soil texture was calculated as follows:

$$\textit{Sand \%} = ((\textit{oven dry soil mass} - (\textit{Rsand} - \textit{RC1}))/(\textit{oven dry soil mass}) \times 100$$

$$\textit{Clay \%} = (\textit{Rclay} - \textit{RC2})/(\textit{oven dry soil mass}) \times 100$$

$$\textit{Silt \%} = 100 - (\textit{Sand \%} + \textit{Clay \%})$$

A non-parametric Kruskal-Wallis test with posthoc Dunn’s test for pairwise multiple comparisons was used to determine whether bulk density (g/cm^3) differed among habitats. Kruskal-Wallis tests were used to determine whether average bulk density by habitat was correlated with bee abundance and richness in emergence traps.

Analyses of variance (ANOVAs) with post-hoc Tukey’s HSD for multiple comparisons were used to determine whether soil texture characteristics differed by site or habitat. Percent silt and percent clay data were square root transformed prior to analysis to improve normality. Significance levels for these tests were adjusted with the Bonferroni correction.

The three soil texture characteristics were strongly intercorrelated (Table 3.11), so principal components analysis was used to reduce the dimensionality of the texture data while preventing issues with multicollinearity (function *prcomp* in R package *stats*; R Core Team, 2013). The first principal component explained over 95% of the variance in the soil texture data and was retained for use in a simple linear regression with bee abundance in traps (Table 3.12). Average bee abundance in each habitat, the dependent variable in the regression, was log(x + 1) transformed prior to analysis to improve normality.

Bee communities collected in nets vs. emergence traps

To determine how the community of soil nesting bees compared with the flower-visiting bee community, I net collected bees visiting open flowers for 10 minutes in 2013 and 20 minutes in 2014 along the 50m transect in each habitat type during suitable weather conditions (temperature >65ºF, wind speed <3.5m/s) for each soil emergence trapping session. Because emergence traps were placed regardless of weather conditions, net collections were sometimes conducted 1-3 days after trap placement.

To visualize differences in the bee communities captured in emergence traps and net-collected from open flowers, I used non-metric multidimensional scaling (NMDS) ordination using Bray-Curtis dissimilarities with Wisconsin double standardization (functions *wisconsin* and *metaMDS,* R package *vegan*). Bee communities were pooled across the two years of sampling for each site. Because of the low abundances of bees in emergence trap samples by site, Bray-Curtis dissimilarities were zero-adjusted using a dummy species with a value of 1 for all sites in the original abundance matrix (Clarke *et al*., 2006). Permutational multivariate analysis of variance (perMANOVA) based on Bray-Curtis dissimilarities with 1000 permutations was used to compare netted and trapped bee communities (function *adonis,* R package *vegan*; Anderson, 2001; McArdle & Anderson, 2001; Oksanen, 2006). Multivariate homogeneity of group dispersions (variances) was confirmed using function *betadisper* in R package *vegan*, a multivariate analogue of Levene's test (Anderson, 2006).

Bee identification

Bee specimens (Hymenoptera: Apoidea) were identified to genus and species using published dichotomous keys (Mitchell, 1960, 1962; LaBerge, 1980; McGinley, 1986; Michener *et al.*, 1994; Gibbs, 2011; Rehan & Sheffield, 2011) and the online keys available through www.discoverlife.org. Emergence trap specimens and all *Lasioglossum* (Dialictus) and *Andrena* specimens were identified by Jason Gibbs (Department of Entomology, Michigan State University). Voucher specimens from this study were deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University.

Suitability of new and mature wildflower restorations as nesting sites for bees

Study sites

This study was conducted in three newly-sown and three mature wildflower restorations in southwest Michigan. Each restoration was paired with an unrestored control habitat within 400 m in order to compare nesting between sites with similar landscape composition and environmental conditions with and without the addition of wildflowers. New restorations were sown into herbicide-treated bare ground adjacent to blueberry fields in fall 2013 or spring 2014 with a mixture of 26 forb species and four grasses. These ranged in size from approximately 0.3 to 0.8 acres. Control habitats for new restorations were grass-dominated blueberry field margins, two of which received regular mowing in summer 2014. These were located between 135 and 350 meters away from the restoration. Mature restorations ranged in age from five to ten years, in size from 4 to 144 acres, and in sown floristic diversity from 22 to 48 forb species. Unrestored control sites for mature restorations were unmowed old field habitats with varying levels of floral diversity, which ranged in distance from approximately 30 to 185 meters from the edge of the wildflower restorations. New and mature restorations were spaced at least 25 km apart (Figure 3.1).

Emergence trapping

In each sample round, ten emergence traps as described above were placed at 5m intervals along each of two haphazardly located 50m transects in the unrestored control and the wildflower planting, for a total of 20 traps per habitat type. Traps were placed after dusk (between 20:00 and 22:00 hours) to ensure that bees were resident in their soil nest during trap placement, and were left for one week prior to collection. Sample rounds were conducted in the same week for one new and one mature restoration and their respective paired unrestored controls, with three sample rounds between June-August 2014.

Bee species richness was characterized for trapped bees using the Chao1 abundance-based richness estimator in the *estimateR* function of R package *vegan*, which corrects for undetected species (Chao, 1987; Oksanen *et al*., 2013). The abundance, richness, and Simpson's (1/D) diversity of bees captured in emergence traps were compared between habitats using nonparametric Kruskal-Wallis tests, as these response variables did not meet the assumption of normality. The abundance data used in this test were bee counts from all emergence traps (n=720), while Chao1 estimated richness and Simpson's diversity were calculated by habitat by site (n=12). Means separation was performed using post-hoc Dunn's tests with Bonferroni correction.

Microhabitat characteristics

Prior to placing each trap, I recorded basic surface characteristics in the trap quadrat (Table 3.2) and cut vegetation to a height of 4-6 inches using manual hedge shears, as described above. Collection jars were half-filled with a 2% soap solution as described above. Collected specimens were strained, then funneled into a 50ml polypropylene vial (Corning Inc., Corning, NY). Vials were filled with 70% ethanol for storage. In the laboratory, bee specimens were sorted out of the vials before being washed, dried, and identified to species. All specimens for this study were identified by Jason Gibbs (Department of Entomology, Michigan State University) using the keys noted above.

Microhabitat characteristics were examined for multicollinearity using a Spearman's rank correlation matrix (Table 3.15). The variables were highly intercorrelated, so I used principal components analysis to reduce the dimensionality of the variables without creating problems with multicollinearity (function *prcomp* in R package *stats*; R Core Team, 2013). Visual examination of the scree plot supported the extraction of the first four principal components for use as predictor variables in a model of bee abundance in traps (Figure 3.4; Table 3.16). Together these four components accounted for 96.6% of the variation in the microhabitat variables.

Table 3.2. Microhabitat characteristics measured in each emergence trap quadrat in three newly-established wildflower plantings, three mature wildflower plantings, and paired unrestored controls in 2014.

Microhabitat characteristic	**Unit of measurement**
Vegetation	% cover (to nearest 1%)
Bare ground	% quadrat area (to nearest 1%)
Leaf litter/thatch	% quadrat area (to nearest 1%)
Wood/rocks	% quadrat area (to nearest 1%)
Slope	Flat, 1-5%, 5-10%, 10-25%, 25-50%, >50%
Aspect	N, NW, W, SW, S, SE, E, NE

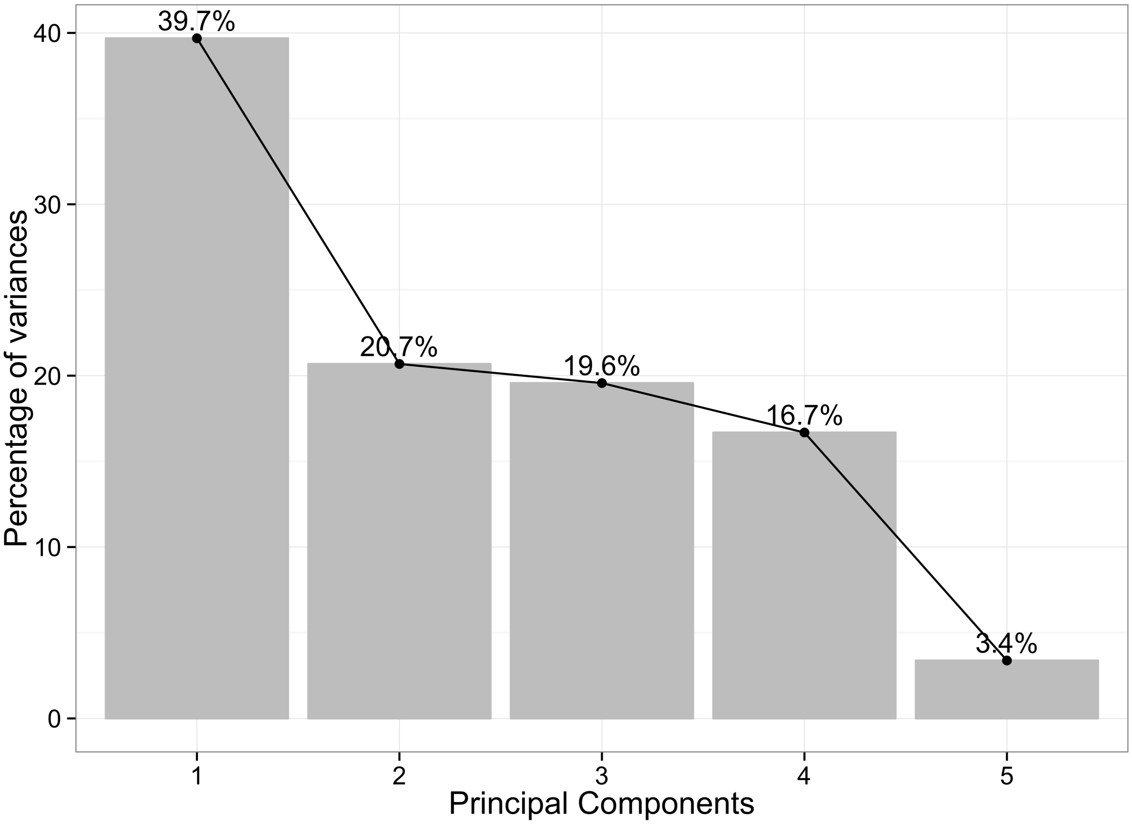

Figure 3.4. Scree plot of the percentage of variation explained by the 5 principal components generated from the microhabitat data from emergence trap quadrats in new wildflower restorations, mature wildflower restorations, and their paired unrestored controls in 2014 (n=720 traps).

As with the previous emergence trap data, bee counts in emergence traps were highly overdispersed. In addition, several traps captured multiple members of the same social species, leading to outliers in the raw abundance data (Table 3.13). Thus, to analyze the effect of microhabitat characteristics on bee nesting, I used binary presence/absence data as the response variable in a logistic regression. Model selection with the four principal components as predictor variables and bee presence/absence in emergence traps as the response variable was conducted using backward stepwise elimination.

Bee community in nets vs. emergence traps

Flower-visiting bees were net collected for 50 minutes in the wildflower planting or unrestored control within 1-2 days of trap placement (20 minutes along each of the two 50m transects and 10 minutes of opportunistic collection). In addition, I counted the number of open flowers of each flowering species in 20 1m^2 quadrats placed at 5m intervals along each 50m transect. Community analyses comparing netted bees with emergence trapped bees were conducted as above. The contribution of individual bee species to the contrast between trapped and netted bee communities was assessed using similarity percentage (SIMPER) analysis (function *simper* in R package *vegan*; Clarke, 1993), which conducts pairwise comparisons of groups of sampling units and finds the average contributions of each species to the overall Bray-Curtis dissimilarity.

Results

Nesting suitability of different habitats on blueberry farms

I captured a total of 47 soil-nesting bees in 42 traps in the four blueberry farm habitats out of a total of 838 trapping events over two years (Table 3.3). Captured bees included specimens from four of five bee families present in Michigan, but were primarily composed of species in the Halictidae and Apidae families (Table 3.3). Four cleptoparasite species were captured in traps: *Nomada illinoensis* Robertson, *Nomada vegana* Cockerell, *Sphecodes davisii* Robertson, and *Sphecodes mandibularis* Cresson. Four species of stem-nesting bees (*Ceratina* spp. and *Hylaeus affinis*) were also captured in emergence traps.

Table 3.3. Bee species collected in emergence traps from different habitat types on four blueberry farms in 2013 and 2014. No. traps represents the number of individual traps (and therefore the minimum number of possible nests) from which these species were collected.

Family ***Species***	**Location captured**				**Total no. captured**	**No. traps**
	Crop field	Flower planting	Field margin	Woods		
Andrenidae						
Andrena canadensis	0	0	3	0	3	1
Andrena miserabilis	0	0	1	0	1	1
Apidae						
Anthophora bomboides	1	0	0	0	1	1
Bombus bimaculatus	0	2	0	1	3	3
Bombus griseocollis	1	0	0	0	1	1
Bombus impatiens	0	3	0	0	3	3
*Ceratina calcarata**	0	0	0	1	1	1
*Ceratina dupla**	0	0	1	0	1	1
*Ceratina strenua**	1	0	0	0	1	1
*Nomada illinoensis***	0	0	0	1	1	1
*Nomada vegana***	1	0	0	0	1	1
Colletidae						
Colletes thoracicus	0	1	0	0	1	1
*Hylaeus affinis**	0	1	0	0	1	1
Halictidae						
Agapostemon sericeus	0	3	1	0	4	3
Agapostemon splendens	0	0	1	0	1	1
Augochlorella aurata	0	2	0	0	2	2
Lasioglossum ellisiae	1	1	1	0	3	3
Lasioglossum fuscipenne	0	0	0	1	1	1
Lasioglossum leucocomum	2	2	0	0	4	3
Lasioglossum macoupinense	1	0	0	0	1	1
Lasioglossum pectorale	0	1	0	0	1	1
Lasioglossum pilosum	0	4	1	0	5	4
Lasioglossum versans	0	0	0	1	1	1
Lasioglossum vierecki	0	2	0	0	2	2
*Sphecodes davisii***	1	1	0	0	2	2
*Sphecodes mandibularis***	0	1	0	0	1	1
Total:	9	24	9	5	47	42

* Stem-nesting bees
** Cleptoparasitic bees

The abundance of soil-nesting bees differed significantly among habitats (Figure 3.7; $\chi^2 = 13.56$, $df = 3$, $p = 0.003$), with the greatest captures in the wildflower plantings compared to those in the wooded areas (posthoc Dunn's test for multiple comparisons with Bonferroni correction, $p = 0.01$) and grassy field margins ($p = 0.03$). Crop fields had an intermediate abundance of soil-nesting bees, but did not have significantly fewer bees than wildflower plantings or more than the other two habitats. Bee species richness in emergence traps did not differ significantly among habitats ($\chi^2 = 5.62$, $df = 3$, $p = 0.13$), nor did Simpson's (1/D) diversity of the trapped bees ($\chi^2 = 3.09$, $df = 3$, $p = 0.38$), though the sample size for each habitat was relatively low.

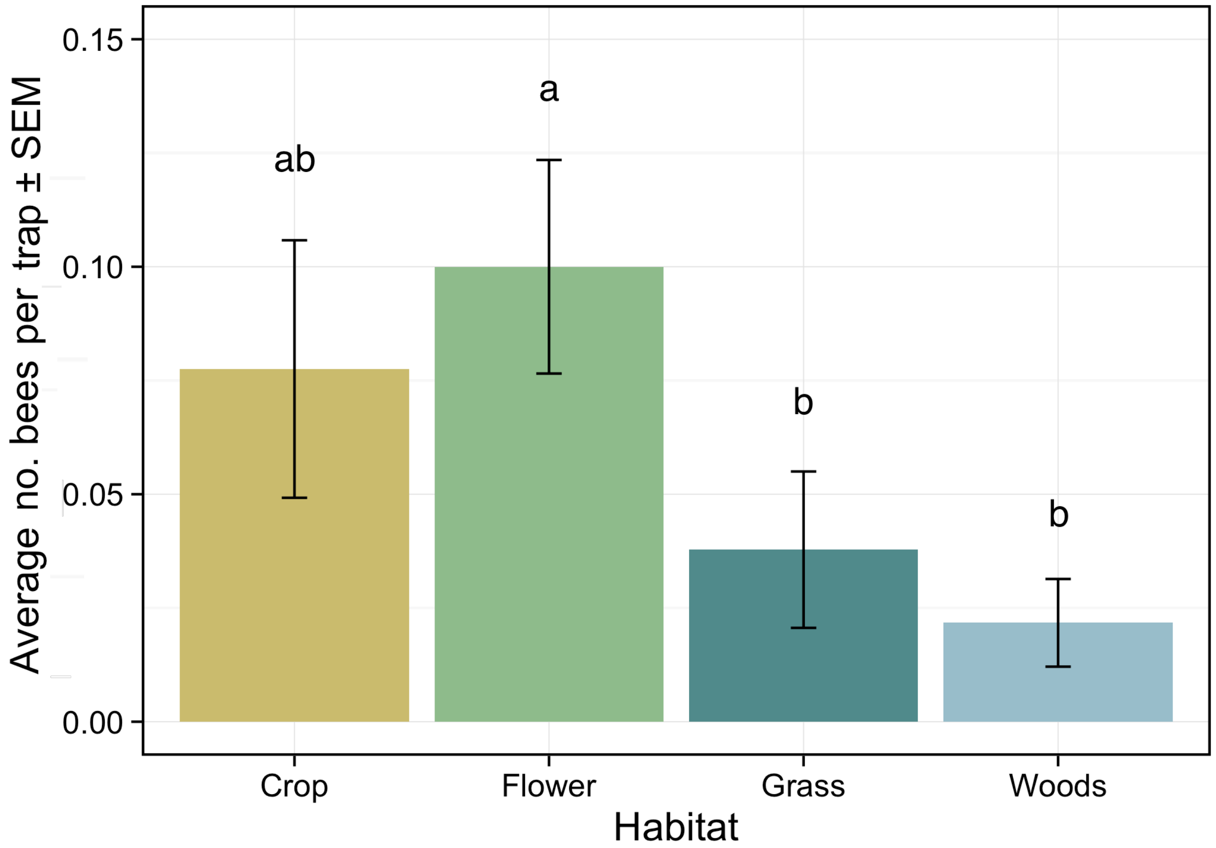

Figure 3.5. Mean number of bees captured in emergence traps in different habitat types on four blueberry farms in 2013 and 2014. Captured bee abundance does not differ significantly among habitats marked with the same letter (posthoc Dunn's pairwise comparisons with Bonferroni correction, α=0.05).

Microhabitat characteristics

Many of the microhabitat characteristics were strongly intercorrelated (Table 3.4), particularly among the percent cover categories. Living vegetation, the dominant percent cover category, was negatively correlated with most of the other cover types. Percent bare ground was strongly negatively correlated with the percent cover of leaf litter and thatch, but positively correlated with the number of cavities and ant nests.

Microhabitat factors loading strongly on the first principal component were leaf litter and thatch cover, which loaded positively, and soil strength (kg/cm^2) and living vegetation cover, which loaded negatively (Table 3.5). Bare ground and the number of ant nests also had weak negative loadings on PC1. Bare ground and the number of small cavities had strong positive loadings on the second principal component, along with weak positive loadings from the number of large cavities and slope and a weak negative loading from vegetation cover (Table 3.5).

The two principal components exhibited nearly equal but opposite relationships with bee abundance in traps, with bee abundance exhibiting a negative relationship with leaf litter and thatch cover (PC1) and a positive relationship with bare ground and the number of small cavities (PC2) (Table 3.6). AIC values for the models containing either one of the two principal components and the model with both components were nearly equal; all models were within 1 AIC value of one another (Table 3.6). Given that bare ground was negatively correlated with vegetation and litter (Table 3.4), these axes had similar explanatory power for bee abundance. Likelihood ratio tests indicated that all three models were significantly better than the null model at $\alpha = 0.05$ (Table 3.6).

Table 3.4. Spearman's rank correlation matrix of 11 microhabitat characteristics measured in each 60cm^2 emergence trap quadrat on four blueberry farms in 2013 and 2014 (n=645 traps).

Microhabitat characteristic	Bare	Vegetation	Rocks	Litter	Wood	Cracks	Small cavities	Large cavities	Ant nests	Soil strength	Slope
Bare ground (%)	1										
Vegetation (%)	**-0.17*****	1									
Rocks (%)	**0.09***	-0.02	1								
Leaf litter/thatch (%)	**-0.56*****	**-0.35*****	**-0.08***	1							
Wood (%)	**-0.22*****	**-0.54*****	-0.01	**0.38*****	1						
Cracked surface (%)	0.02	**-0.13*****	0.03	**0.09***	**0.13*****	1					
No. cavities (<2mm)	**0.22*****	**-0.08***	-0.02	**-0.09***	-0.03	0.04	1				
No. cavities (>2 mm)	**0.16*****	**-0.18*****	-0.03	0.01	0	0.07	**0.16*****	1			
No. ant nests	**0.34*****	0.05	-0.04	**-0.26*****	**-0.25*****	-0.06	0.04	-0.02	1		
Soil strength (kg/cm^2)	-0.03	**0.35*****	**0.11****	**-0.21*****	**-0.16*****	-0.04	0.01	**-0.16*****	**0.08***	1	
Slope (%)	0.05	-0.04	-0.04	0.05	**0.13*****	0.01	**0.1***	0.05	-0.06	**-0.15*****	1

*significant at $p = 0.05$, **$p = 0.01$, ***$p = 0.001$

Table 3.5. Factor loadings for the first two principal components from the microhabitat characteristics analysis. Variables with factor loadings greater than 0.4 are in bold.

Microhabitat characteristic	**PC1**	**PC2**
Bare ground (%)	-0.25	**0.53**
Vegetation (%)	**-0.44**	-0.39
Leaf litter/thatch (%)	**0.54**	-0.18
Rocks (%)	-0.11	0.06
Wood (%)	0.32	0.05
Surface cracks (%)	0.11	0.19
No. small cavities	-0.12	**0.41**
No. large cavities	0.12	0.34
No. ant nests	-0.36	0.22
Soil strength (kg/cm^2)	**-0.40**	-0.20
Slope (%)	0.09	0.35

Table 3.6. Model coefficients (β), *z*, *p*, and Akaike's information criterion (AIC) values for the competing zero-inflated models of bee abundance in traps, and the *p*-values from likelihood ratio tests compared with a null model.

Model	**β ± SE**	***z***	***p***	**AIC**	***p*-value from likelihood ratio test**
Combined model (PC1+ PC2)					
PC1	-0.18 ± 0.13	-1.33	0.183	237.63	0.049*
PC2	0.14 ± 0.10	1.34	0.181		
Individual models					
PC1	-0.26 ± 0.11	-2.31	0.021*	237.35	0.035*
PC2	0.19 ± 0.09	2.23	0.026*	237.56	0.039*

*significant at $\alpha = 0.05$

Table 3.7. Mean values by habitat for the microhabitat characteristics with large factor loadings on PC1 and PC2. Values within a column followed by the same letter are not significantly different (posthoc Dunn's pairwise comparisons with Bonferroni correction, α=0.05).

Habitat	No. traps	Vegetation (%)	Leaf litter or thatch (%)	Bare ground (%)	No. small cavities	Soil strength (kg/cm^2)
Crop	128	32.3 ± 2.9 b	35.4 ± 2.9 bc	31.5 ± 2.9 a	0.32 ± 0.07 a	0.46 ± 0.04 c
Flower	240	83.2 ± 1.3 a	37.3 ± 2.0 b	9.0 ± 1.0 c	0.13 ± 0.04 b	0.75 ± 0.03 b
Grass	238	80.8 ± 1.2 a	27.5 ± 1.6 c	12.4 ± 1.1 b	0.05 ± 0.02 bc	1.27 ± 0.06 a
Woods	230	37.6 ± 1.9 b	84.7 ± 1.6 a	2.8 ± 0.7 d	0.02 ± 0.01 c	0.59 ± 0.02 c

Microhabitat characteristics loading on the first two principal components were not independent of habitat (PC1: $F = 229.6$, $df = 3, 641$, $p < 0.001$. PC2: $F = 55.5$, $df = 3, 641$, $p < 0.001$; Table 3.7; Figure 3.6). For the first principal component, which was positively associated with leaf litter and thatch cover and negatively associated with living vegetation cover, all habitat types were significantly different, with woods and crop fields on the positive side of the axis and wildflower plantings and grassy field margins on the negative side of the axis (all $p < 0.001$; Figure 3.6). Crop fields fell significantly higher on PC2, which is positively associated with bare ground and the number of small cavities, than the other three habitats (all $p < 0.001$), which did not differ from each other.

All of the individual microhabitat characteristics that loaded heavily (factor loading > 0.4) on the first two principal components varied significantly by habitat type (Table 3.7). On the first principal component, percent cover of living vegetation was significantly different by habitat ($\chi^2 = 371.0$, $df = 3$, $p < 0.001$), with significantly more vegetation cover in wildflower plantings and grassy field margins than in crop fields or woods. Leaf litter/thatch cover varied significantly among habitats ($\chi^2 = 331.1$, $df = 3$, $p < 0.001$), with more litter in woods than other habitats. Soil surface strength (kg/cm^2) also differed significantly among habitats ($F = 62.19$, $df = 3, 382$, $p < 0.001$). Grassy field margins had the highest soil surface compaction, followed by wildflower plantings, wooded areas, and crop fields, in that order (Table 3.7). On the second principal component, the percent bare ground in emergence trap quadrats differed significantly by habitat ($\chi^2 = 207.0$, $df = 3$, $p < 0.001$). Crop fields had the most bare ground per quadrat, followed by field margins, wildflower plantings, and woods (Table 3.7). Finally, the habitat types also differed in the number of small cavities measured per quadrat (χ^2 = 32.2, *df* = 3, *p* < 0.001); on average, more cavities were counted in crop fields than in other habitats. Wildflower plantings also had significantly more small cavities than woods (*p* = 0.02), but not grassy field margins.

None of the variables with large factor loadings on the first principal component were significant predictors of nesting bee presence in logistic regression models (Table 3.8). However, both variables loading heavily on the second principal component, the percent bare ground and the number of small cavities, were significant predictors of nesting bee presence (Tables 3.8 and 3.9). The logit model containing both variables (percent bare ground + number of small cavities) exhibited the best fit of the tested models (Table 3.8). The combined model indicated that the number of small cavities in a trap quadrat was a better predictor of trap capture than the percent bare ground; with every additional small cavity counted in a quadrat, the odds of capturing a bee increased by a factor of 1.96 (95% confidence interval: 1.37 - 2.84; Table 3.9). Bare ground exhibited a lower odds ratio than the number of small cavities; with every 1% increase in bare ground in a quadrat, the odds of bee capture increased by a factor of 1.01 (95% confidence interval: 1.00 – 1.03).

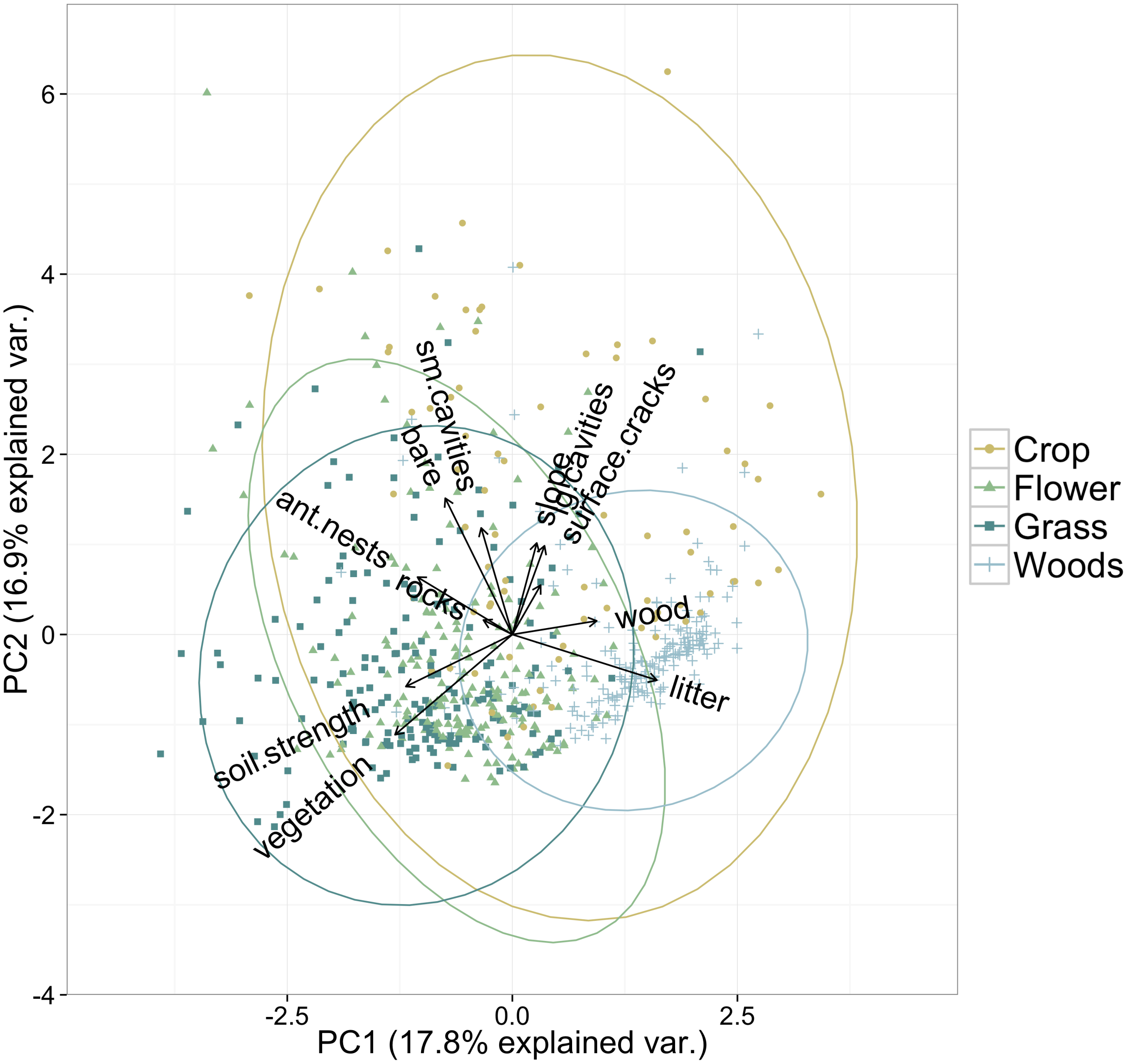

Figure 3.6. Biplot of first two principal components in the microhabitat PCA. Each dot represents an individual emergence trap quadrat (n=645 traps). Ellipses represent 95% confidence around the group mean for each habitat type.

Table 3.8. Model coefficients (β), *z*- and *p*-values for parameters, residual deviances, degrees of freedom, and Akaike's information criterion (AIC) values for the combined and individual logistic regression models of microhabitat variables as predictors of bee presence in emergence traps.

Model	**β ± SE**	***z***	***p***	**Residual deviance**	***df***	**AIC**
Combined model						
small cavities	0.68 ± 0.18	3.7	<0.001	295.59	833	301.59
bare ground (%)	0.01 ± 0.01	2.21	0.03			
Individual models						
small cavities	0.76 ± 0.18	4.28	<0.001	299.79	834	303.79
bare ground (%)	0.02 ± 0.01	2.99	0.003	307.7	834	311.7
leaf litter (%)	-0.01 ± 0.004	-1.36	0.17	313.32	834	317.32
vegetation (%)	-0.002 ± 0.004	-0.63	0.53	314.84	834	318.84
soil strength (kg/cm^2)	-0.34 ± 0.38	-0.89	0.37	204.17	643	208.17†

†*Soil strength model AIC value not directly comparable (measured on subset of quadrat values)*

Table 3.9. Logistic regression model assessing the number of small cavities and percent bare ground as predictors of the presence of bees in emergence traps.

Microhabitat characteristic	**Odds ratio (95% confidence)**	**β ± SE**	**Wald χ^2**	***k***	***p***
Small cavities	1.96 (1.37-2.84)	0.68 ± 0.18	256.4	1	< 0.0001
Bare ground (%)	1.01 (1.00-1.03)	0.01 ± 0.01	13.7	1	0.0002

Soil characteristics

Bulk density (g/cm^3) of surface soil differed significantly among habitats ($F = 91.12$, $df = 3, 155$, $p < 0.001$), with significantly higher average bulk density in grassy field margins and flower plantings than in crop fields or wooded areas (Tukey's HSD, all $p < 0.001$; Table 3.10). Soil in crop fields was significantly more dense than soil in wooded areas ($p < 0.001$). However, mean bulk density was not significantly correlated with bee abundance or richness in emergence traps ($F_{abundance} = 2.76$, $df = 1,14$, $p = 0.12$; $F_{richness} = 1.67$, $df = 1,14$, $p = 0.22$).

All soils were categorized as sands or loamy sands, with percent sand ranging from 80.0-95.6% across the sixteen samples (Table 3.10). Percent sand and silt did not differ among sites or habitats (all *p*-values > 0.35). Percent clay differed significantly among habitats ($F = 6.34$, $df = 3$, $p = 0.008$), with significantly more clay in soils sampled from crop fields and wildflower plantings than from field margins (Table 3.10). Mean bee abundance and Chao1 estimated richness by habitat were not related to the soil texture principal component ($F_{abundance} = 1.70$, $df = 1,14$, $p = 0.21$; $F_{richness} = 0.41$, $df = 1,14$, $p = 0.53$; Table 3.12).

Table 3.10. Soil physical properties in the crop field, grassy field margin, wildflower restoration, and wooded areas on four blueberry farms in SW Michigan.

Habitat	**Soil texture (%)**			**Bulk density**	**Soil strength**
	Sand ± SE	Clay ± SE	Silt ± SE	**(g/cm^3)** ± SE	**(kg/cm^2)** ± SE
Crop field	91.2 (1.7) a	3.1 (0.4) a	5.6 (1.5) a	1.29 (0.07) b	0.31 (0.04) d
Field margin	94.4 (0.0) a	1.3 (0.0) b	4.4 (0.0) a	1.60 (0.04) a	1.54 (0.05) a
Wildflower	89.8 (3.8) a	3.1 (0.8) a	7.0 (3.1) a	1.56 (0.03) a	0.91 (0.09) b
Woods	90.0 (2.1) a	1.2 (0.1) ab	8.8 (2.1) a	0.94 (0.09) c	0.59 (0.04) c

Values are means ± 1 SE (in parentheses). Values within a column with the same letter are not significantly different (p = 0.05).

Table 3.11. Spearman's rank correlation matrix of soil texture characteristics measured on soil samples collected across different habitat types on four blueberry farms in 2013 (n=16).

	Sand (%)	Silt (%)	Clay (%)
Sand (%)	1		
Silt (%)	-0.98***	1	
Clay (%)	-0.54*	0.47	1

*significant at $p = 0.05$, **$p = 0.01$, ***$p = 0.001$

Table 3.12. Factor loadings on the first principal component for soil texture.

	Factor loading on PC1
Sand (%)	-0.75
Silt (%)	0.65
Clay (%)	0.10

Bee communities collected in nets vs. emergence traps

There was a marginally significant difference in the bee communities captured by the two collection methods (perMANOVA; $F = 1.63$, $df = 1, 6$, $p = 0.06$). NMDS ordination with 95% confidence ellipses around the group means for emergence trapped bee communities and netted bee communities showed visual separation of the two collection methods (Figure 3.7).

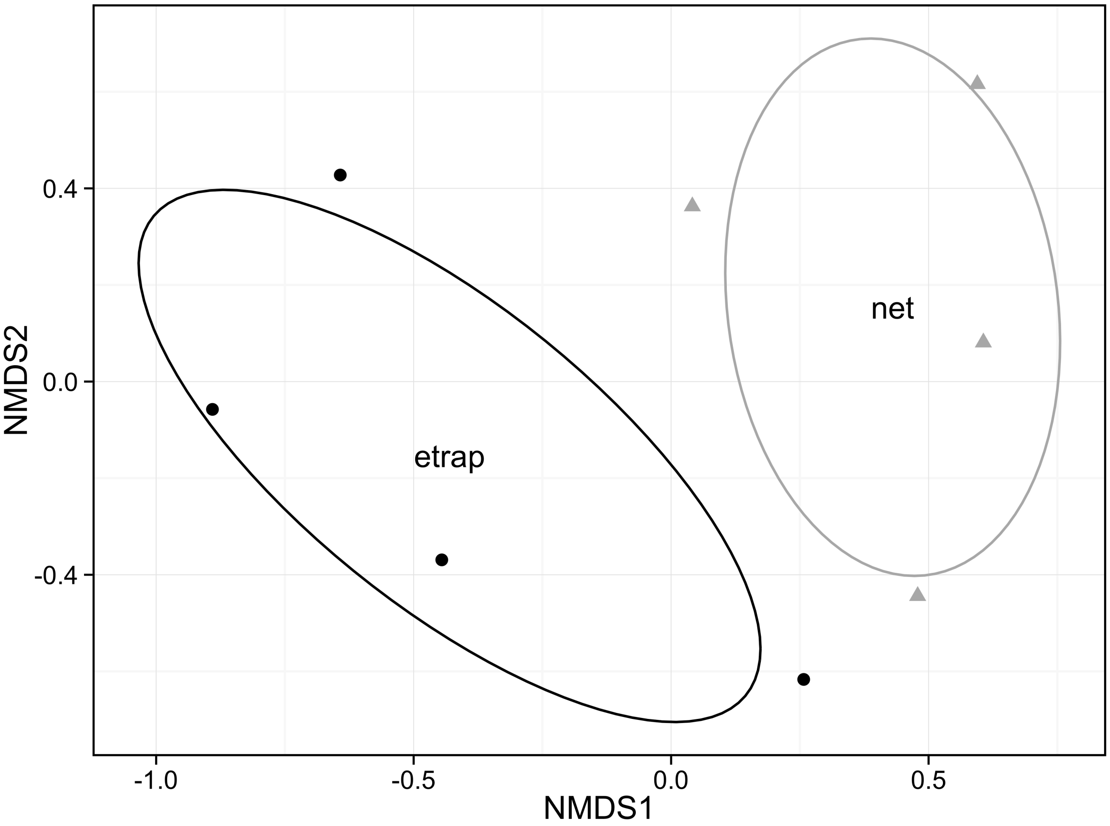

Figure 3.7. Non-metric multidimensional scaling of the community of bees captured in emergence traps (etrap, black circles) and netted on open flowers (net, gray triangles) at four blueberry farms in SW Michigan. Ellipses represent 95% confidence ellipses around the group means.

Suitability of new and mature wildflower restorations as nesting sites for bees

I captured a total of 159 bees in 89 traps in the three newly-established and three mature wildflower plantings and their paired unrestored controls, out of a total of 720 trapping events over three sample rounds in 2014 (Table 3.13). The majority of the captured bees were subsocial members of the genus *Lasioglossum* (Hymenoptera: Halictidae), with several traps capturing large numbers of the same species, presumably from a single nest (Table 3.13). Two stem-nesting species (*Ceratina dupla* Say and *Hylaeus affinis* (Smith)) were also abundant in the traps. One specimen of the *Penstemon* oligolege *Osmia distincta* Cresson was captured in an old field control site; the nesting substrate of this species has never been described (Tepedino *et al*., 2006).

The abundance of captured soil-nesting bees differed among habitat types ($\chi^2 = 44.27$, $df = 3$, $p < 0.001$), with significantly more bees trapped in mature wildflower restorations than in new restorations or controls paired with new restorations (Figure 3.8). Mature restorations averaged more bees per trap than their nearby control sites (Figure 3.8), but this difference was not significant ($p = 0.11$).

Bee species richness differed by habitat ($\chi^2 = 8.64$, $df = 3$, $p = 0.03$), with significantly higher estimated richness in mature wildflower restorations and their controls than in the unrestored controls paired with new restorations (Figure 3.9). Species richness did not differ between the new and mature restorations or between mature restorations and their paired controls. Simpson's (1/D) diversity of bees in emergence traps did not differ by habitat ($\chi^2 = 3.76$, $df = 3$, $p = 0.29$).

Table 3.13. Bee species collected in emergence traps from three newly-established and three mature wildflower restorations and paired unrestored controls in 2014. No. traps represents the number of individual traps (and therefore the minimum number of possible nests) from which these species were collected.

Family *Species*	**Location captured**				**Total no. captured**	**No. traps**
	New Control	New Restoration	Mature Control	Mature Restoration		
Andrenidae						
Andrena imitatrix	0	0	1	0	1	1
Perdita octamaculata	0	0	0	1	1	1
Apidae						
Bombus impatiens	0	0	0	1	1	1
*Ceratina dupla**	0	0	2	5	7	3
Melissodes agilis	0	1	0	0	1	1
Colletidae						
Colletes nudus	0	0	0	1	1	1
*Hylaeus affinis**	0	0	6	21	27	22
Halictidae						
Agapostemon sericeus	0	0	2	0	2	1
Augochlorella aurata	2	0	4	5	11	8
Augochloropsis metallica	0	0	0	3	3	1
Halictus confusus	0	0	2	0	2	2
Halictus rubicundus	0	3	0	0	3	2
Lasioglossum anomalum	0	0	2	8	10	6
Lasioglossum cinctipes	0	0	1	0	1	1
Lasioglossum ellisiae	0	4	0	0	4	1
Lasioglossum foveolatum	0	0	1	0	1	1
Lasioglossum hitchensi	0	5	7	6	18	8
Lasioglossum illinoensis	0	0	0	4	4	1
Lasioglossum imitatum	0	0	1	0	1	1
Lasioglossum leucocomum	0	2	0	33	35	8
Lasioglossum leucozonium	0	3	9	0	12	7
Lasioglossum oceanicum	0	0	1	0	1	1
Lasioglossum paraforbesii	0	0	0	3	3	1
Lasioglossum pectorale	0	0	2	3	5	5
Lasioglossum perpunctatum	0	0	0	1	1	1
Lasioglossum pilosum	0	2	0	0	2	2
Megachilidae						
*Osmia distincta***	0	0	1	0	1	1
Total:	2	20	42	95	159	89

* Stem-nesting bees

** Nesting substrate unknown (Tepedino *et al*., 2006)

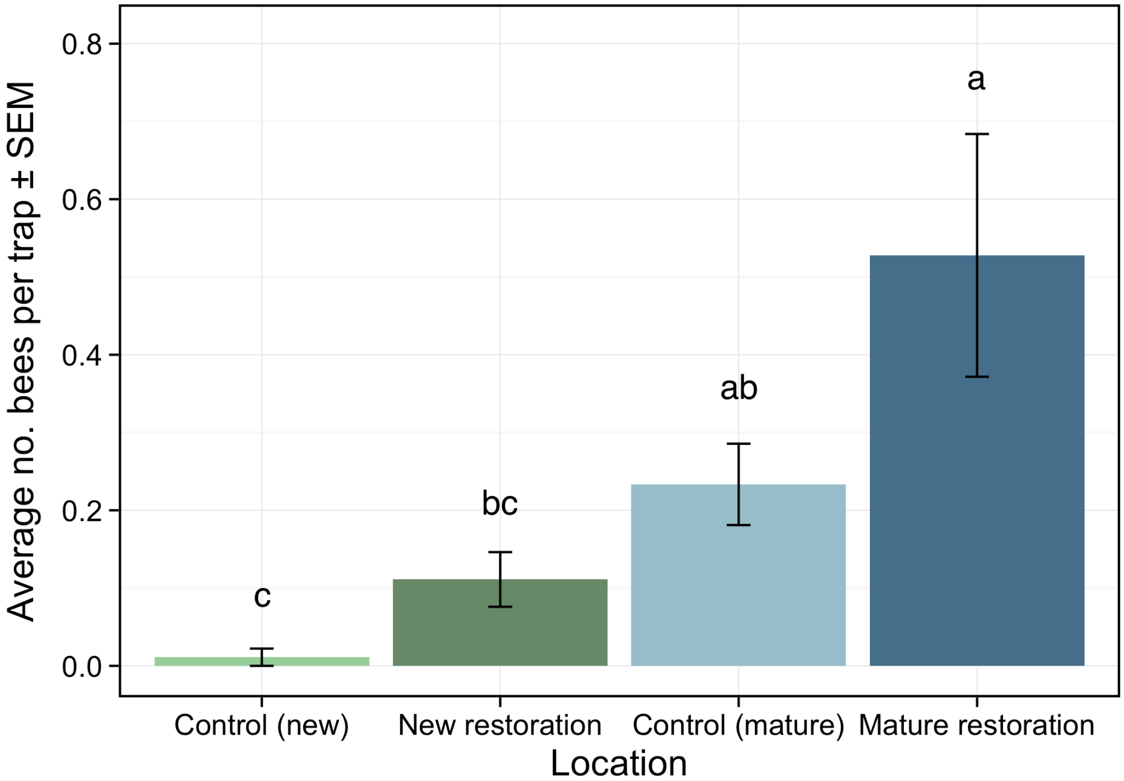

Figure 3.8. Mean number of bees collected per emergence trap in newly-established wildflower plantings, mature wildflower plantings, and paired unrestored controls. Locations with the same letter are not significantly different (posthoc Dunn's pairwise comparisons with Bonferroni correction, α=0.05).

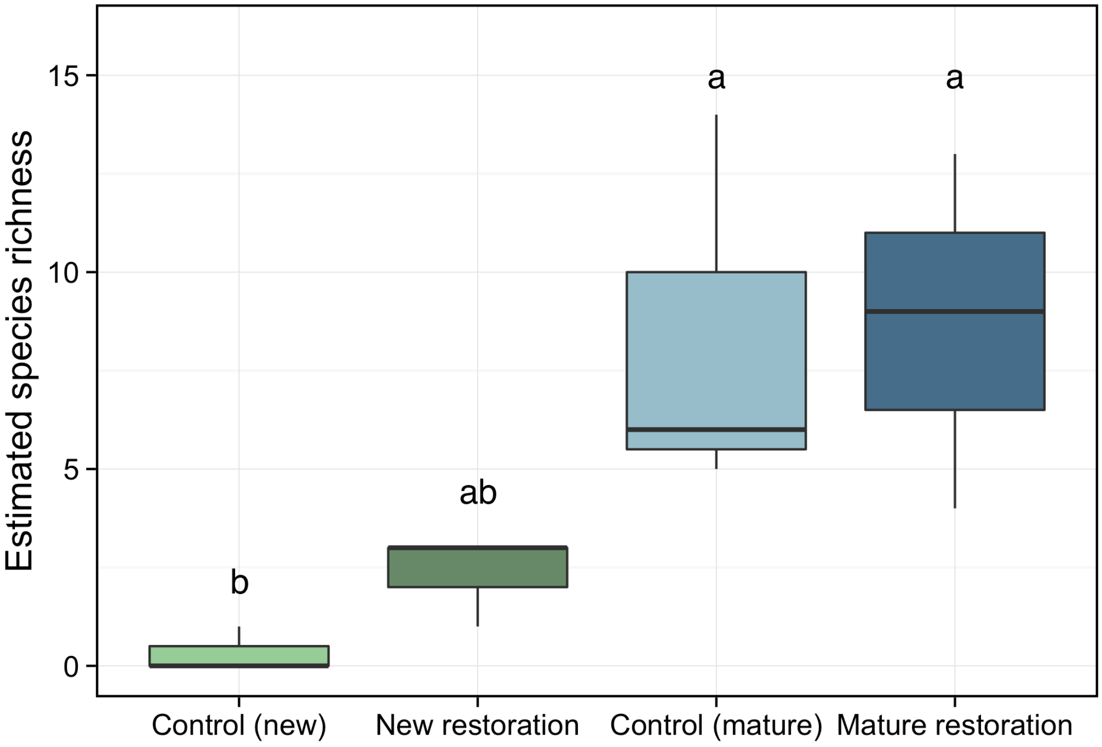

Figure 3.9. Boxplot of Chao1 estimated species richness of bees collected in emergence traps in in newly-established wildflower plantings, mature wildflower plantings, and paired unrestored controls. Locations with the same letter are not significantly different (posthoc Dunn's pairwise comparisons with Bonferroni correction, α=0.05).

Table 3.14. Microhabitat characteristics measured in emergence trap quadrats at three new wildflower restorations, three mature wildflower restorations, and paired unrestored control sites (n = 720 traps). Values within a column followed by the same letter are not significantly different (posthoc Dunn's pairwise comparisons with Bonferroni correction, α=0.05).

Habitat	**Bare ground (%) ± SEM**	**Vegetation (%) ± SEM**	**Wood/rocks (%) ± SEM**	**Leaf litter/thatch (%) ± SEM**
Control (new)	1.6 ± 0.6 b	95.3 ± 0.8 a	0.6 ± 0.2 b	57.8 ± 2.7 ab
New restoration	24.4 ± 2.2 a	72.2 ± 2.3 b	1.1 ± 0.2 ab	11.0 ± 1.2 c
Control (mature)	6.1 ± 1.6 b	82.7 ± 1.8 b	2.2 ± 0.3 a	47.9 ± 2.4 b
Mature restoration	1.7 ± 0.5 b	85.2 ± 1.3 b	0.6 ± 0.1 b	63.6 ± 2.8 a

Table 3.15. Spearman's rank correlation matrix of microhabitat characteristics measured in emergence trap quadrats at new wildflower restorations, mature wildflower restorations, and paired unrestored control sites (n = 720 traps).

	Bare ground (%)	Vegetation (%)	Wood and rocks (%)	Leaf litter or thatch (%)	Slope
Bare ground (%)	1				
Vegetation (%)	-0.54^{***}	1			
Wood and rocks (%)	0.11^{**}	-0.17^{***}	1		
Leaf litter/thatch (%)	-0.56^{***}	0.08^{*}	0.01	1	
Slope	-0.11^{**}	0.20^{***}	-0.01	0.07	1

*significant at $p = 0.05$, **$p = 0.01$, ***$p = 0.001$

Microhabitat characteristics

The microhabitat characteristics were highly intercorrelated (Table 3.15), and all of the percent cover categories differed significantly by habitat (Table 3.14). New restorations had significantly more bare ground than other habitats. Mature restorations had more leaf litter/thatch than other habitats, though not significantly more than the control habitats paired with new restorations. Control habitats paired with mature restorations had significantly more wood and/or rocks than mature restorations or new controls (wood and rock categories were not separated). Control habitats paired with new restorations, which were primarily grassy field margins adjacent to blueberry fields, had significantly more living vegetation than any other habitat type.

The microhabitat variable with the highest factor loading on PC2 was percent wood and rocks, which loaded positively on the axis (Table 3.16). Percent leaf litter and thatch also had a weak positive loading on the axis, but no factor besides wood and rocks had a loading over 0.4. On PC3, the largest factor loading was a negative loading for slope, but percent leaf litter/thatch also had a strong positive loading (Table 3.16).

Backward stepwise elimination led to the selection of a logit model with the second and third principal components as predictor variables (AIC = 500.28). Individual models with PC2 and PC3 had delta AIC values over 2 (AIC = 502.43 and 502.67, respectively), indicating that the more parsimonious models were not viable alternatives to the PC2+PC3 model. A likelihood ratio test indicated that the model fit for the PC2+PC3 model was significantly better than the null model ($\chi^2 = 7.46$, $df = 2$, $p = 0.02$). Bee presence was positively correlated with both model terms (Table 3.17).

Table 3.16. Factor loadings on the first four principal components for microhabitat characteristics in emergence trap quadrats in new wildflower restorations, mature wildflower restorations, and their paired unrestored controls in 2014 (n=720 traps). Factor loadings greater than 0.4 are in bold.

Microhabitat characteristic	**PC1**	**PC2**	**PC3**	**PC4**
Bare ground (%)	**0.66**	0.03	-0.13	-0.16
Vegetation (%)	**-0.62**	-0.16	-0.10	**0.41**
Wood and rocks (%)	0.06	**0.90**	0.04	**0.43**
Leaf litter/thatch (%)	-0.37	0.35	**0.42**	**-0.71**
Slope	-0.20	0.22	**-0.89**	-0.34

Table 3.17. Logistic regression model assessing the second and third principal component axes as predictors of the presence of bees in emergence traps.

Model term	**Odds ratio (95% confidence interval)**	**β ± SE**	**Wald χ^2**	***df***	***p***
PC2	1.22 (1.00-1.46)	0.19 ± 0.10	298.5	1	<0.001
PC3	1.28 (1.00-1.67)	0.25 ± 0.13	298.4	1	<0.001

Bee communities collected in nets vs. emergence traps

NMDS ordination of trapped and netted bees indicated that the bee communities collected by the two methods had little overlap (Figure 3.10). The bee communities differed significantly between the two collection methods (perMANOVA; $F = 2.65$, $df = 1, 22$, $p = 0.02$). Twenty species contributed to the first 70% of the dissimilarity between the two methods (Table 3.18), including a mix of soil-nesting and stem-nesting species. The top contributors included two stem-nesting bees, *Ceratina calcarata* Robertson and *Hylaeus affinis* (Smith), and two halictine soil-nesting bees, *Lasioglossum hitchensi* Gibbs and *L. leucocomum* (Lovell).

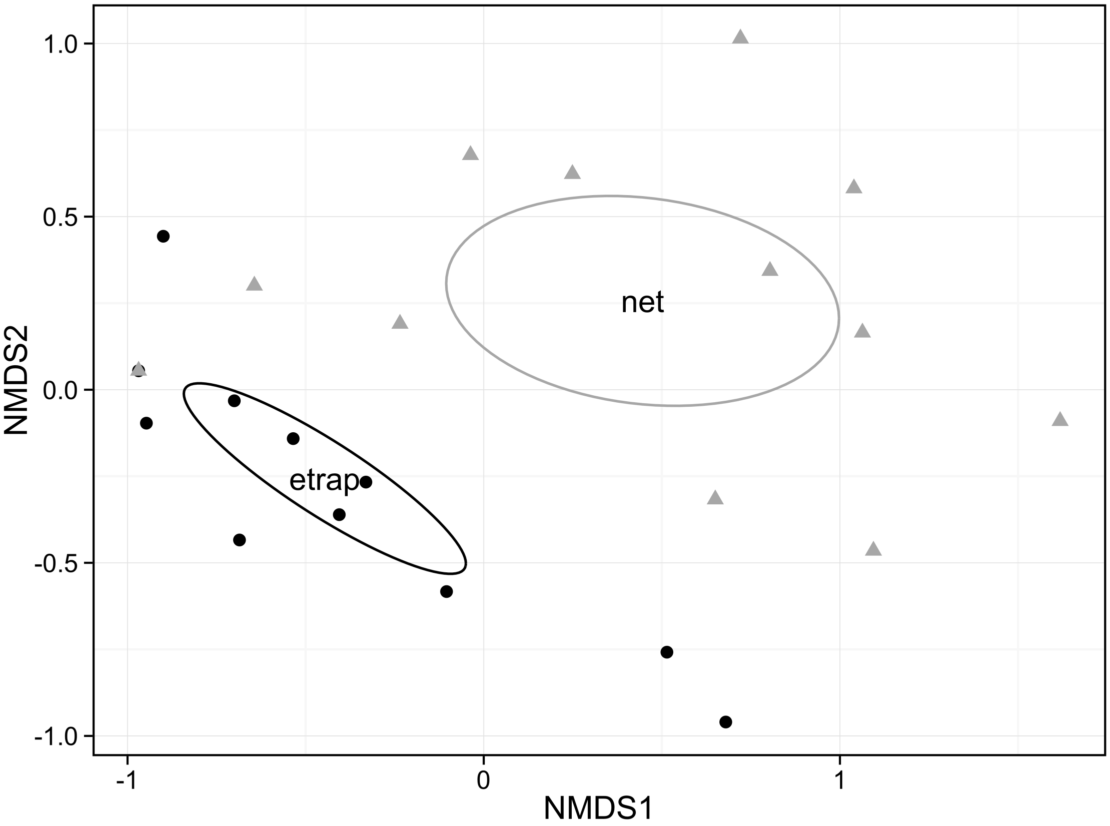

Figure 3.10. Non-metric multidimensional scaling of the community of bees captured in emergence traps (etrap, black circles) and netted on open flowers (net, gray triangles) in mature wildflower restorations, newly-established restorations, and paired unrestored habitats for each restoration in SW Michigan. Ellipses represent 95% confidence ellipses around the group means.

Table 3.18. Bee species most responsible for differentiating bee communities by collection method (SIMPER analysis).

Species	Average contribution ± SD (%)	Total no. in traps	Total no. in nets	Nesting substrate	Cumulative contribution to contrast
Ceratina calcarata	7.0 ± 9.8	0	23	Stem	8.1%
Lasioglossum hitchensi	5.7 ± 8.9	18	5	Soil	14.8%
Lasioglossum leucocomum	5.6 ± 10.9	35	9	Soil	21.4%
Hylaeus affinis	4.3 ± 6.4	27	4	Stem	26.4%
Augochlorella aurata	3.8 ± 5.5	11	11	Soil	30.9%
Bombus impatiens	3.3 ± 4.5	1	13	Soil	34.7%
Hylaeus modestus	3.1 ± 8.7	0	18	Stem	38.3%
Ceratina mikmaqi	2.9 ± 7.4	0	13	Stem	41.7%
Lasioglossum leucozonium	2.9 ± 6.7	12	1	Soil	45.1%
Ceratina dupla	2.7 ± 5.7	7	2	Stem	48.3%
Bombus griseocollis	2.5 ± 3.8	0	10	Soil	51.2%
Halictus ligatus	2.3 ± 3.9	0	9	Soil	53.9%
Andrena wilkella	2.3 ± 3.0	0	9	Soil	56.5%
Lasioglossum pectorale	2.2 ± 4.3	5	7	Soil	59.1%
Lasioglossum anomalum	2.1 ± 4.1	10	2	Soil	61.5%
Lasioglossum lineatulum	2.1 ± 7.2	0	12	Soil	64.0%
Halictus rubicundus	1.7 ± 6.6	3	1	Soil	66.0%
Lasioglossum imitatum	1.5 ± 3.7	1	7	Soil	67.8%
Ceratina strenua	1.5 ± 4.9	0	3	Stem	69.5%
Bombus bimaculatus	1.4 ± 2.7	0	5	Soil	71.2%

Discussion

Using emergence traps in blueberry farms, I found that wildflower plantings support a greater abundance of soil-nesting bees than unrestored field perimeters or woodland in the surrounding landscape. Blueberry fields had intermediate captures. However, species richness and diversity of soil-nesting bees did not differ across the sampled habitats. In addition, I found evidence to suggest that the abundance of nesting bees increases as wildflower plantings mature, as there were significantly more bees nesting in mature wildflower plantings than in newly-established wildflower plantings.

Nesting bees were also more species-rich in mature wildflower plantings than new restorations, although not more diverse.

Previous work has shown that planting wildflowers in resource-limited landscapes can attract abundant and diverse bee communities to forage on those patches (Pywell *et al.*, 2005, 2007; Carvell *et al.*, 2007; Morandin & Kremen, 2013; Blaauw & Isaacs, 2014a, 2014b). This study complements this previous work by showing that bees preferentially nest in these undisturbed wildflower patches, indicating that wildflower plantings provide bees with two limiting resources in these landscapes: food and nesting sites. Other on-farm habitats may not be as well-suited for nesting: the crop field and its margins have high levels of disturbance, including tillage and pest management inputs, while wooded areas have thick layers of litter that may act as a barrier to nest formation.

Bee nesting was not consistently associated with specific microhabitat variables across studies. On blueberry farms, bare ground was a significant predictor of bee nesting, but it did not emerge as an important predictor of nesting in the restoration age study, perhaps because variability in the percent bare ground was low in most habitats in this study. The availability of patches of bare ground has been consistently associated with bee nesting and/or ground-nesting bee abundance, though the strength of the association is variable (Potts *et al.*, 2005; Hopwood, 2008; Exeler *et al.*, 2009; Morandin & Kremen, 2013; Sardiñas & Kremen, 2014). Potts *et al.* (2005) found that species richness of soil-nesting bees collected via timed net sampling in post-fire habitat patches was positively associated with the percent bare ground in those habitats ($p = 0.02$). The percent bare ground was also positively associated with nesting in the Sardiñas and Kremen (2014) emergence trap study ($p = 0.09$). Both of these studies, however, were conducted in fire-dependent scrub habitats in Mediterranean climates, where variability in percent exposed soil is likely to be greater than in temperate prairie restorations (*see* Table 3 in Potts *et al*., 2005 for means of microhabitat characteristics in that environment). When variability in exposed soil is low, as in our restoration age study, bee choice of nest site may be based on other factors, such as proximity to floral resources.

The number of small cavities (<2 cm diameter) counted in emergence trap quadrats was the best predictor of bee presence in traps in the blueberry habitat study (Table 3.9). Interestingly, Sardiñas and Kremen (2014) found a significant negative relationship between the number of cavities and nesting bee abundance. However, their study placed traps before the first emergence of bees and therefore measured pre-existing cavities from at least the season prior to trapping, while the cavities I measured may have been a combination of pre-existing cavities and active bee nests. More work is needed to determine whether bees choose to nest in or to avoid pre-existing cavities, as well as to determine the likelihood that small, round cavities in the ground are active bee nests. If untrained observers are able to accurately identify active bee nests by sight simply by counting cavities of a certain size and shape, then there may be faster ways to determine bee nesting abundance in different habitats than emergence trapping.

In the restoration age study, bee presence in emergence traps was positively associated with percent cover of leaf litter and dried thatch as well as wood and rocks, both of which included different types of pithy stems (e.g. *Rubus* spp. canes were counted as wood, while dried stems of various tall grasses were counted as thatch). We captured several species of stem-nesting bees in emergence traps, which may explain the association with these two cover categories (Table 3.13). Alternatively, the association may be an artifact of the correlation between mature wildflower restorations and higher levels of thatch (Table 3.14); again, it is possible that nesting bees may have been attracted to floral resources rather than specific microhabitat characteristics.

Emergence trapping and hand netting of bees collected distinct subsets of the total bee communities utilizing different habitat types for nesting or foraging. Differences in collections of closely related species in nets or traps may reveal subtle niche partitioning. For example, while all of the morphologically and genetically similar members of the *Ceratina* genus nest in pithy stems, the species exhibit subtle preferences for nesting in different plant species with exposed pith (Vickruck *et al*., 2011; Vickruck & Richards, 2012). We captured several *Ceratina dupla* in emergence traps, but no *C. calcarata, C. mikmaqi,* or *C. strenua*, all of which were captured in nets at the same sites (Table 3.18). *Ceratina dupla* may be using a different type of pithy substrate from the rest of the genus. Similarly, two closely related species in the stem-nesting genus *Hylaeus* were associated with different collection methods: *Hylaeus affinis* was fairly abundant in emergence traps, with a few netted specimens, while *H. modestus* was captured only in nets. These bees have long been considered nearly morphologically indistinct (Sheffield *et al*., 2009; Grundel *et al*., 2011), and the challenge of reliable morphological delineation of the two species means little is known about possible differences in nesting biology. The differences in collection methods suggest there may be as-yet unknown niche partitioning based on nesting substrate. Alternatively, these differences in collection may simply be a sampling artifact; the spatial variability in nest sites and relatively low captures of emerging bees mean that it’s likely that there were nesting species that were missed.

In addition, emergence traps captured several species of cleptoparasites in the *Nomada* and *Sphecodes* genera in blueberry farm habitats. The apid genus *Nomada* consists of cross-family cleptoparasites of andrenid bees, while the halictid genus *Sphecodes* are a mixture of generalist and specialist nest parasites with hosts in various bee families (Bogusch *et al*., 2006; Habermannová *et al*., 2013). Host associations and their degree of specialization are not known for many cleptoparasites of soil-nesting bees, though it has been suggested that soil nests are parasitized more frequently than aboveground nests in twigs and other cavities (Wcislo, 1987, 1996; Wcislo & Cane, 1996; Bogusch, 2003). While cleptoparasites are sometimes captured while nectaring on flowers, they are generally more rare in floral collection records because they do not collect pollen, but instead co-opt the pollen resources of their host (Minckley *et al*., 1999). Emergence traps may allow for better quantification of the presence and overall proportion of cleptoparasitic species in wild bee communities than hand netting or pan trapping. Interestingly, while the abundance of soil-nesting bees was found to be higher in wildflower plantings than other habitat types in farm landscapes, cleptoparasites – which might be expected to track the nesting abundance of potential hosts - were spread relatively evenly through the different farm habitats, with cleptoparasites captured in the crop field, wooded areas, and wildflower restorations on blueberry farms. No cleptoparasites were captured in the three mature wildflower restorations sampled in the restoration age study. More work is needed to determine whether increasing abundance of soil-nesting bees over time in wildflower plantings is associated with increasing populations of cleptoparasites and associated risk of parasitism for soil-nesting bees, but these initial results suggest that wild bee cleptoparasites are not concentrated in wildflower plantings.

Emergence traps are a promising technique for developing our understanding of bee nesting preferences and resource requirements, and for increasing the richness of bees sampled during community studies (Sardiñas & Kremen, 2014). However, the traps require large investments in time and resources for variable – and sometimes quite low – returns in terms of trap captures. To maximize return on investment, it is crucial to select the most cost- and time-effective trapping methodology. The first trapping method, for the on-farm study conducted from 2013-14, maximized replication with our 40 emergence traps by moving the traps to new locations every 2-3 days, and minimized logistical issues with labor inputs by setting the traps out during daylight hours. However, this method yielded very low capture rates overall, with an average of 0.05 ± 0.01 bees per trap, or about 1 bee per 20 traps on average, and 1 bee per 10 traps in the wildflower plantings. We revised the methodology for the restoration age study by placing traps after dusk and leaving them out for slightly longer (one week) prior to collection. This method increased logistical challenges during the peak of field season, as the driving distance to sites ranged from 125 to 193 km from campus and hand netting of bees needed to be conducted in suitable weather conditions, typically earlier in the day. However, this method yielded significantly higher bees per trap, with an average of 0.22 ± 0.03 bees captured per trap across all habitats, or around 1 bee for every 4-5 traps. In the mature wildflower plantings, we captured about 1 bee for every 2 traps using this method (0.53 ± 0.16 bees per trap). By contrast, Sardiñas and Kremen (2014) deployed 40 larger 1.2m^2 emergence traps in the same locations for the duration of the flight season (May-

October), returning approximately every 12 days to collect emerging bees and refill the collection jars. This method yielded 252 bees, with 85% of traps capturing at least one bee. These methods are not directly comparable, both because the total number of trapping hours was much higher in the California study and because the study locations (the Mediterranean climate of California vs. the northern temperate climate of Michigan) are likely to differ in bee species richness and abundance. However, it is worth noting that placing traps in early spring, rather than in midsummer as in our study, maximizes the chance of capturing an emerging bee at some point during the season.

In choosing a method for emergence trap placement, it is also important to consider the unit of measurement needed to answer a particular research question. The method used here, which aimed to maximize replication with a limited number of traps, provided an estimate of abundance of nesting bees at each site for the short windows of time represented by each sample round. Because I did not leave the traps in one place for the entire growing season, and therefore could not capture all of the bees that might have been present in one $60cm^2$ area across multiple flight seasons, this method does not provide an estimate of nesting density. The density of nesting bees might have important consequences for the magnitude of bees' effects on belowground processes, such as soil bioturbation. Cane (2003) suggests that in the absence of a large aggregation of soil-nesting bees, such as the managed alkali bee, soil-nesting bees are generally minor agents of biogeomorphology and bioturbation. However, Colloff *et al*. (2010) determined that the soil macropores generated by ground-nesting bees and other soil macroinvertebrates are important for soil hydrological function. Density measurements of soil-nesting bees would therefore be useful in determining bees' overall contributions to soil physical and chemical properties in different environments.

Developing effective conservation strategies for wild bees in agricultural landscapes begins with sound information on bee resource requirements, including knowledge of which resources may be limiting in different environments, and how bees respond to different management approaches. Floral resources are widely regarded as the primary limiting resource for bees in human-altered landscapes, and studies have nearly universally shown that the installation of floral resources increases the diversity and abundance of wild bees in these landscapes (Carvell *et al.*, 2007; Carvalheiro *et al.*, 2012; Morandin & Kremen, 2013; Blaauw & Isaacs, 2014b; Jönsson *et al.*, 2015; Wood *et al.*, 2015). Much less is known about whether nesting resources are a limiting factor for bee communities, though it has been suggested for a variety of nesting guilds in different environments (Potts & Willmer, 1997; Kremen *et al.*, 2002; Williams *et al.*, 2010; Murray *et al.*, 2012; Xie *et al.*, 2013).

Management approaches for wild bee nesting differ by nesting guild. Widely available artificial nesting materials for cavity and tunnel-nesting bees have been shown to attract diverse and abundant nesting assemblages (Medler, 1966; Tscharntke *et al.*, 1998b; Bosch & Kemp, 2001; Sheffield *et al.*, 2008; Junqueira *et al.*, 2012), but there are few proven methods for enhancing nesting by soil-dwelling bees. The creation or maintenance of patches of bare ground, particularly in areas receiving morning or midday sun exposure, has been widely suggested as a possible management technique to attract soil-nesting bees (Shepherd *et al.*, 2003; Gregory & Wright, 2005; Wild Farm Alliance, 2007; Hopwood, 2008; Mader *et al.*, 2010; Shepherd & Vaughan, 2011; Shepherd, 2012);

however, there remains little empirical evidence that these practices work. This study provides evidence from farm landscapes that wildflower restorations increase nesting by soil-nesting bees relative to surrounding habitats, and guidance on a method that can be used to assess the response of bees to the availability of nesting resources.

CHAPTER 4:

CONCLUSIONS AND FUTURE DIRECTIONS

In this thesis, I have explored how the distribution of resources and stressors affect wild bee abundance, richness, and community composition in the highbush blueberry agroecosystem. The data from two years of field sampling at farms in southwest Michigan that were sampled almost a decade before, and at sites where habitat enhancements have been established, revealed that wild bees are affected by various factors that all interact at the farm level to influence these insect communities.

Long term monitoring of bee populations is rare, especially in the United States, but this is necessary to determine how temporal or spatial changes in bee habitat quality or quantity will affect these insects (Williams *et al*., 2001; Westphal *et al*., 2008; Lebuhn *et al*., 2013). By revisiting previously-sampled farms where pesticide use has increased over recent years, I found that the abundance, richness, diversity, and community composition of wild bees continue to exhibit strong negative responses to insecticide program risk (Tuell & Isaacs, 2010). Solitary bee species, including several important *Vaccinium* pollinators such as *Andrena carolina*, show slightly greater sensitivity to insecticide risk than social species, but the margin of difference is small.

While these results indicate a need for concern about the possible long-term impacts on bees of pest management in fruit crops, extensive and continuous long-term monitoring, with additional sites in unmanaged natural areas, is needed to determine the degree and scope of any possible wild bee declines in this system (Williams *et al*., 2001; Droege *et al*., 2003; Lebuhn *et al*., 2013). Using the results from 11 multiyear studies of wild bee populations for estimates of average variability, Lebuhn *et al*. (2013) estimated that a national monitoring program with 200–250 carefully selected sampling locations, each sampled twice annually over 5 years, would provide sufficient power to detect small

(2–5%) annual declines in the number of species and in the total abundance of wild bees. Other estimates have called for more frequent sampling through the season for accurate detection of changes in regional bee communities, up to every 7-10 days for faunal surveys (Banaszak *et al.*, 2014). Pan traps have been nearly universally cited as the most efficient, cost-effective, and relatively unbiased sampling method for standardized monitoring programs (Cane *et al.*, 2001; Droege *et al.*, 2003, 2010; Westphal *et al.*, 2008; Lebuhn *et al.*, 2013), with some caveats (Wilson *et al.*, 2008; Baum & Wallen, 2011). An ongoing debate remains about whether repeated lethal sampling of bees causes declines in wild pollinators in monitored areas (Lebuhn *et al.*, 2015; Tepedino *et al.*, 2015), but a recent multiyear study suggests that bee populations may be robust to this level of disturbance (Gezon *et al.*, 2015). Long-term monitoring across space and time, not just within the small window of blueberry bloom, is needed for accurate estimation of the status of wild bees in this system and beyond (Winfree, 2010; Lebuhn *et al.*, 2013; Gezon *et al.*, 2015).

For blueberries in particular, I would recommend that long term monitoring to determine changes in bee communities be established on a set of blueberry farms stratified by insecticide use (e.g. unmanaged, low-intensity management, and high-intensity management), with similar landscape composition at the local level. This landscape caveat may be challenging to fulfill, as most unmanaged blueberry fields in southwest Michigan that I am aware of are not surrounded by highly-managed blueberry, unlike the managed fields included in this study. In addition to the unmanaged blueberry sites, which provide a control habitat as similar as possible to managed blueberry, several monitoring sites in natural areas as far removed from intensive agricultural fields as possible would be helpful for distinguishing the effects of insecticide use and landscape. Ideally, monitoring would be conducted at multiple time points through the season, with about one sample per month from May-September at each site to maximize coverage of different species' flight periods (Banaszak *et al*., 2014).

Additional work is needed to determine how life history traits shape bee responses to pesticide exposure, and conversely how long-term exposure to pesticides may affect bee community structure and functional diversity (Brittain & Potts, 2011). My study found no effect of pest management on the functional trait diversity of bee communities in highbush blueberry fields. In the long term, however, continued differences in sensitivity of social and solitary species to insecticide risk could lead to non-random changes in community structure with consequences for wild plant and crop pollination (Larsen *et al*., 2005; Brittain & Potts, 2011). Long-term monitoring of a set of sites using consistent trapping methodology would allow for detection of these types of community-level changes.

The second part of my research, which involved the use of emergence traps to quantify the abundance of soil-nesting bees nesting in different habitats, adds an important piece to our understanding of wildflower restorations as a conservation strategy for wild bees in farm landscapes. Previous work has shown that the addition of floral resources into landscapes with scarce or fragmented floral resource patches increases the abundance and richness of wild bees in those landscapes (Marshall *et al*., 2006; Carvell *et al*., 2007; Pywell *et al*., 2007; Morandin & Kremen, 2013; Blaauw & Isaacs, 2014; Jönsson *et al*., 2015; Williams *et al*., 2015). Morandin & Kremen (2013) suggested that the ability of floral restorations to export pollinators to nearby crops could be the result of consistent, undisturbed nesting sites as well as the availability of rich floral resources. This study complements recent molecular surveys by Wood *et al*. (2015) in providing empirical evidence that these types of restorations increase nesting by soil-nesting bees, thereby providing dual benefits to pollinators in restored areas. Most pollinators of blueberry - aside from managed honey bees - nest in the soil, so wildflower restorations are a suitable choice for growers looking to support populations of blueberry-pollinating bees on farms.

Wildflower restorations located an appropriate distance away from crop fields may also act as refugia for wild bees in intensively-managed farm landscapes, attracting bees to floral resources outside of treated crop areas and reducing the possibility of pesticide exposure. Growers must weigh the benefits of placing wildflower plantings close to crop fields to achieve pollination and biocontrol benefits (Blaauw & Isaacs, 2012, 2014) with the possibility that these areas will receive spray drift later in the season, possibly creating a sink for pollinators nesting and foraging in restorations close to crop fields (Davis *et al*., 1991; Otto *et al*., 2009). Several authors have suggested buffer zones for pesticide applications near hedgerows to protect butterflies and other organisms from the lethal and sublethal effects of insecticides, as well as to sustain the flowering plants that might be killed by herbicide use close to hedgerows (Cuthbertson & Jepson, 1988; Davis *et al*., 1991; Longley & Sotherton, 1997; Dover & Sparks, 2000). Estimates of appropriate buffer distances from pesticide applications for honey bee hives range from 5 to 40 meters depending on spray physical properties, formulations, and application conditions (Davis & Williams, 1990). Similar recommendations may be needed for the optimal placement of conservation plantings, with careful consideration of the typical application methods (e.g. aerial or ground applications) and chemistries used for pest and disease management and their potential for drift (Barret *et al*., 1981; Longley *et al*., 1997).

My work with emergence traps provides support for the assertion of Sardiñas & Kremen (2014) that this methodology can provide useful insights into bee nesting requirements as well as the total community composition of different sites beyond what's typically captured in pan traps or nets. However, the high cost of currently available emergence traps means that they require careful consideration of different methodologies to receive the best return on investment. I would advise future researchers interested in using these traps to consider the appropriate method to use to answer their specific research questions, bearing in mind the tradeoffs of using different trapping approaches. The method that I used to maximize replication with a limited number of traps is time-intensive and logistically difficult to integrate into a fieldwork program involving midday bee collections. By contrast, the method employed by Sardiñas & Kremen (2014) requires less intensive labor inputs and provides a useful estimate of season-long nest density, but is limited in the area it can cover by the high cost of traps.

Bearing these considerations in mind, I believe the logical next step is to determine season-long nest density of bees in different habitat types. I began sampling bees using emergence traps in mid-June following blueberry bloom, when floral resources were most abundant in wildflower plantings. It is possible that sampling in the same habitats in early spring would discover higher numbers of bees nesting in forests or forest margins, close to early-blooming resources such as flowering trees and shrubs. This early-season sampling would also be helpful in determining the specific habitat use and requirements of blueberry-pollinating bees. Mandelik *et al.* (2012) found that different habitat types provide complementary floral resources for bees at different times of the year, with concurrent shifts in bee community distribution in the landscape over the course of the growing season; the same pattern may be true for the use of different habitats for nesting. In addition, more accurate estimates of nest density in different habitats will allow for a) better parameterization of pollinator abundance models based on land cover types (e.g. Lonsdorf *et al.*, 2011), and b) better estimation of the effects of soil-nesting bees on soil physical and chemical properties, which have been mostly ignored in studies of the effects of belowground organisms on soil properties (Anderson, 1994; Lavelle, 1996). For example, nest construction and food accumulation by subterranean ants have been found to affect the vertical distribution of nutrients and physical properties of soil relative to surrounding soil environments (Dostál *et al.*, 2005). These types of belowground changes can lead to changes in overall soil fertility and the diversity and biomass production of aboveground plant communities (Hooper *et al.*, 2000; Wardle *et al.*, 2004). Understanding the effects of soil-nesting bees on soil physical and chemical properties would allow for better valuation of their total contributions to ecosystem function.

In general, my research indicates that wild bee communities are shaped by complex interactions of resources and stressors. Functional traits may be key to understanding differences in species' responses to these environmental factors, as well as understanding how communities may change over time with unidirectional stressors like high levels of pesticide exposure. Further research into wild bee environmental responses should explicitly consider species-specific ecology and functional traits. While there has been great interest at the national level in pollinator conservation over the last decade, with pollinator-specific language incorporated into many different funding opportunities from the US Department of Agriculture, we still know little about the basic ecology of many bee species. In particular, a greater emphasis is needed on research into the subterranean ecology of bees, so that information on nesting requirements can be incorporated into conservation strategies for soil-nesting bees.

For blueberry growers, this research suggests that growers interested in conserving wild bees for pollination need to employ pest management practices that minimize risk to non-target organisms. These practices include applying sprays after dusk, minimizing spray drift, using integrated pest management approaches to minimize the number of applications for target pests, and choosing insecticides with lower toxicity to bees whenever possible. In addition, growers can provide nesting and floral resources to support wild bee populations on farms through the installation of perennial wildflower restorations in areas protected from pesticide drift.

APPENDICES

APPENDIX A:

GPS COORDINATES FOR FIELD SITES

Table A. GPS coordinates for the 15 blueberry fields in which bees were sampled during bloom by J.K. Tuell between 2004-6 and by EM in 2013 and 2014.

Site	N	W
1	42˚16.075	-086˚13.997
2	42˚20.869	-086˚13.355
3	42˚21.885	-086˚17.217
4	42˚24.749	-086˚06.378
5	42˚32.148	-086˚12.896
6	42˚34.917	-086˚09.107
7	42˚37.589	-086˚10.117
8	42˚41.677	-086˚08.920
9	42˚43.631	-086˚06.638
10	42˚49.122	-086˚10.236
11	42˚50.604	-086˚09.902
12	42˚52.051	-086˚07.578
13	42˚52.905	-086˚09.369
14	42˚57.208	-086˚06.568
15	42˚59.413	-086˚09.451

Table B. GPS coordinates for the four blueberry farms sampled using emergence traps in 2013 and 2014. Coordinates are for the wildflower restoration at each site.

Site	N	W
1	42°12.919	-086°20.338
2	42°15.790	-086°14.004
3	42°32.330	-086˚17.217
4	42°26.458	-086°05.249

Table C. GPS coordinates for the new and mature wildflower restorations sampled using emergence traps in 2014.

Site	Type	N	W
1	New	42°22.940	-085°54.880
2	New	42°17.920	-085°50.257
3	New	42°58.103	-086°08.540
4	Mature	42°20.931	-085°44.345
5	Mature	42°21.220	-085°35.288
6	Mature	43°01.041	-085°50.286

APPENDIX B:

COLLECTED WILD BEE SPECIES & ASSOCIATED FUNCTIONAL TRAITS

Table D. Wild bee species captured in pan traps and nets at 15 blueberry fields during bloom by J.K. Tuell between 2004-2006 and EM in 2013 and 2014, and their associated functional traits. Trait information was taken from Wolf & Ascher (2008), Bartomeus *et al*. (2013), and Gibbs *et al*. (2011). Key to nest location: "Soil (R)" = species that rent rather than excavate soil nests, and "Clepto" = cleptoparasitic species. Key to sociality, "E" = eusocial, "F" = facultatively social, and "S" = solitary. Key to lecty (diet specialization): "P" = polylectic and "O" = oligolectic. Body size was categorized from inter-tegular distance, where available, or based on educated guesses (Bartomeus *et al*., 2013). Key to body size: "S" = small, "M" = medium, and "L" = large (Table 2.2). Service-providing bees are those that have been recorded collecting pollen from *Vaccinium corymbosum* L. and close relatives (see reference column); a "no" in the service-providing column means that the species has not been recorded visiting *Vaccinium* flowers, or is a cleptoparasite or an oligolege on other types of plants.

	Total no. captured					Functional traits					
Species	2004	2005	2006	2013	2014	Nest location	Sociality	Lecty	Body size	Service providing	Ref
Agapostemon sericeus	1	3	4	4	0	Soil	F	P	M	Yes	3
Agapostemon splendens	2	1	0	2	2	Soil	F	P	M	Yes	4
Agapostemon texanus	0	2	1	4	0	Soil	F	P	M	Yes	2
Agapostemon virescens	3	5	3	2	3	Soil	F	P	M	Yes	5
Andrena algida	1	1	0	0	0	Soil	S	P	M	No	
Andrena alleghaniensis	8	21	18	0	1	Soil	S	P	M	Yes	2
Andrena andrenoides	0	1	0	0	0	Soil	S	P	M	No	
Andrena arabis	0	0	1	0	0	Soil	S	O	M	No	
Andrena barbilabris	0	8	2	1	0	Soil	S	P	M	No	
Andrena carlini	57	55	17	0	7	Soil	S	P	L	Yes	1
Andrena carolina	111	303	113	8	16	Soil	S	O	M	Yes	1,2,3,10
Andrena ceanothi	4	2	9	2	0	Soil	S	P	L	Yes	6
Andrena cf. *morrisonella*	1	0	0	0	0	Soil	S	P	M	Yes	3
Andrena cf. *w-scripta*	0	0	0	0	1	Soil	S	P	M	Yes	2
Andrena clarkella	0	1	0	0	0	Soil	S	O	M	Yes	6
Andrena commoda	2	2	0	0	0	Soil	S	P	M	No	
Andrena confederata	1	0	0	0	0	Soil	S	P	M	No	

Table D (cont'd)

Andrena crataegi	17	10	16	0	3	Soil	S	P	M	Yes	2
Andrena cressonii	9	23	13	3	9	Soil	S	P	M	Yes	1
Andrena dunningi	1	0	0	1	2	Soil	S	P	M	Yes	2
Andrena erigeniae	0	2	0	0	1	Soil	S	O	S	No	
Andrena erythrogaster	0	1	0	0	0	Soil	S	O	M	No	
Andrena erythronii	0	0	1	0	0	Soil	S	O	M	No	
Andrena forbesii	5	0	7	1	3	Soil	S	P	M	Yes	2,7
Andrena hilaris	3	0	0	0	0	Soil	S	P	M	No	
Andrena hippotes	7	5	4	0	1	Soil	S	P	M	No	
Andrena imitatrix	31	26	21	1	6	Soil	S	P	M	Yes	1,2
Andrena imitatrix or *morrisonella*	8	27	18	0	0	Soil	S	P	M	Yes	1,2,3
Andrena integra	2	0	0	0	0	Soil	S	O	M	No	
Andrena mandibularis	0	2	0	0	0	Soil	S	P	M	Yes	2
Andrena mariae	1	0	0	0	0	Soil	S	O	M	No	
Andrena milwaukeensis	1	0	0	0	0	Soil	S	P	M	Yes	2
Andrena miranda	0	0	0	1	0	Soil	S	P	M	Yes	6
Andrena miserabilis	9	45	43	3	4	Soil	S	P	M	Yes	2, 3
Andrena morrisonella	3	4	3	0	0	Soil	S	P	M	Yes	3
Andrena nasonii	7	14	11	4	9	Soil	S	P	M	Yes	3
Andrena neonana	1	0	0	0	0	Soil	S	P	M	No	
Andrena nigrae	3	0	11	0	0	Soil	S	O	M	No	
Andrena nigrihirta	0	1	7	0	0	Soil	S	P	M	No	
Andrena nivalis	1	0	0	0	0	Soil	S	P	L	Yes	1,2,10
Andrena nuda	15	4	7	0	1	Soil	S	P	M	No	
Andrena perplexa	15	6	3	3	2	Soil	S	P	M	Yes	3
Andrena persimulata	0	0	1	0	0	Soil	S	O	M	No	

Table D (cont'd)

Andrena pruni	2	1	1	0	0	Soil	S	P	M	Yes	7
Andrena rehni	2	0	0	0	0	Soil	S	P	M	No	
Andrena robertsonii	1	1	2	0	0	Soil	S	P	M	No	
Andrena rugosa	10	4	6	1	3	Soil	S	P	M	Yes	2
Andrena salictaria	1	5	0	0	0	Soil	S	O	M	Yes	2
Andrena sp.	2	10	2	1	8	Soil	S	P	M	Unknown	
Andrena spiraeana	0	1	0	0	0	Soil	S	P	M	No	
Andrena vicina	53	49	26	4	2	Soil	S	P	M	Yes	1
Andrena wilkella	0	0	0	1	0	Soil	S	P	M	Yes	1,3
Augochlora pura	41	13	11	15	17	Wood	S	P	M	Yes	1
Augochlorella aurata	68	32	72	40	15	Soil	E	P	M	Yes	3
Augochloropsis metallica	1	0	0	0	0	Soil	S	P	M	Yes	1,7
Bombus bimaculatus	7	0	2	1	10	Soil (R)	E	P	L	Yes	2
Bombus citrinus	15	0	1	1	0	Clepto	C	C	L	No	
Bombus fervidus	0	3	3	7	9	Soil (R)	E	P	L	Yes	7
Bombus griseocollis	3	0	4	0	4	Soil (R)	E	P	L	Yes	11
Bombus impatiens	1	2	0	1	53	Soil (R)	E	P	L	Yes	10
Bombus perplexus	3	0	0	0	0	Soil (R)	E	P	L	Yes	2
Bombus vagans	0	0	0	0	9	Soil (R)	E	P	L	Yes	2
Ceratina calcarata	43	59	44	15	33	Stem	F	P	S	Yes	7
Ceratina dupla	1	0	0	0	0	Stem	F	P	S	Yes	2
Ceratina mikmaqi	16	15	6	7	2	Stem	F	P	S	Yes	7†
Ceratina strenua	9	6	0	3	2	Stem	F	P	S	Yes	7
Colletes inaequalis	0	15	3	1	5	Soil	S	P	L	Yes	3
Colletes thoracicus	24	4	0	1	3	Soil	S	P	L	Yes	3
Colletes validus	0	2	0	0	0	Soil	S	P	L	Yes	3,10
Eucera atriventris	1	0	0	0	1	Soil	S	P	L	No	

Table D (cont'd)

Eucera hamata	0	1	0	5	1	Soil	S	P	L	No	
Halictus confusus	2	27	4	1	7	Soil	F	P	S	Yes	2
Halictus ligatus	17	20	11	2	25	Soil	E	P	M	Yes	2
Halictus parallelus	2	1	2	5	10	Soil	E	P	L	Yes	5
Halictus rubicundus	3	7	3	1	4	Soil	F	P	M	Yes	3,8,10
Hoplitis pilosifrons	1	1	0	0	2	Stem	S	P	M	No	
Hoplitis producta	1	2	0	2	0	Stem	S	P	S	No	
Hoplitis spoliata	0	1	0	0	0	Stem	S	P	S	No	
Hylaeus affinis	1	2	1	0	1	Cavity	S	P	S	Yes	1
Hylaeus illinoisensis	1	1	2	0	0	Cavity	S	P	S	No	
Hylaeus mesillae	0	1	0	0	0	Cavity	S	P	S	Yes	2
Hylaeus sp.	0	2	0	0	0	Cavity	S	P	S	Unknown	
Lasioglossum abanci	0	0	0	0	2	Soil	E	P	S	No	
Lasioglossum acuminatum	5	3	4	2	7	Soil	F	P	M	No	
Lasioglossum admirandum	11	3	4	2	5	Soil	E	P	M	Yes	2
Lasioglossum anomalum	1	4	2	1	25	Soil	E	P	S	No	
Lasioglossum atwoodi	0	0	0	1	0	Soil	E	P	S	No	
Lasioglossum bruneri	3	1	0	0	0	Soil	E	P	S	No	
Lasioglossum cattellae	0	1	1	0	0	Soil	E	P	S	No	
Lasioglossum coeruleum	5	1	3	0	3	Wood	E	P	S	No	
Lasioglossum coriaceum	60	17	12	42	61	Soil	F	P	M	Yes	1,3
Lasioglossum cressonii	80	17	17	34	39	Wood	E	P	S	Yes	1,7
Lasioglossum ellisiae	6	5	16	3	13	Soil	E	P	S	No	
Lasioglossum ephialtum	0	0	0	8	1	Soil	E	P	S	No	
Lasioglossum floridanum	3	4	0	0	0	Soil	E	P	S	No	
Lasioglossum foxii	2	3	3	0	1	Soil	S	P	S	Yes	2
Lasioglossum fuscipenne	4	1	1	0	6	Soil	F	P	M	No	

Table D (cont'd)

Lasioglossum hitchensi	23	9	10	0	7	Soil	E	P	S	No	
Lasioglossum illinoense	0	1	0	0	0	Soil	E	P	S	No	
Lasioglossum imitatum	25	72	27	0	39	Soil	E	P	S	Yes	2
Lasioglossum laevissimum	0	0	0	0	1	Soil	E	P	S	Yes	1
Lasioglossum leucocomum	8	28	20	8	39	Soil	E	P	S	Yes	10
Lasioglossum leucozonium	64	27	56	12	18	Soil	S	P	M	Yes	2
Lasioglossum lineatulum	5	20	0	0	12	Soil	E	P	S	No	
Lasioglossum lustrans	0	0	1	0	0	Soil	S	O	S	No	
Lasioglossum macoupinense	3	2	4	9	9	Soil	S	P	S	No	
Lasioglossum nelumbonis	1	0	0	1	2	Soil	E	O	S	No	
Lasioglossum nigroviride	2	1	7	0	4	Soil	E	P	M	No	
Lasioglossum nymphaearum	1	1	2	1	0	Soil	E	P	S	No	
Lasioglossum oblongum	5	5	3	0	2	Wood	E	P	S	Yes	2
Lasioglossum obscurum	2	0	0	0	2	Soil	E	P	S	No	
Lasioglossum oceanicum	0	0	0	0	4	Soil	E	P	S	No	
Lasioglossum paradmirandum	0	0	0	0	1	Soil	E	P	S	No	
Lasioglossum pectorale	11	14	14	14	19	Soil	S	P	S	Yes	5
Lasioglossum perpunctatum	4	3	3	1	1	Soil	E	P	S	Yes	2
Lasioglossum pilosum	29	112	40	68	85	Soil	E	P	S	Yes	2
Lasioglossum planatum	1	0	0	0	0	Soil	E	P	S	No	
Lasioglossum quebecense	1	1	0	0	0	Soil	S	P	M	Yes	1,10
Lasioglossum sagax	1	0	0	0	0	Soil	E	P	S	No	
Lasioglossum smilacinae	0	0	0	0	3	Soil	E	P	M	Yes	7
Lasioglossum subviridatum	1	2	0	4	0	Wood	E	P	S	No	
Lasioglossum timothyi	6	2	1	8	0	Soil	E	P	S	No	
Lasioglossum versans	8	1	4	3	1	Soil	E	P	S	Yes	1
Lasioglossum versatum	22	2	2	0	1	Soil	E	P	S	Yes	7

Table D (cont'd)

Lasioglossum vierecki	1	6	0	0	2	Soil	S	P	S	No	
Lasioglossum viridatum	1	1	1	1	1	Soil	E	P	S	Yes	2
Lasioglossum zephyrum	0	1	0	0	1	Soil	E	P	S	Yes	7
Lasioglossum zonulum	0	0	0	1	2	Soil	S	P	M	Yes	2
Megachile addenda	1	0	0	0	0	Cavity	S	P	M	No*	
Megachile gemula	1	0	0	0	0	Cavity	S	P	L	Yes	1
Megachile mucida	0	2	0	0	0	Cavity	S	P	L	No	
Megachile rotundata	0	0	1	0	0	Cavity	S	P	M	Yes	2,8
Nomada cressonii	0	1	0	0	0	Clepto	C	C	M	No	
Nomada denticulata	0	2	0	0	1	Clepto	C	C	M	No	
Nomada maculata	0	1	0	0	0	Clepto	C	C	M	No	
Nomada ovata	0	1	0	0	0	Clepto	C	C	M	No	
Nomada sp.	33	47	13	1	0	Clepto	C	C	M	No	
Osmia albiventris	1	0	0	0	0	Cavity	S	P	M	No	
Osmia atriventris	0	1	1	0	3	Cavity	S	P	M	Yes	9
Osmia bucephala	4	2	0	0	1	Cavity	S	P	L	Yes	7
Osmia caerulescens	0	0	0	0	1	Cavity	S	P	M	No	
Osmia conjuncta	1	2	0	0	0	Cavity	S	P	M	No	
Osmia cornifrons	0	0	1	0	0	Cavity	S	P	L	Yes	5
Osmia felti	1	0	1	0	0	Cavity	S	P	M	Yes	1
Osmia georgica	0	0	0	0	1	Cavity	S	P	M	No	
Osmia pumila	4	4	4	0	5	Cavity	S	P	M	Yes	1
Osmia virga	0	1	0	0	0	Cavity	S	P	M	Yes	2
Sphecodes cressonii	0	0	0	0	1	Clepto	C	C	M	No	
Sphecodes confertus	2	0	0	0	0	Clepto	C	C	S	No	
Sphecodes dichrous	0	0	0	0	1	Clepto	C	C	M	No	
Sphecodes ranunculi	2	0	0	0	0	Clepto	C	C	M	No	

Table D (cont'd)

Sphecodes sp.	2	0	2	0	0	Clepto	C	C	M	No	
Xylocopa virginica	2	1	0	3	22	Wood	F	P	L	Yes	1

References: 1) Cane *et al.,* 1985; 2) Stubbs *et al.,* 1992; 3) Tuell *et al*., 2009; 4) Deyrup *et al*., 2002; 5) Adamson, 2011; 6) Sheffield *et al.,* 2003; 7) MacKenzie & Eickwort, 1996; 8) Javorek *et al.,* 2002; 9) Stubbs & Drummond, 1997; 10) Moisan-Deserres *et al.,* 2014; 11) Benjamin *et al*., 2014.

† Inferred from other *Ceratina* references, as *Ceratina mikmaqi* was first described from the *Ceratina dupla* Say species complex in 2011 (Rehan & Sheffield, 2011).

* *Megachile addenda* is an excellent pollinator of cranberry (*Vaccinium macrocarpon*) (Cane, 1996), but has not been recorded on *Vaccinium corymbosum*

APPENDIX C:

RECORD OF DEPOSITION OF VOUCHER SPECIMENS

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 used in this research. Voucher recognition labels bearing the voucher number have been attached to pinned specimens.

Voucher Number: 2015-01

Author and title of thesis: Emily A. May, “Wild bee community responses to farm management practices, wildflower restorations, and landscape composition.”

Museum where deposited: Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Table E. List of voucher specimens. Each record represents one pinned adult specimen. Species determinations (“Det”) were made by Dr. Jason Gibbs (JG) and the author (EM).

Unique ID	Family	Genus-Species	Date collected	Sex	Det
13-0392	Halictidae	*Agapostemon sericeus*	5/29/13	F	EM
13-0093	Halictidae	*Agapostemon splendens*	5/20/13	F	EM
13-0130	Halictidae	*Agapostemon texanus*	5/21/13	F	EM
13-0310	Halictidae	*Agapostemon virescens*	5/29/13	F	EM
14-0112	Andrenidae	*Andrena alleghaniensis*	5/24/14	F	JG
14-1027	Andrenidae	*Andrena asteris*	9/18/14	F	JG
13-0025	Andrenidae	*Andrena barbilabris*	5/20/13	F	JG
14-1452	Andrenidae	*Andrena canadensis*	9/3/14	F	JG
13-0418	Andrenidae	*Andrena carlini*	5/30/13	F	JG
13-0317	Andrenidae	*Andrena carolina*	5/29/13	F	JG
13-0292	Andrenidae	*Andrena ceanothi*	5/29/13	F	JG
14-0076	Andrenidae	*Andrena cf. w-scripta*	5/26/14	F	JG
14-0786	Andrenidae	*Andrena commoda*	6/27/14	F	JG
14-0006	Andrenidae	*Andrena crataegi*	5/21/14	M	JG
14-0508	Andrenidae	*Andrena cressonii*	5/24/14	F	JG
13-0342	Andrenidae	*Andrena dunningi*	5/30/13	F	JG
14-0282	Andrenidae	*Andrena erigeniae*	5/21/14	F	JG
13-0210	Andrenidae	*Andrena forbesii*	5/30/13	F	JG
14-0509	Andrenidae	*Andrena hippotes*	5/24/14	F	JG
14-1024	Andrenidae	*Andrena hirticincta*	9/8/14	F	JG
14-0252	Andrenidae	*Andrena imitatrix*	5/29/14	M	JG
13-0204	Andrenidae	*Andrena miserabilis*	5/30/13	F	JG

Table E (cont'd)

13-0079	Andrenidae	*Andrena nasonii*	5/21/13	F	JG
14-0559	Andrenidae	*Andrena nuda*	5/24/14	F	JG
13-0194	Andrenidae	*Andrena perplexa*	5/30/13	F	JG
14=1010	Andrenidae	*Andrena placata*	8/15/14	F	JG
13-0001	Andrenidae	*Andrena rugosa*	5/17/13	F	JG
13-0097	Andrenidae	*Andrena vicina*	5/20/13	F	JG
14-0799	Andrenidae	*Andrena wilkella*	6/24/14	F	JG
13-028	Megachilidae	*Anthidium oblongatum*	6/21/13	F	JG
13-007	Apidae	*Anthophora bomboides*	6/19/13	F	EM
14-1034	Apidae	*Anthophora terminalis*	9/8/14	F	JG
14-0837	Apidae	*Apis mellifera*	6/30/14	F	EM
13-0356	Halictidae	*Augochlora pura*	5/29/13	F	EM
13-0295	Halictidae	*Augochlorella aurata*	5/29/13	F	EM
14-1346	Halictidae	*Augochloropsis metallica*	6/10/14	F	JG
13-0419	Apidae	*Bombus bimaculatus*	5/30/13	F	EM
13-0082	Apidae	*Bombus citrinus*	5/20/13	F	EM
13-0052	Apidae	*Bombus fervidus*	5/21/13	F	EM
13-0420	Apidae	*Bombus griseocollis*	5/30/13	F	EM
13-0406	Apidae	*Bombus impatiens*	5/21/13	F	EM
14-0976	Apidae	*Bombus vagans*	8/5/14	F	EM
13-0337	Apidae	*Ceratina calcarata*	5/29/13	F	EM
14-1449	Apidae	*Ceratina dupla*	8/7/14	F	JG
13-0319	Apidae	*Ceratina mikmaqi*	5/29/13	F	EM
13-0343	Apidae	*Ceratina strenua*	5/30/13	F	EM
13-0369	Colletidae	*Colletes inaequalis*	5/29/13	F	EM
14-1454	Colletidae	*Colletes nudus*	7/17/14	F	JG
14-0638	Colletidae	*Colletes thoracicus*	5/26/14	F	EM
13-0217	Colletidae	*Colletes thoracicus*	5/30/13	M	EM
13-057	Halictidae	*Dieunomia heteropoda*	7/17/13	F	EM
14-0001	Apidae	*Eucera atriventris*	5/20/14	M	EM
14-0004	Apidae	*Eucera hamata*	5/20/14	M	EM
14-0438	Halictidae	*Halictus confusus*	5/25/14	F	EM
14-0253	Halictidae	*Halictus ligatus*	5/29/14	F	EM
14-0150	Halictidae	*Halictus parallelus*	5/29/14	F	EM
14-0599	Halictidae	*Halictus rubicundus*	5/24/14	F	EM
14-0717	Megachilidae	*Heriades carinata*	6/16/14	F	JG
14-0554	Megachilidae	*Hoplitis pilosifrons*	5/25/14	F	JG
13-0388	Megachilidae	*Hoplitis producta*	5/29/13	F	EM
14-0898	Megachilidae	*Hoplitis spoliata*	7/22/14	F	JG
14-0065	Colletidae	*Hylaeus affinis*	5/26/14	M	JG
14-0956	Colletidae	*Hylaeus annulatus*	8/5/14	F	JG
14-0790	Colletidae	*Hylaeus mesillae*	6/24/14	F	JG

Table E (cont'd)

14-0828	Colletidae	*Hylaeus modestus*	7/10/14	F	JG
14-0266	Halictidae	*Lasioglossum abanci*	5/21/14	F	JG
14-0289	Halictidae	*Lasioglossum acuminatum*	5/21/14	F	JG
13-0129	Halictidae	*Lasioglossum admirandum*	5/21/13	F	JG
14-0473	Halictidae	*Lasioglossum anomalum*	5/24/14	F	JG
13-0073	Halictidae	*Lasioglossum atwoodi*	5/21/13	F	JG
14-0249	Halictidae	*Lasioglossum coeruleum*	5/29/14	F	JG
14-0110	Halictidae	*Lasioglossum coriaceum*	5/24/14	F	EM
13-0230	Halictidae	*Lasioglossum cressonii*	5/30/13	F	JG
13-0298	Halictidae	*Lasioglossum ellisiae*	5/29/13	F	JG
14-0407	Halictidae	*Lasioglossum ephialtum*	5/24/14	F	JG
13-049	Halictidae	*Lasioglossum floridanum*	7/1/13	F	JG
14-1474	Halictidae	*Lasioglossum foveolatum*	7/17/14	F	JG
14-0342	Halictidae	*Lasioglossum foxii*	5/20/14	F	JG
14-0348	Halictidae	*Lasioglossum fuscipenne*	5/20/14	F	EM
13-0256	Halictidae	*Lasioglossum hitchensi*	5/30/13	F	JG
14-0261	Halictidae	*Lasioglossum imitatum*	5/21/14	F	JG
14-0321	Halictidae	*Lasioglossum laevissimum*	5/20/14	F	JG
14-0456	Halictidae	*Lasioglossum leucocomum*	5/24/14	F	JG
14-0595	Halictidae	*Lasioglossum leucozonium*	5/30/14	F	JG
14-0470	Halictidae	*Lasioglossum lineatulum*	5/24/14	F	JG
14-0873	Halictidae	*Lasioglossum lustrans*	7/25/14	F	JG
14-0081	Halictidae	*Lasioglossum macoupinense*	5/29/14	F	JG
13-0355	Halictidae	*Lasioglossum nelumbonis*	5/29/13	F	JG
14-0405	Halictidae	*Lasioglossum nigroviride*	5/24/14	F	JG
14-0275	Halictidae	*Lasioglossum oblongum*	5/21/14	F	JG
14-0304	Halictidae	*Lasioglossum obscurum*	5/20/14	F	JG
13-0247	Halictidae	*Lasioglossum oceanicum*	5/30/13	F	JG
14-0621	Halictidae	*Lasioglossum paradmirandum*	5/30/14	F	JG
13-0314	Halictidae	*Lasioglossum pectorale*	5/29/13	F	JG
14-0516	Halictidae	*Lasioglossum perpunctatum*	5/24/14	F	JG
14-0371	Halictidae	*Lasioglossum pilosum*	5/24/14	F	JG
14-0286	Halictidae	*Lasioglossum smilacinae*	5/21/14	F	JG
13-0593	Halictidae	*Lasioglossum subviridatum*	7/25/13	F	JG
14-0810	Halictidae	*Lasioglossum tegulare*	7/17/14	F	JG
13-0116	Halictidae	*Lasioglossum timothyi*	5/21/13	F	JG
14-1000	Halictidae	*Lasioglossum trigeminum*	8/20/14	F	JG
13-0349	Halictidae	*Lasioglossum versans*	5/29/13	F	JG
14-0283	Halictidae	*Lasioglossum versatum*	5/21/14	F	JG
14-0335	Halictidae	*Lasioglossum vierecki*	5/25/14	F	EM
13-0255	Halictidae	*Lasioglossum viridatum*	5/30/13	F	JG
14-0388	Halictidae	*Lasioglossum zephyrum*	5/24/14	F	JG

Table E (cont'd)

14-0618	Halictidae	*Lasioglossum zonulum*	5/30/14	F	JG
14-1401	Megachilidae	*Megachile brevis*	8/18/14	F	EM
14-0923	Megachilidae	*Megachile centucularis*	7/21/14	F	JG
14-0924	Megachilidae	*Megachile gemula*	8/15/14	M	JG
14-0732	Megachilidae	*Megachile latimanus*	6/25/14	F	JG
14-0962	Megachilidae	*Megachile mendica*	8/5/14	F	JG
14-0918	Megachilidae	*Megachile petulans*	7/21/14	M	JG
14-0872	Megachilidae	*Megachile pugnata*	7/30/14	M	JG
14-0739	Megachilidae	*Megachile texana*	6/25/14	M	JG
14-1422	Apidae	*Melissodes agilis*	8/14/14	F	JG
14-0968	Apidae	*Melissodes bimaculata*	8/5/14	F	JG
13-058	Apidae	*Melissodes communis*	7/17/13	F	EM
14-0974	Apidae	*Melissodes desponsa*	8/5/14	M	JG
14-1045	Apidae	*Melissodes druriella*	9/9/14	F	JG
13-046	Apidae	*Melissodes subillata*	7/1/13	F	JG
14-0687	Apidae	*Nomada articulata*	6/16/14	F	JG
14-0043	Apidae	*Nomada denticulata*	5/29/14	F	JG
13-008	Apidae	*Nomada illinoensis*	6/19/13	M	JG
14-1466	Apidae	*Nomada vegana*	7/8/14	M	JG
14-0408	Megachilidae	*Osmia atriventris*	5/20/04	F	EM
14-0639	Megachilidae	*Osmia bucephala*	5/26/14	F	EM
14-0417	Megachilidae	*Osmia caerulescens?*	5/20/14	M	EM
14-1429	Megachilidae	*Osmia distincta*	6/24/14	F	JG
14-0240	Megachilidae	*Osmia georgica*	5/29/14	M	EM
14-0634	Megachilidae	*Osmia pumila*	5/25/14	F	EM
14-0699	Andrenidae	*Perdita halictoides*	6/16/14	F	JG
14-1407	Andrenidae	*Perdita octomaculata*	8/18/14	F	JG
14-1033	Andrenidae	*Pseudopanurgus nebrascensis*	9/8/14	F	JG
14-0809	Halictidae	*Sphecodes cf. coronus*	7/7/14	M	JG
14-0334	Halictidae	*Sphecodes cressonii*	5/25/14	F	JG
13-009	Halictidae	*Sphecodes davisii*	6/19/13	F	JG
14-0219	Halictidae	*Sphecodes dichrous*	5/20/14	F	JG
13-021	Halictidae	*Sphecodes mandicularis*	7/19/13	F	JG
13-0410	Apidae	*Xylocopa virginica*	5/21/13	F	EM

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