

**SUPPLEMENTING EAST TENNESSEE LANDSCAPES FOR
POLLINATORS WITH NATIVE PERENNIALS**

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DEDICATION

To everyone that helped me along this windy road, this is for you.

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ABSTRACT

Tennessee, home to the Great Smoky Mountains, is a biodiversity hotspot for many plant and animal species, yet it receives relatively few conservation dollars (Jenkins et al., 2015). Despite East Tennessee's biodiversity hotspot status, little is known about the abundance or diversity of insect pollinators. In order to both estimate pollinator communities in East Tennessee and pollinator forage preferences for native Tennessee plants, we established four plots comprised of three plant families across five common land use types (Urban, Semi-natural, Cattle Pasture, Mixed Use Agriculture, and Organic Agriculture). Each plot represented a plant family, while the one plot included a combination of all three plant families.

Over two field seasons, we collected nearly 7,300 insect specimens with a total sampling effort of 101.3 hours. A majority of the specimens we collected were wild bees, over 4,500 individuals from 99 species. The plant species with the highest visitation rate was *Pycnanthemum muticum*. The treatment with the highest visitation rate was our Mixed treatment. In other words, the most diverse plots, at the family level, were the most attractive to pollinators. We were also able to characterize the pollinator community in the region, thus providing species-level data for bees found across three eastern Tennessee counties. We expanded our findings to explore potential landscape level effects on pollinator communities. Through landscape analysis, we did not find any relationships between species richness or abundance and land cover

classification. However, these findings may be largely due to the relative heterogeneity at each of the study sites. We found the highest abundances and species richness in our agriculture study sites, which offers substantial support to the incorporation of native perennial plantings in agricultural systems. We found the Organic Agriculture block to have the greatest bee species abundance and bee species richness.

Ultimately, as the first study in East Tennessee to document pollinator forage preferences for native perennial plantings across multiple land use types, we found strong support for the integration of native perennial plantings to support pollinator conservation across the region.

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INTRODUCTION

Many agricultural crops depend on insect pollination (Klein et al., 2007) and the demand for these insect-pollinated crop plants is increasing at a faster rate than wind-pollinated plants (Aizen et al., 2008). In East Tennessee, there are over 50 small horticultural farms that mainly grow pollinator-dependent plants (*Nourish Knoxville, personal communication*). Although land managers often rent honey bee hives for pollination services, wild bees may be able to provide sufficient pollination services (Russo et al., 2017) and have been identified as more efficient pollinators for some crops (Garibaldi et al., 2013; Kennedy et al., 2013).

Despite our reliance on insect pollinators, increased agricultural intensification and urbanization have led to decreases in natural areas, which previously provided crucial habitat for a range of pollinators (Kremen et al., 2002). Moreover, as farm ownership has transitioned from many small farms to fewer larger farms, land use has become more specialized to one type of management, e.g. row crop or pasture (Benton et al., 2003). Increased acreage and the removal of nonproductive lands and field boundaries allows for large land parcels to have identical agriculture use (Robinson & Sutherland, 2002). At the farm scale, before the introduction of synthetic weed and pest controls, mixed crop varieties and tillage were common control measures. However, common agricultural practices have shifted toward maximizing yield through modern machinery, leading to simplified crop rotations and overall reduced crop variety (Robinson & Sutherland, 2002) promoting spatial and temporal uniformity (Benton et al., 2003).

Bees require a variety of floral resources and nesting substrates, as outlined in Chapter 1, adding to the complexity of restoring or supplementing degraded landscapes for pollinator conservation. However, establishing native plantings in agricultural landscapes has been shown to increase pollinator diversity and abundance (Bennett & Isaacs, 2014; Garibaldi et al., 2014; Isaacs et al., 2009; Morandin et al., 2014; Morandin & Kremen, 2013a, 2013b; Tuell et al., 2008; Williams et al., 2015). Although these efforts have largely been tested in agricultural landscapes, studies have also researched the role of native plants in urban systems and found forage preferences for native over non-native plants in urban gardens (Baldock et al., 2019).

Following these findings, we aimed to characterize the pollinator community and the role of native perennial plantings as forage resources in East Tennessee (Chapter 2). We collected flower-visiting insects on 18 selected plant species from three plant families for two field seasons, 2019 and 2020. The goal of our study was to both describe the bee community in the region and provide local planting recommendations for local pollinator conservation initiatives.

Bees vary substantially in body size and are capable of foraging at a wide range of distances; thus, it is vital to analyze the effects of the greater landscape. Increased agriculture in the landscape has been found to negatively affect bee species richness and abundance (Connelly et al., 2015; Nicholson et al., 2017; Russo et al., 2015; Watson et al., 2011), while increased natural areas in the landscape have been found to have a positive relationship with bee species richness and abundance (Cusser et al., 2016; Greenleaf & Kremen, 2006; Klein et al., 2012; McKechnie et al., 2017; Nicholson

et al., 2017; Smith et al., 2013; Watson et al., 2011). Given the established effects of agricultural intensification and natural areas in the surrounding landscape, we investigated the potential impacts of land cover in Chapter 3.

CHAPTER I

AN OVERVIEW OF BEE BIOLOGY AND FLORAL RESOURCE USE

Abstract

This thesis addresses the role of floral resource supplementation and land-use in supporting wild pollinators, with a special focus on bee pollinators. As such, within this literature review, we provide a background on bee biology and ecology, as well as an overview of the effects of land-use on bee community composition.

Bee biology

Bees are functionally classified as solitary, parasitic, social, and social parasites (Danforth et al., 2019). Social bees include the well-studied Eastern bumble bee (*Bombus impatiens*) or European honey bee (*Apis mellifera*). However, much less is known about solitary bees that make their nests in a variety of substrates or cavities above ground. Defined by adult female solitary bees construct and provision their nests, either through digging or identifying available cavities (Michener, 2007). Females provide the necessary pollen requirements for male or female eggs to mature and emerge independently the following season. Males generally emerge first, followed by the females. Adult males are strictly nectarivores, but may be found with free or released pollen attached to their hairs. Parasitic bees also do not consume or collect pollen but rely solely on nectar in adulthood (Michener, 2007).

Foraging

Short-lived flowers provide both nectar and pollen throughout the entirety of their lives, while longer-lived flowers offer pollen and nectar for a short time at first bloom, but these resources then vary throughout the remaining bloom period (Maloof & Inouye, 2000). Other flowers will present nectar first, followed by pollen, or the reverse. The

variation in floral resource presentation may play a role in which bees visit these flowers because many bees will take both pollen and nectar from the same flower, if available (Michener, 2007). Bees can “learn” how to handle a floral type and exhibit floral constancy, allowing for increased forage efficiency, or increased collection of more pollen grains per unit time (Michener, 2007).

Specialization in flowers refers to strong directional selection on traits related to pollination, such as floral tubes or “unusual rewards” that restrict the type of visitor that can access floral rewards. Alternatively, generalization in flowers describes an open floral design with rewards that are attractive and accessible to most flower visitors (Minckley & Roulston, 2006). However, in order to determine specialization, there must be observation and experimentation to characterize pollinator visitation to flowers with limited visitors (Minckley & Roulston, 2006).

Short-lived solitary bees are limited to flowering plants during their emergence period. These bees have a limited window of activity and, as univoltine organisms (species that only have one brood per year) they may be able to fulfill their floral resource requirement utilizing one host plant (Minckley1994; Minckley & Roulston, 2006).

The mutualistic relationships between plants and their pollinators also affect the abundance of floral resources and the population size of both interacting organisms. Larsson and Franzén (2007) found a linear relationship between the critically endangered endemic European mining bee species, *Andrena hattorfiana*, and its host plant *Knautia arvensis* (*Caprifoliaceae*) (Larsson & Franzén, 2007). Declines in *K.*

arvensis populations across Europe are thought to be the driver of *A. hattorfiana* decline.

Floral resources

Pollen serves as a food source for numerous adult insects beyond bees (Roulston et al., 2000) such as Collembola (Scott & Stojanovich, 1963), thrips (Thysanoptera) (Kirk, 1984), beetles (Coleoptera) (Mann & Crowson, 1981), flies (Diptera) particularly Syrphidae (Haslett, 1983) and midges (Downes, 1955), butterflies (Ehrlich & Raven, 1964), and moths (Hahn & Brühl, 2016). Bees and Masarinae wasps, however, are the only groups that actively collect pollen for their larvae (Danforth et al., 2019). Very few non-bee insects, such as wasps in the subfamily Masarinae, family *Vespidae*, and one documented species of *Sphecidae* wasp, collect and provide their larvae with pollen (Danforth et al., 2019; Minckley & Roulston, 2006).

Bees collect pollen from a range of flowering plants and, much like the variation of sugar concentration in nectar, pollen protein levels also vary between plants (Roulston et al., 2000; Vaudo et al., 2020). Crude protein levels in pollen may be greater than 60% or as low as 2.5% (Buchmann, 1986), but protein is not the only important nutrient found in pollen. Other highly nutritious compounds such as amino acids, lipids, sterols, and starches were also found in pollen (Danforth et al., 2019).

Pollen quality and quantity can determine body size and sex ratio in solitary bees. The amount of pollen consumed by a bee larva determines intraspecific body size (Jauker et al., 2016; Roulston & Cane, 2002). Smaller-bodied female bees have lower provisioning abilities, thus producing smaller females (Seidelmann et al., 2010).

Additionally, these smaller female bees produce more male-biased brood, as male larvae are smaller and require less pollen (Danforth et al., 2019). As males provide only reproductive resources, these heavily male-skewed broods can reduce the viability of a population, further highlighting the importance of reliable and adequate pollen resources.

Nicolson et al. (2007) describe nectar as one of the most abundant foods available globally, largely comprised of fructose, glucose, and sucrose (Nicolson et al., 2007). Nectar production in flowers is reflective of the coevolutionary dynamics between plants and pollinators (Burger, 1981). Researchers have documented relationships between floral biomass and nectar volume secretion (Galletto & Bernardello, 2004; Nicolson et al., 2007; Opler et al., 1983; Szabo, 1984). In other words, larger flowers have larger nectaries that produce larger quantities of nectar.

Nectar is generally viewed as a reward or incentive for pollinators to visit flowers and purposefully or inadvertently carry plant pollen. Other behaviors such as frequency of visitation, number of flowers visited, time spent collecting nectar per flower, and even movement entering, probing, or exiting the flower are also impacted by a plant's nectar rewards (Rathcke, 1992). These pollinator behaviors then determine the pollen deposition, removal and transfer, transport, and reproductive success of the plant (Rathcke, 1992). Overall, increased nectar rewards should encourage greater pollinator visitation, thus positively impacting a plant's reproductive success (Heil, 2011; Neiland & Wilcock, 1998).

The nectaries of a flower are responsible for nectar secretion. Nectaries can be found almost anywhere in a flower, or another part of the plant (Pacini & Nepi, 1970). The sugary liquid provides carbohydrates crucial to the dietary needs of pollinators, but nectar also includes other compounds, such as water and amino acids (Baker & Baker, 1973; Gardener & Gillman, 2002). Some pollinators, such as honey bees and flies, can detect and prefer experimentally manipulated nectar solutions with varying amino acid concentrations (Kim & Smith 2000; Potter & Bertin 1988).

However, for insect pollinators, this crucial liquid substance is largely needed to support adult insects. In eusocial insects, such as honey bees or bumble bees, larvae depend on a nectar-pollen mixture. Alternatively, solitary bees require nectar to maintain stamina during multiple foraging trips for pollen or nesting resources or even the energy requirement for hovering. For lepidopterans, in their adult form, nectar is typically the only floral resource they consume.

Plants visited by pollinators with high energy requirements (e.g. hummingbirds, Sphingidae, bats) exhibit higher nectar sugar concentrations and nectar volume as compared to flowers visited by smaller pollinators with relatively lower energy requirements like flies and bees (Cruden et al., 1983). Generally, flowers visited by diurnal pollinators produce and present nectar during the day, while plants that require nocturnal pollinators produce nectar at night (Nepi & Pacini, 2007).

Specialization in Lamiaceae

Some flowers in the Lamiaceae family have anthers located deep within an elongated corolla (Danforth et al., 2019). The location of the anthers causes bees and

other visitors to insert their heads deep into the corolla and vibrate their flight muscles to extract its pollen. This leads to pollen deposition on the face, head, or dorsum, but due to varying modifications of facial hairs (setae), Lamiaceae specialist bees can use their forelegs to groom the pollen from their face to their scopae (Danforth et al. 2019). Danforth et al. (2019), describe this behavior as “nototribic” and the specific facial modifications exist in all of the bee families of North America.

Specialization in Fabaceae

Plants in the Fabaceae family have complex floral phenotypes handled by behaviorally specialized bees, such as flowers with keels, poricidal anthers, or primarily pollen-rewarding flowers, and exhibit high P:L ratios (Vaudo et al., 2020). This specialized behavior has been described as “buzz pollination”. Buchmann (1985) described buzz pollination as vibration caused by a bee’s flight muscles to release pollen from a plant’s anthers and the subsequent buzzing sound led to the name buzz pollination/sonication. Female bees seize the flower’s anther column with their legs, then curl the metasoma below the flower and begin to vibrate anywhere from a millisecond to several seconds. Although the bee’s flight muscles allow for this vibration, the wings remain closed (Danforth et al., 2019). Various members from all seven bee families were reported to be capable of buzz pollination (Cardinal et al., 2018). Many genera from Apidae, Colletidae, and Halictidae demonstrate floral sonication, while few Andrenidae, Megachilidae, or Melittidae do. Non-buzz pollinated Fabaceae serve as the preferred host for Masarine wasps, Andrenidae, and Megachilidae (Danforth et al., 2019). Furthermore, the pollen of buzz-pollinated flowers is protein-rich (Danforth et al.,

2019; Roulston et al., 2000). These pollen grains are small, which also showed some association to increased protein content (Roulston et al., 2000).

Specialization in Asteraceae

The flowers of the Asteraceae family generally have compact inflorescences or flower heads. These flower heads remain open for longer periods, thus supporting multiple species with varying emergences (Neff & Simpson, 1990). Although Asteraceae have an attractive floral display, there is evidence that Asteraceae pollen contains secondary defense chemistry (Danforth et al., 2019; Mueller & Kuhlmann, 2008). This means their pollen is toxic or provides very low nutritional value for generalist bees. Despite the observed toxicity, generalist bees regularly mix different pollen types, which may allow them to consume some toxic pollen (Danforth et al., 2019).

Other resources collected by bees

Genera from the bee families Apidae and Megachilidae often forage for plant material to serve as a nest lining. Some materials include leaves, resins, trichomes, or floral oils (Danforth et al., 2019). These plant materials increase bee fitness by protecting developing offspring. For example, resin serves as brood nest construction material providing waterproof, antibiotic, and hardening properties.

Leaves are also used in nest construction, mainly by *Megachile* and *Osmiini*. Leaves may be transferred whole, cut, or even masticated into a paste. Unlike unchewed leaves, leaf paste forms a wall between brood cells or as a wall at either end of the nest. Species in the *Megachilidae* may also use flower petals (Bohart & Youssef,

1972; Michener, 1953) or even plastic bags (MacIvor & Moore, 2013) to line their nest cells.

CHAPTER II

**USING NATIVE PERENNIALS TO CHARACTERIZE POLLINATOR
COMMUNITIES IN EAST TENNESSEE**

Abstract

Native perennial plantings are an example of a popular, multidisciplinary approach to pollinator conservation. These plants can provide habitat, pollen, and nectar to native and non-native insects, thereby promoting their abundance and diversity. Because little is known about insect pollinators in East Tennessee or their forage preferences, few guidelines are available for such conservation plantings. To better understand these plant-pollinator interactions, we established long-term communities of native Tennessee plants representing three families: Asteraceae, Fabaceae, and Lamiaceae. At five research sites, we planted four research plots. Each of the three plant families was represented by a plot with six species, and we included a fourth plot with two species of each of the three families (Mixed plot). Throughout each flowering period, we evaluated the relative attractiveness of each species and estimated pollinator visitation rates to their inflorescences. Over two years, we collected nearly 7,300 total insect specimens; more than 4,500 were wild bees representing 99 species. We found the most attractive plant, in terms of visitation rate (number of floral visitors per unit floral area per unit time), to be *Pycnanthemum muticum*. Among the different plot types, the Mixed plot (containing two species of each plant family) received the highest average visitation rate. Our results demonstrate that native plants can be utilized for pollinator conservation across multiple land use types.

Introduction

Over time, land use has become more specialized into one management type, for example, row crop or pasture (Benton et al., 2003). As farms have become larger, land use diversity has decreased, and the landscape has become more homogenized, sometimes including large acreages of monocultures (Robinson & Sutherland, 2002). Before the introduction of synthetic weed and pest controls, mixed crop varieties and tillage were common control measures, but modern machinery and attempts to maximize yield and efficiency have led to simplified crop rotations and reduced crop diversity (Robinson & Sutherland, 2002). Overall, modern agricultural practices promote spatial and temporal uniformity (Benton et al., 2003). Both the duration of land use in agricultural production, as well as the spatial extent of the intensive agricultural land use have increased over time (Benton et al., 2003). These historical shifts have led to biodiversity loss and biotic homogenization across the globe (Deguines et al., 2014; Freitas et al., 2009; Kremen et al., 2002; Tscharntke et al., 2005). For example, the conversion of landscapes to agricultural use leads to habitat fragmentation that impacts plant species richness across longer spatial and temporal scales, and habitat loss that has more immediate and localized effects (Alofs et al., 2014). Because of this, recent conservation efforts have been directed at diversifying and supplementing agricultural landscapes with communities of native plant species, with demonstrable increases in pollinator abundance in many cases (Schulte et al., 2017).

There are many threats to pollinators, but the most critical threats are those that impact habitat quality or extent (Alofs et al., 2014; Carvell et al., 2006). Native

perennials can provide vital resources, such as pollen and nectar, and nesting habitats for native and non-native insects (Danforth et al., 2019; Isaacs et al., 2009). Native plants are also ideal for establishing conservation habitat for pollinating insects because they exhibit adaptations that allow them to thrive within their native regions, including resilience to environmental conditions such as seasonal variation, soil conditions, or pest pressures.

Although pollinators may not exclusively rely on native plants to fulfill nectar and pollen resource requirements, bee abundance and richness are higher on native plants, compared to non-natives (Morandin & Kremen, 2013). Some bee species are highly specialized on native plant hosts and females will forage extended distances to collect pollen exclusively from native plants. For example, for *Osmia lignaria*, female reproductive success (and the number of offspring) correlated with distance to seminatural habitat where preferred native plants were found (Williams & Kremen 2007). These findings highlight the importance of conservation initiatives that specifically promote native plantings. Strategic placement of native perennial plantings can also improve multiple ecosystem services including water quality and soil health (Kremen & Miles, 2012; Schulte et al., 2017). Plant diversity within these conservation schemes allows bees to choose from a variety of pollen and nectar resources with varying nutrient levels (Vaudo et al., 2015). Diversity of floral resources provided by native perennials also allows for extended flowering periods, as opposed to limited bloom times of annual crop flowers (Tuell et al., 2008).

We established plots of 18 species of native perennials of three plant families, with high functional diversity. We used these plantings to characterize pollinator abundance, species richness, and community composition. Abundance is important as common species may be the drivers of ecosystem services, as compared to species richness (Winfree et al., 2015). However, species richness provides a key component for biodiversity metrics (Hillebrand et al., 2018) and the diversity of pollinating insects has been repeatedly linked to crop yield and quality (Garibaldi et al., 2013; MacInnis & Forrest, 2019).

Following similar studies in the United States and Europe (Frankie et al., 2009; Hanley et al., 2014; Isaacs et al., 2009; Morandin & Kremen, 2013a; Tuell et al., 2008; Williams et al., 2015), we developed the following hypotheses. First, we expected most of our insect collections to be comprised of wild bees (Frankie et al., 2009; Hanley et al., 2014; Isaacs et al., 2009; Morandin & Kremen, 2013a; Tuell et al., 2008).

Secondly, we expected our plants to be more attractive in year two, as perennials will be larger and more robust in their second year of establishment (Ehrlén & Lehtilä, 2002), thus increasing pollinator abundance in 2020 collections.

Thirdly, as plants within the Asteraceae have been found to be the most attractive to pollinators due to their large floral displays (Tuell et al., 2008; Williams et al., 2015), we hypothesized the Asteraceae plot to be the most attractive plot overall.

To our knowledge, this is the first study in East Tennessee specifically looking into the role of native perennial plants and their insect pollinators. One previous study assessed pollinators in the region (Wilson et al., 2016), but focused on insect visitors to

horticultural crop flowers and excluded pollinator forage preferences and an assessment of the populations of Tennessee bees in multiple land use types.

Objectives

- 1) To quantify pollinator abundance and richness in East Tennessee
- 2) To determine native plant forage preferences for native and non-native pollinating insects
- 3) To provide evidence-based native planting recommendations for pollinator conservation in Tennessee

Methods

All research sites were located on the University of Tennessee properties in East Tennessee (Anderson, Cumberland, and Knox counties). In 2019, we began with 4 sites 1) Urban Gardens, 2) Semi-natural, 3) Cattle Pasture, and 4) Mixed Use Agriculture. In 2020, we expanded to include a fifth site representing 5) Organic Agriculture. Each of the sites represents a block in the experimental design, comprising a full set of experimental treatments, here species composition.

At each site, we established four plots, one containing six species of each plant family (Asteraceae, Fabaceae, and Lamiaceae) and one featuring two species of each family (Mixed family plot). These plots were approximately 50 meters apart. Within each plot, we planted four individuals each of six native perennial species, such that the composition of the plots in each site was fixed (Fig. 1, all figures and tables located in the appendix). As each block served as a replicate of the experimental treatments (four plots), there were five replicates for the study in 2020 and four replicates in 2019.

Plot Setup

For each of the replicated 3m x 2m plots, we eliminated grass through hand-weeding and hoeing. Additionally, all sites except the Organic Agriculture site received one application of glyphosate three weeks before planting. We distributed compost and commercially available topsoil throughout each plot before planting the selected native perennials.

All plants were purchased as plugs from the same nursery and placed approximately 50cm apart within the plots. After planting, we added a soil amendment (e.g. compost) and a layer of commercially available mulch to each plot for moisture retention and weed suppression. The plants were hand-watered regularly during dry periods, and all plots within a site received the same amount of water. The plots were enclosed with chicken wire fencing to deter herbivores.

Selected Plant Families and Species

We selected the plant families based on specific qualities attractive to pollinators. Asteraceae have an attractive, open flowering display and extended flowering periods (Isaacs et al., 2009). Flowering plants in the Fabaceae family contain high protein pollen (Danforth et al., 2019; Pywell et al., 2005; Vaudo et al., 2020) and Lamiaceae flowers produce significant quantities of nectar (Danforth et al., 2019). We selected our native perennial study species (Table 1) based on the Lady Bird Johnson Wildflower Center database, the Southeast Region Pollinator Plants List published by The Xerces Society, nutrient content (Vaudo et al., 2020), and plant availability from a local nursery.

Due to variation in pollen protein content among plant species, supplementing habitat with an array of plant species can support the nutritional needs of a diverse community of pollinators (see Chapter 1). The reported pollen protein to lipid ratio of our selected plant families by Vaudo et al., (2020) is as follows: Asteraceae 1.06 ± 0.1 ug/mg, Lamiaceae ~ 1.2 ug/mg, and Fabaceae 3.8 ± 0.5 ug/mg.

From each of the three plant families, we chose six representative species (Table 1). The six Asteraceae species were: *Helianthus occidentalis*, *Coreopsis lanceolata*, *Eurybia saxicastelli*, *Stokesia laevis*, *Helianthus hirsutus*, and *Verbesina occidentalis*. The six Lamiaceae species were: *Conradina verticillata*, *Pycnanthemum muticum*, *Lycopus virginicus*, *Physostegia leptophylla*, *Blephilia subnuda*, and *Collinsonia canadensis*. The six Fabaceae species were *Amorpha herbacea*, *Senna marilandica*, *Baptisia albescens*, *Lespedeza hirta*, *Baptisia tinctoria*, and *Thermopsis villosa*. The Mixed family plot contained: *H. occidentalis*, *S. marilandica*, *C. verticillata*, *B. albescens*, *C. lanceolata*, and *P. muticum*. The plants in the Mixed plot treatment were selected from the available plant species based on their commercial availability.

Data Collection

Weekly visits were made to each site to conduct pollinator collections. For each pollinator collection, we recorded the date, time, site location, plot name, cloud cover, sun, temperature at the time of collection, number of inflorescences per plant, and the collector. We conducted pollinator collections between the hours of 0900h-1600h as this is when most pollinators are active (Danforth et al., 2019). We did not conduct collections during times of rain or excessive cloud cover.

Pollinator collections began each season (2019/2020) as the first plants began to bloom. We monitored all individuals of a given plant species within a plot for 5 minutes and collected any insects seen touching the reproductive parts of the flowers using a handheld insect-collecting vacuum. We repeated the same procedure for each plant species until all flowering plant species within a plot were sampled for five minutes. The specimens were stored in a freezer and later pinned, labeled, and sorted taxonomically. We used voucher specimens to identify the specimens and our identifications were verified by a taxonomist (Sam Droege, USGS).

We calculated floral display as the number of open inflorescences in a given collection event multiplied by the average size of the inflorescence (length and width) for each plant species. We calculated the average size of the inflorescences by randomly selecting 10-20 different inflorescences per plant species, and measuring them to the nearest tenth of a millimeter with a digital caliper (Russo et al., 2019).

Data Analysis

Floral display is a strong determinant of pollinator visitation (Russo et al., 2019, 2020; Williams et al., 2015). We created a linear model for pollinator abundance with floral display as the fixed effect. We log transformed both floral display and abundance to normalize their distributions. We also created an additional linear model for abundance that included floral display (log transformed) as a fixed effect and block as a random effect using the sjPlot package in R (Lüdecke, 2021). We then calculated the conditional and marginal coefficient using the r.squaredGLMM function in R from the MuMIn package (Barton, 2018; Russo et al., 2019).

To better determine the relative attractiveness of our individual selected plant species, we also calculated the visitation rate to their flowers. The visitation rate of floral visitors acts as a proxy for pollinator forage preferences, as patterns have been documented between visitation and floral area (Rowe et al., 2020). We calculated the visitation rate using the number of total insects collected during a 5-minute sample, then divided this number by the size of the floral display during the sample for each plant species. We also calculated the visitation rate to these flowers by bee specimens only.

In addition to comparing visitation rate among the plant species, we compared the average visitation rate across the four treatments (Asteraceae, Fabaceae, Lamiaceae, and Mixed).

Results

Pollinator Collections

For two field seasons combined (2019/2020), we collected 7,294 insects during a total of 101.33 hours sampling effort. Most (5,108, 70%) of our collected specimens were bees (Table 2) and 2,186 (30%) were non-bee flower-visiting insects (Table 3). We collected a total of 99 different bee species and 53 non-bee families. Additionally, we collected 7 previously unreported bee species in Tennessee. The following species were considered new species records: *Andrena placata*, *Ceratina cockerelli*, *Heriades leavitti/variolosa*, *Lasioglossum lionotum*, *Lasioglossum pruinsum*, *Lasioglossum rozeni*, and *Sphecodes heraclei* (Sam Droege, USGS). We compared the average number of insects collected per block between 2019 and 2020 collection years, and ultimately found slightly lower average abundances for our 2020 collections (Fig. 2).

Total Bees Collected

Over our two-year study, we collected 4,563 wild bees and 545 honey bees (*Apis mellifera*). These individuals represent 28 different bee genera, with a majority from *Lasioglossum*, *Halictus*, *Apis*, *Augochlorella*, *Ceratina*, and *Bombus* (Table 2).

2019 Collections

In year 1 (2019), we conducted a pilot study on the first four sites. We collected 1,806 flower visiting insects, with a total sampling effort of 27.17 hours from late June to mid-October. Roughly three quarters of the specimens were bees, primarily (~88%) wild bees, representing 55 species. The remaining bee specimens were honey bees (*Apis mellifera*). We sorted all non-bees, approximately 467 individuals, into 6 orders: Coleoptera, Hemiptera, Diptera, Lepidoptera, Hymenoptera (non-bee), and Mecoptera. These orders were further identified to 34 families (Table 4).

2020 Collections

In year 2 (2020), we conducted the first full season of pollinator collections. The pollinator collections began in March and ended in October 2020 with a total sampling effort of 74.17 hours. We collected 5,488 total specimens, representing five insect orders and 54 non-bee insect families. Most of these specimens were bees: 3,380 wild bees of 87 species and 389 *A. mellifera*. In year 2, we collected 41 bee species that were not collected in year 1. Only two previously uncollected species were collected at Block 5 (*Andrena near simplex* and *Melissodes sp. A*). The remaining 39 species were collected at blocks that were in their second year of growth. We sorted all non-bees, approximately 467 individuals, representing 6 orders: Coleoptera, Hemiptera, Diptera,

Lepidoptera, Hymenoptera (non-bee), and Mecoptera. These 6 orders were further identified to 44 families (Table 5).

Floral Phenology

In both field seasons, and across all sites, 17 of 18 plant species flowered. All species in the Asteraceae and Lamiaceae families flowered. However, none of the individuals of *Thermopsis villosa* in the Fabaceae family flowered at any site.

The plants bloomed in the following order: *Conradina verticillata*, *Coreopsis lanceolata*, *Blephilia subnuda*, *Baptisia albescens*, *Stokesia laevis*, *Physostegia leptophylla*, *Pycnanthemum muticum*, *Senna marilandica*, *Amorpha herbacea*, *Baptisia tinctoria*, *Helianthus hirsutus*, *Helianthus occidentalis*, *Collinsonia canadensis*, *Eurybia saxicastelli*, *Lespedeza hirta*, *Lycopus virginicus*, and *Verbesina occidentalis* (Fig. 3). Multiple plant species flowered at the same time in most weeks, with the exception of weeks 1 and 2. At week 22, we observed the most plants in flower (15 different species). There was no discernable pattern in bloom timing across plant families. Some plant species were still flowering at the end of the field season (e.g., *Verbesina occidentalis*).

Floral Display

The plant species varied in their average floral display (Fig. 4). Asteraceae species had larger floral displays compared to Fabaceae and Lamiaceae. *Helianthus hirsutus*, for example, had a floral display of $13246\text{mm}^2 \pm 2160\text{mm}^2$ on average per collection, while the Fabaceae species with the largest floral display, *Senna marilandica*, had a floral display of $1484\text{ mm}^2 \pm 291\text{ mm}^2$ on average per collection.

There was a significant positive linear relationship between the log-transformed floral display and insect abundance (effect size = 0.33, $N = 5$, $P < 0.001$, Fig. 5). The linear model had a marginal R^2 value of 0.35 and a conditional R^2 value of 0.38 (Fig. 6).

Visitation Rate

Among the plant species, *Pycnanthemum muticum* had the highest visitation rate of any plant species in 2020 for total insects (Figure 7a), and had the second highest visitation rate when we looked exclusively at bee visitors (Fig. 7b). The plant with the average highest bee visitation rate was *Lespedeza hirta* (Fig. 7b). At the treatment level, the Mixed family treatment had the highest, and the Asteraceae treatment the lowest, average visitation rate for both study years (Fig. 8).

Discussion

Overall, we found our forage preference hypothesis was not supported. In agreement with previous research studies, we found floral display to be a significant predictor for abundance (Russo et al., 2019, 2020; Williams et al., 2015). However, unlike similar studies (Tuell et al., 2008; Williams et al., 2015), we did not find our Asteraceae plot to be the most attractive, nor did plants in the Asteraceae family have the highest visitation rates. Instead, the Mixed family treatment had the highest average visitation rate for both study years, while the Asteraceae had the lowest average visitation rate. It is interesting to note that plants in the Lamiaceae family had higher visitation rates even though the Asteraceae family had larger floral displays. As the Mixed treatment included all three plant families, this suggests that the presence of the

other two families either led to increases in the visitation rate to the Asteraceae in the Mixed plots, or the Lamiaceae and Fabaceae were more attractive in the Mixed plots.

In the second year, we found many bee species that were not collected in the first year. Only two of them were collected in the new block, while the rest were new to sites we had sampled in the first year. We may have found so many new bee species in the second year of the study due to various factors; for example, we had a lower sampling effort in the first year of the study and fewer plants bloomed in their first year. It is also possible that plants were more attractive in their second year, attracting more pollinator species, rather than a larger abundance as we expected.

Conclusion

Our data indicate that native plants provide vital nectar and pollen resources to a wide array of flower visiting insects. Most of the specimens collected were wild bees, thus furthering the much-needed empirical support that native plants can support wild bees, specifically in East Tennessee. Our results provide a first glance at both the pollinator abundance and diversity in East Tennessee, and allow us to compare the forage preferences of pollinators among native plants. The continuous bloom offered by our selected plants can provide forage resources to support increased flower-visiting insect species richness (Williams et al., 2015), thus highlighting the importance of incorporating multiple plant species for pollinator conservation efforts across land use types. We provided baseline data for not only pollinator species in the region, but also plant species that can be incorporated for native plantings. We suggest further research is required to better understand the visitation rate to each plant species, for all

pollinating insects. Additionally, it would be interesting to investigate the nesting resources provided by habitat provisioning in native pollinator plots throughout the year.

CHAPTER III

EFFECT OF LAND COVER ON POLLINATOR COMMUNITIES

Abstract

Globally, there is substantial concern regarding the contribution of land-use change and anthropogenic disturbance to declines in populations of beneficial insects. These concerns led to increased interest in biodiversity conservation, including providing supplemental habitat for these insects, especially in degraded landscapes. Promoting conservation efforts within landscapes requires an understanding of the spatial configuration of land-use types and landscape heterogeneity. As pollinators are mobile organisms, spatial analysis can provide additional context to many pollinator study findings. Using data from our two-year experiment, we calculated the average pollinator abundance and species diversity at each site. We then analyzed the surrounding landscape around each of our research sites using ArcGIS and the National Land Cover Database to determine if there were any relationships between the observed abundance or species diversity at our research sites and the surrounding landscapes. Overall, we found the highest abundance and species richness in the agricultural sites, but we could not identify a significant relationship between land cover and species diversity or abundance. However, as we increased the spatial scale, we found increased landscape heterogeneity at each research site, which may play a significant role in pollinator abundance and richness, but was unexplored in this study, thus warranting further investigation.

Introduction

Agriculture is a multibillion-dollar industry in Tennessee (NASS USDA 2018), but the influence of this agricultural land-use on current populations of local, wild pollinators has not been adequately assessed in the state. Few studies have looked at pollinators in eastern Tennessee and, to our knowledge, none have assessed current populations and potential effects of land use.

Landscape-level factors such as habitat fragmentation and habitat loss have been identified as drivers of pollinator decline (Cunningham, 2000). Highly fragmented landscapes are unable to support pollinator populations, and the amount of remaining habitat may determine species survival (Boscolo & Metzger, 2011; Ferreira et al., 2015). Habitat loss can have varying effects according to scale. Regional level habitat loss not only causes reduced habitat availability, but may also increase patch isolation, limiting population sizes (Ferreira et al., 2015). The impacts of local habitat loss can lead to reduced forage resources, resulting in increasing forage distances, which may impact different types of bees in different ways. In European grasslands, Jauker et al., (2013) found that small bodied and solitary bees were particularly vulnerable, as compared to other body sizes of bees, while other studies found larger, social bees were more vulnerable (Benjamin et al., 2014; Bommarco et al., 2010), indicating a strong negative effect of field-scale agricultural intensity. However, both (Benjamin et al., 2014; Jauker et al., 2013) found an effect of large scale agricultural intensification of 1500m, which negatively impacted small bees. At the family level, bee genera within Halictidae, were found to be most impacted by habitat loss (Benjamin et al., 2014; Jauker et al., 2013).

Mixed sociality in the Halictidae family may be an important distinction at the genus level. Certain genera may have better resource acquisition in highly fragmented landscapes through sociality (Bommarco et al., 2010), but no data is available to compare individual species populations or nests to determine which groups outperform others. Finally, kleptoparasitic bees were not found to be impacted by reduced habitat or homogenous landscapes, as compared to non-parasitic species (Jauker et al., 2013). The stability of parasitic bee populations may further negatively impact the already vulnerable solitary species.

Similar findings were reported in urban areas, where certain individual bee groups were found in higher numbers (Cardoso & Gonçalves, 2018). Urban area studies are critical as urbanization is the leading driver behind local extinction rates and losses in native species (McKinney, 2002). Due to the nature of development, negative effects of urbanization have long-term implications. Buildings and roads generally maintain their original land use for extended amounts of time and are rarely converted back to green areas. Alternatively, undeveloped areas within cities, such as parks or green areas that may foster pollinators are usually the first to be converted (McFrederick & LeBuhn, 2006). Although development is replacing natural areas, in a review of bees in urban landscapes, Hall et al., (2017) found global evidence of native bee richness and abundance in cities. Even in studies that did not find increased native bee richness or abundance in urban areas (Bates et al., 2011; Cardoso & Gonçalves, 2018; Hernandez et al., 2009), cavity nesting bees were found in greater abundance, overall, as compared to ground nesting bees and there were fewer floral specialists

present (Bates et al., 2011; Cane, 2005; Cane et al., 2006; Cardoso & Gonçalves, 2018; Matteson & Langellotto, 2011). However, diversity has also been demonstrated to be negatively impacted by urbanization (Ahrné et al., 2009; Kearns & Oliveras, 2009; Matteson & Langellotto, 2011). Other studies point to resource availability (Ahrné et al., 2009; Kearns & Oliveras, 2009; McFrederick & LeBuhn, 2006), such as food and nesting, rather than development intensity, as one key driver of pollinator decline.

Ground nesting bees may be in lower abundance in urbanized landscapes due to different nesting behavior, as compared to cavity nesting bees (Bates et al., 2011; Cane, 2005; Cane et al., 2006; Cardoso & Gonçalves, 2018; Matteson & Langellotto). Impervious surfaces, such as roads, sidewalks or parking lots, may prevent nest excavation for ground nesting bees (Cardoso & Gonçalves, 2018). The constant disturbance of mowing, weeding, seeding and removal of brush or debris might also make urban habitats less suitable for other pollinators (McFrederick & LeBuhn, 2006). On the other hand, cavity nesting bees can utilize a range of nesting habitats found in disturbed urban landscapes, such as weep holes in brickwork. In contrast, natural land cover can provide greater resource availability and connectivity between habitat patches and has been identified as providing crucial habitat for wild pollinators (Garibaldi et al., 2011). Thus, maintaining some high-quality natural land cover is essential to mitigate the negative effects of habitat loss.

Our study sites represented common land use types, urban, semi-natural and agriculture (Cattle Pasture, Mixed Use Agriculture and Organic). We used a landscape

analysis to provide insight into the pollinator communities in these areas and how they may be affected by general land use.

Objectives

- 1) To examine the effect of landscape composition on pollinator communities
- 2) To analyze potential relationships between pollinator abundance and land-use
- 3) To analyze potential relationships between species diversity and land-use

Methods

Study Sites

We chose five sites, representing three common landscapes in East TN: urban, semi-natural, and agricultural. The University of Tennessee Knoxville Gardens (UT Gardens), (1) in Knoxville, TN represented the urban landscape for our study. The UT Gardens comprises 10 acres of native and non-native plants, shrubs, and tree species surrounded by the Tennessee River, highways, buildings, and parking lots, near downtown Knoxville, TN. The semi-natural landscape was the UT Arboretum (2) in Oak Ridge, TN approximately 20 miles west of Knoxville, TN. The property comprises 250 acres of semi-managed forests and woody plants, with a high diversity of protected natural habitat and native plant species. The location of the Arboretum is also close to major highways, residential homes, and the Oak Ridge National Laboratory.

To assess pollinator communities in agricultural land, we selected three sites that represented common cropping systems and land uses in the region: organic agriculture, conventional row crops, and cattle pasture. The Cattle Pasture site (3) and Mixed Use Agriculture site (4) were both at the Plateau AgResearch & Education Center (PREC)

located in Crossville, TN approximately 80 miles west of Knoxville, TN. The 2,000-acre conventional farm is used for cattle, cash crops, and horticulture research. The two independent replicates were placed on opposite sides of the property, approximately one mile apart. The Organic Crops Unit (Organic Agriculture) at the East Tennessee AgResearch and Education Center (ETREC) (5) served as our Organic Agriculture site. The agriculture research facility is located 8 miles south of Knoxville on 90-acre dedicated to organic horticulture and field crop research. Outside of those 90 acres is residential housing and some small-scale independent farm operations.

We used the data from our 2019/2020 field experiment to evaluate the bee community at each of the sites (Chapter 2). We calculated average bee abundance (Fig. 10) and species diversity using Shannon's Diversity Index (Fig. 11) from the fixed plant community plots at each site. We used ArcGIS and the US National Land Cover Database (NLCD) (Dewitz, 2019), to classify the land cover surrounding each of our research sites at 500m, 1000m, and 2000m with the Asteraceae plots as the center (Fig. 14). These three radii were chosen based on differences in forage distances for pollinators, specifically bees, as there is some correlation with body size and forage distance capabilities (Greenleaf et al., 2007). Smaller bodied, solitary bees have an estimated forage range of 150-600m for some bee species (Gathmann & Tscharntke, 2002), while large body bees such as *Bombus* spp. have been documented to forage well over 2000m (Rao & Strange, 2012; Redhead et al., 2016).

The NLCD has more than 20 different land cover classifications, including categories for vegetation, and various land-use densities. We aggregated the classes

into four general land-use types: water, developed, agriculture, and natural. For example, there are three different classifications for developed land-use, low, medium, and high, and all three were aggregated to represent developed land use. The NLCD defined developed land as constructed materials and impervious surfaces such as commercial and residential housing, roadways, and even lawn grasses. Areas classified as water included open water and areas with minimal soil and vegetation. Natural included different forest types, wetlands, shrubland, and non-grassland herbaceous land cover. Agriculture comprised of land cover categorized as pastureland, cultivated crops, or grasslands by the NLCD. Finally, we used the Zonal Statistics as Table tool in ArcGIS Pro to determine the total number of cells per land cover classification. We then used that total to create a percentage of each land cover classification for each radius (Table 5). We hypothesized that, as a forestry research facility, the Arboretum should have the highest proportion of natural land cover, at any radius, of all our selected sites.

We used these generalized land cover types (specifically natural habitat) as a proxy for suitable pollinator habitat directly around our plots and in the surrounding areas. We then estimated the relationship between land cover type and pollinator abundance and richness across the landscapes. We hypothesized that landscape context has some effect on pollinator diversity or abundance; specifically, greater proportions of natural land cover in the landscape can better promote more abundant and diverse pollinator populations.

Data Analysis

We used pollinator collection data from the experiment described in Chapter 2. To determine differences in bee abundance at each of the sites, we averaged the abundance per sample, per plot. There were 4 plots at each site, for a total of 20 plots across all sites. In addition to bee abundance, we calculated species diversity using Shannon's Diversity Index, as this accounted for evenness of the bee community.

To determine the model that best predicted the effect of the four land cover classifications and the three different radii on abundance and species richness, we used the *dredge* function from the MuMIn package in R (Barton, 2018; Russo et al., 2019). The response variables included species richness and abundance, separately, and each radius with an accompanied land cover served as the covariates. For this analysis, we used plot as a random effect. Additionally, we tested for a correlation between the average pollinator abundance and the proportion of natural land cover at three radii: 500m, 1000m, and 2000 (Fig. 15). We also tested for correlations between the average pollinator abundance at each of the sites and the major land cover classes (agriculture, developed and natural) at the 2000m radius (Fig.16).

Results

Bee Abundance & Species Diversity

We found all three agriculture sites had higher abundance compared to the Urban Gardens and Semi-natural sites (Fig. 10). The Organic Agriculture site had the highest average abundance, while the Semi-natural site had the lowest. Using,

Shannon's Diversity Index, we found the Cattle Pasture site to have the highest species diversity, with an index of 16, but it also had the largest confidence intervals of the five sites, suggesting high variation (Fig. 11). The next highest species diversity was at the Mixed Use Agriculture site (index of 14), followed closely by the Semi-natural site. The Urban site had an index of 12 and lastly, the Organic Agriculture site had the lowest species diversity index of 7.

Spatial Analysis Results

The Urban Gardens had the highest proportion of developed land coverage at any given radius (Table 2). The Arboretum, identified as the Semi-natural site, had the highest proportion of natural land cover at the smallest radius, 500m, but showed just as much natural cover as the Organic Agriculture site at 1000m and the Mixed Use Agriculture site at 2000m, respectively.

Additionally, the Arboretum had the second highest proportion of land cover classified as developed at any scale. For the agriculture sites, in general, as the spatial scale increased, the percentage of land classified as agriculture decreased, while the percentage of land classified as natural increased. The Mixed-Use Agriculture had the largest land cover classified as natural at both the 500m and 2000m scale and had the lowest percentage of developed at any scale as compared to the Cattle Pasture and Organic Agriculture.

Through model comparisons, and ranking order depending on AIC score, the results showed no one radius was more predictive than any other. The results suggested the best predictive model included all land cover types at any of the

three radii, thus we were unable to identify a relationship between land cover and species diversity (Fig. 17) or abundance (Fig. 18). Additionally, through comparisons between abundance and proportion of natural land cover (Fig. 15), we found that the proportion of natural land cover around the sites did not serve as a viable explanatory variable for the observed abundance. We observed the highest R^2 value between natural land cover and bee abundance at the 2000m radius ($y = 5.66x + 3.83$, $R^2 = 0.10$).

Following these findings, we compared abundance and all three major land cover types at the 2000m radius (Fig.16). We found the developed land cover provided the highest R^2 value ($y = -4.88x + 7.51$, $R^2 = 0.22$) with a slightly negative relationship, as compared to the agriculture ($y = 5.78x + 4.81$, $R^2 = 0.18$) and natural ($y = 5.66x + 3.83$, $R^2 = 0.10$) land covers that both had slightly positive relationship with abundance (Fig. 16).

Discussion

We expected to see lower abundance and species diversity in the agricultural sites, and higher abundance in the Semi-natural site. We also expected to find increased species diversity and abundance in our Semi-natural site as studies within forested habitats found increased bee species diversity and abundance in open canopies and increased herbaceous plant cover and diversity (Hanula et al., 2015; Romey et al., 2007). However, our data did not support these findings. All three agriculture sites (Cattle Pasture, Mixed Use Agriculture, and Organic Agriculture) had higher abundances and species diversity compared to the Semi-natural site.

Our findings from the Semi-natural site may be due to lack of floral resources in forests or other historical variables such as fire suppression in the region, even though trees provide multiple resources to bees, including pollen, nesting habitat and material, honeydew, and resins (Requier & Leonhardt, 2020; Winfree, Griswold, & Kremen, 2007). Moreover, understory floral resource abundance is assumed to be strongest in early spring when light can pass through the canopy, which may not coincide with the flowering time of our study plant species (Winfree et al., 2007). This limited flowering window may best support early emergence solitary bees and their brood parasites (Harrison et al., 2018). These bees generally have shorter flight seasons and smaller range sizes (Harrison et al., 2019) and may explain findings of lower pollinator richness and abundance in forested sites as compared to other land uses (Winfree et al., 2011; Winfree et al., 2007). We found the highest average species diversity in our conventional agriculture systems, that share various land uses, including horticulture, forests, row crops and cattle pasture, suggesting landscape heterogeneity may be more important than previously considered for pollinator conservation (Winfree et al., 2007).

Bees are considered central place foragers (Michener, 2007) and they travel constantly to forage for food and other resources. Highly fragmented and isolated landscapes can increase forage distance requirements, ultimately reducing forage performance and fitness (Klein et al., 2017). Foraging distance differs between bee species and body size, with more literature available for larger-bodied bees. Large-bodied bees have an estimated forage range from 1-2 kilometers, but may differ depending on local resource availability (Cane, 2005). Even when resources are

available, if their supply is limited, it may be unable to support the production of future generations (Cane, 2005). Although we did not identify any significant relationship between land cover and abundance or species richness, our results indicate that at larger radii, the land cover surrounding our plots can be defined as a heterogeneous landscape, with no one site having >70% of a single land cover type (Fahrig et al., 2011; Kremen et al., 2007). Bees are not dependent upon a single patch, therefore, landscape heterogeneity can provide matrix complexity with different patch types, to meet resource demands (de Lima et al., 2020; Kremen et al., 2007; Tschardt et al., 2005).

Our findings may provide an opportunity for more specific and robust landscape analysis. For example, the Urban Gardens site, at the smallest spatial scale has only 6% natural land cover. The NLCD layer overlooks multiple potential floral resources such as small-scale horticulture plots and gardens. A potential resolution is a bottom-up approach where researchers can use their own observations, with assistance from land managers when necessary, to classify landscapes and build high resolution data layers (Samuelson & Leadbeater, 2018). Although time consuming, this information can provide localized data in real-time, aligning within the data collection timeframe.

Conclusion

Our study provides the first look at potential relationships between observed pollinator communities and land cover in East Tennessee. Although our results did not support any clear patterns, our work offers an opportunity for future research to uncover the complexity of spatial configuration. The landscape heterogeneity observed at larger spatial scales may be beneficial to both bee species' diversity and abundance. The

observed high species diversity and abundance found in the agriculture sites provides additional support for perennial plantings in agricultural landscapes.

CONCLUSION

This study serves as the first in East Tennessee to document pollinator forage preferences for different perennial plantings across multiple land use types. We found native perennials can support a multitude of flower visiting insects, especially wild bees. We found the highest species abundances and richness in our agriculture study sites, which offers substantial support to the incorporation of native perennial plantings in agricultural systems. We found a single species to be the most attractive, but treatment that comprised of all three plant families had the highest average visitation rate. The plot with greatest plant species diversity was the most attractive during any one pollinator collection. We were also able to quantify the pollinator community in the region, thus providing species level data for bees found across three eastern Tennessee counties.

Although we did not find any relationships between species richness or abundance and land cover classification at any radii, these findings warrant further exploration. Additionally, future work could address patterns in the different species or functional groups of bees collected at each site that were not explored, both in terms of the landscape level effects, relative plant preferences, and treatment level effects. Our work illustrates the potential for native perennials to serve as a promising resource for pollinator conservation across multiple common land uses in East Tennessee.

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APPENDIX

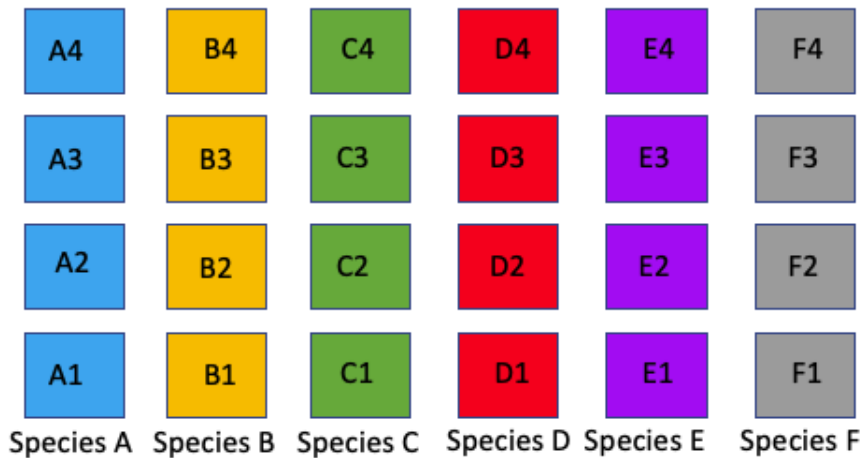


Figure 1. Plot Design

Design of each plot or treatment across all blocks. There are 6 different plant species and four individuals per species, totaling 24 individuals per plot. Each color represents a plant species.

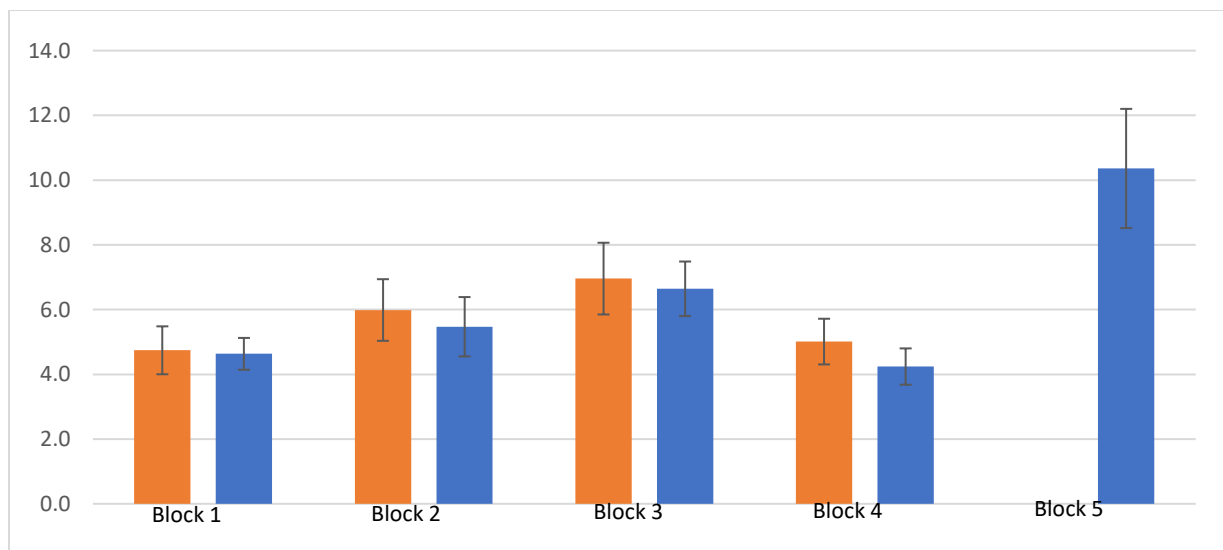


Figure 2. Average Pollinator Abundance per Block

Orange bars represent 2019 collections and 2020 in blue. Block 5 was established in 2020 and had the highest average abundance (10.4 ± 1.8). Block 4 had the lowest abundance in 2019 (5.0 ± 0.7) and 2020 (4.2 ± 0.6). 2020 blocks did not have higher abundance than 2019 blocks.

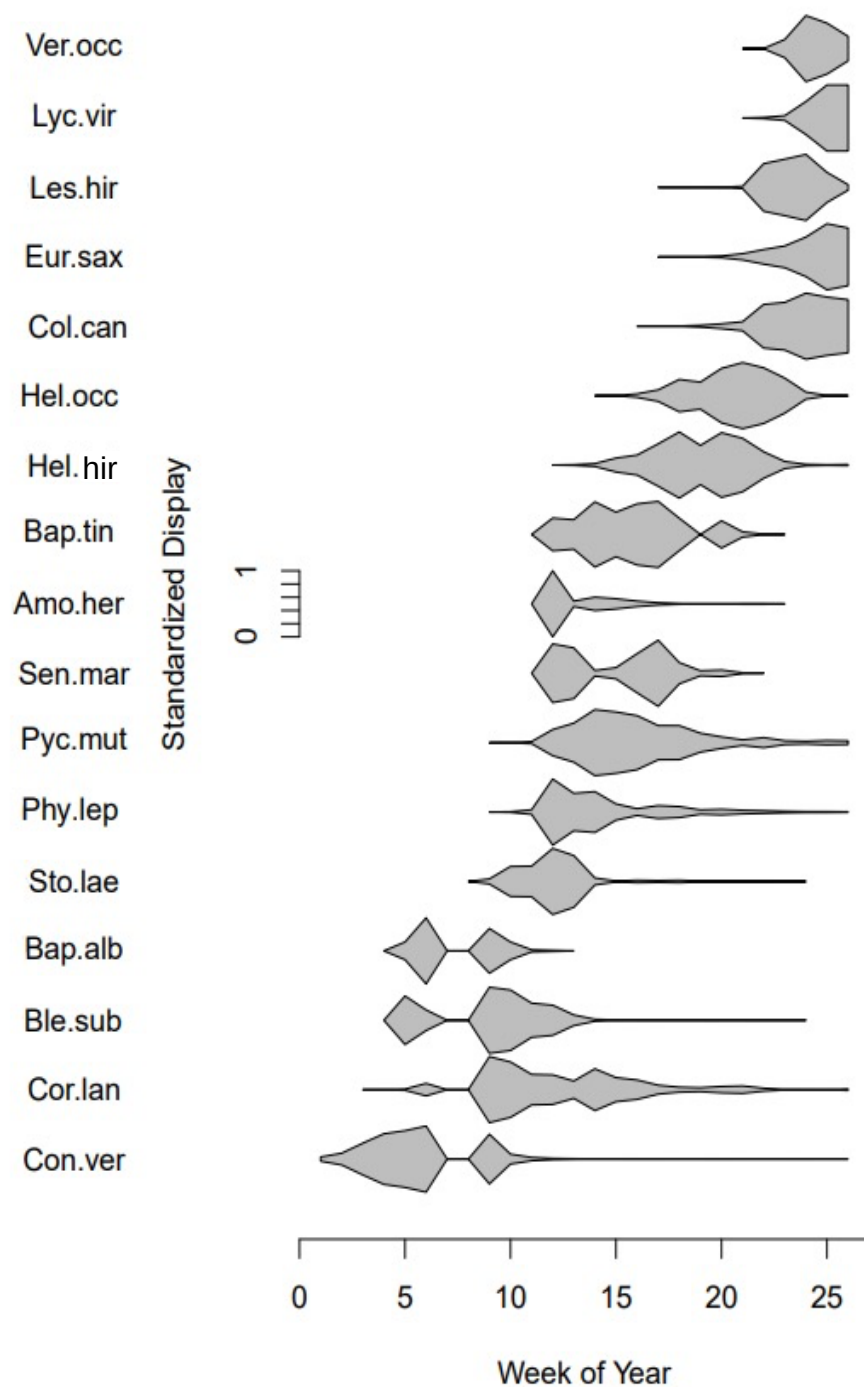


Figure 3. Floral Phenology

Duration and peak floral phenology for all species that bloomed. We calculated floral phenology by averaging the total number of inflorescences per plant species, summed across all blocks, per week. We standardized floral display on a 0-1 scale (feature scaling). Lines depict the start of each plant species bloom period and the shape and thickness of each line represents the average standardized floral display per week. Plant species are represented by abbreviations of the first three letters of genus and species.

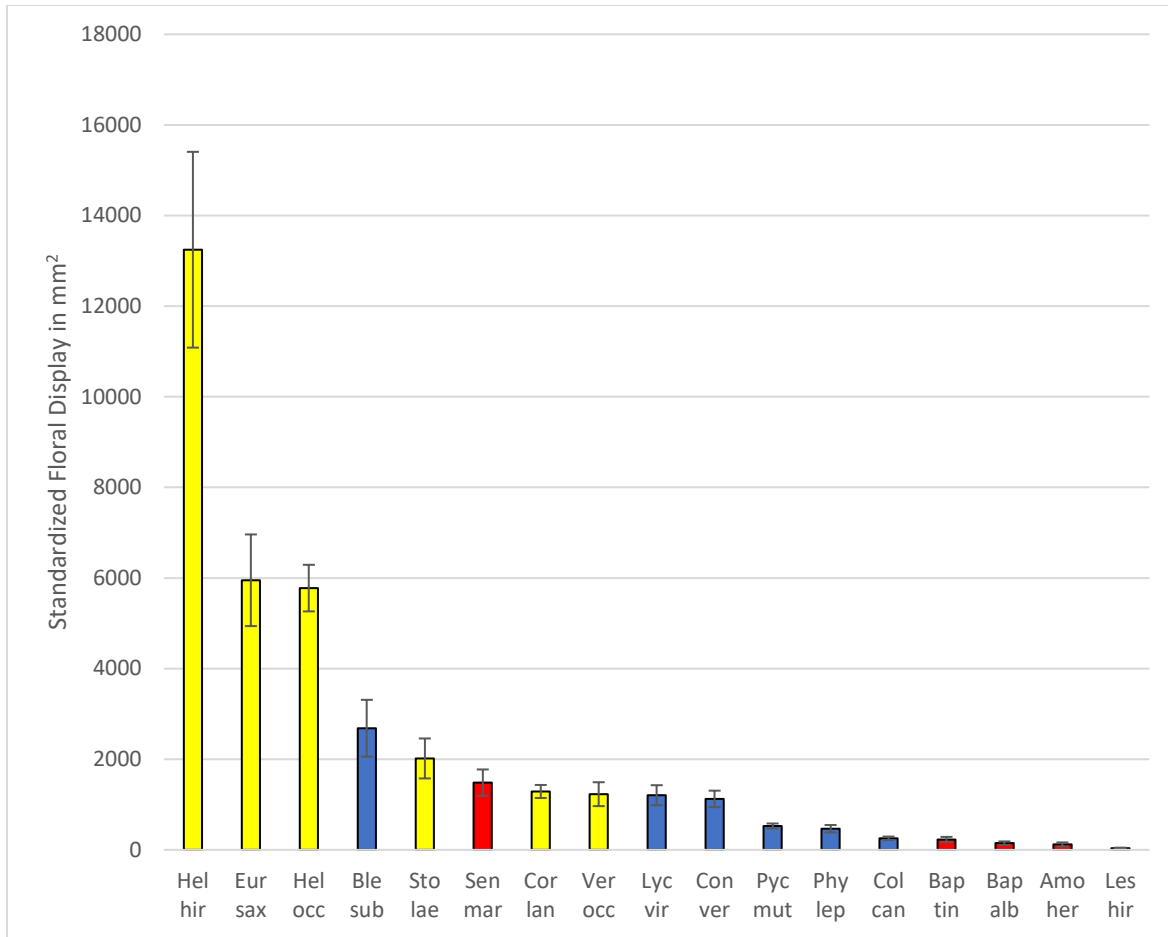


Figure 4. Average Floral Display per Plant Species per Individual Sample

We calculated floral display by taking the average size of an inflorescence in mm² multiplied by the number of inflorescences for each plant species per individual sample. We then calculated the average of the total floral display for Asteraceae (yellow), Lamiaceae (blue), and Fabaceae (red).

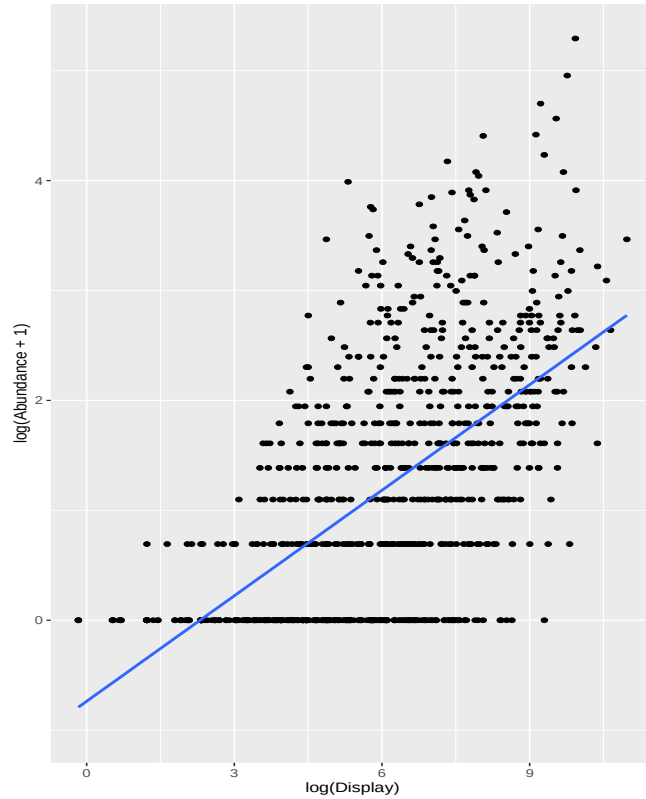


Figure 5. Floral Display and Abundance

Linear model of floral display (log transformed) on the x-axis and pollinator abundance (log transformed) on the y-axis. Floral display was calculated by the average size of the inflorescence per plant species, multiplied by the number of inflorescences. Each black dot represents one sampling event.

<i>Predictors</i>	<i>log(Abundance + 1)</i>		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	-0.76	-1.02 – -0.51	<0.001
Display [log]	0.33	0.30 – 0.36	<0.001
Random Effects			
σ^2	0.84		
τ_{00} Block	0.04		
ICC	0.05		
N _{Block}	5		
Observations	890		
Marginal R^2 / Conditional R^2	0.350 / 0.382		

Figure 6. Linear Model Summary Output, Abundance and Floral Display

Linear model summary output for Fig 9, pollinator abundance (log transformed), and floral display (log transformed). Floral display was treated as a fixed effect and block as a random effect using the sjPlot package in R.

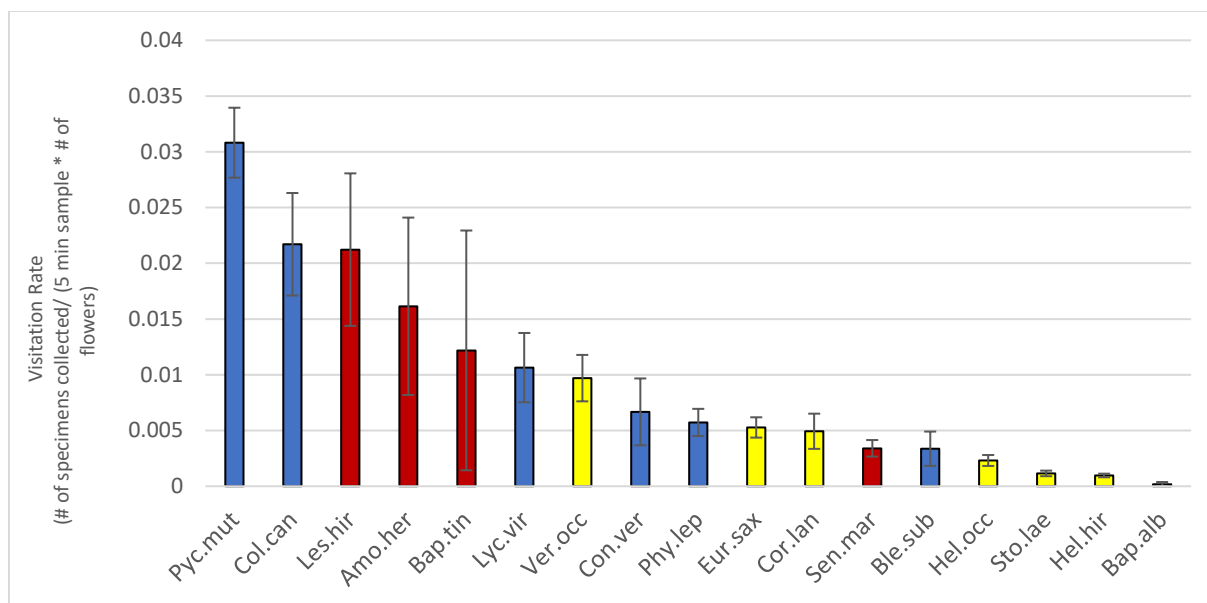


Figure 7a. Average Visitation Rate Per Plant Species 2020

Calculated by the number of insect visitors per unit floral area, per sample, averaged across all blocks and collections. Each plant species is labeled with an abbreviation of the first three letters from the genus and species name. The color of each bar represents each plant family; Asteraceae (yellow), Fabaceae (red), and Lamiaceae (blue). *Pycnanthemum muticum* had the highest visitation rate ($0.03. \pm 0.003$).

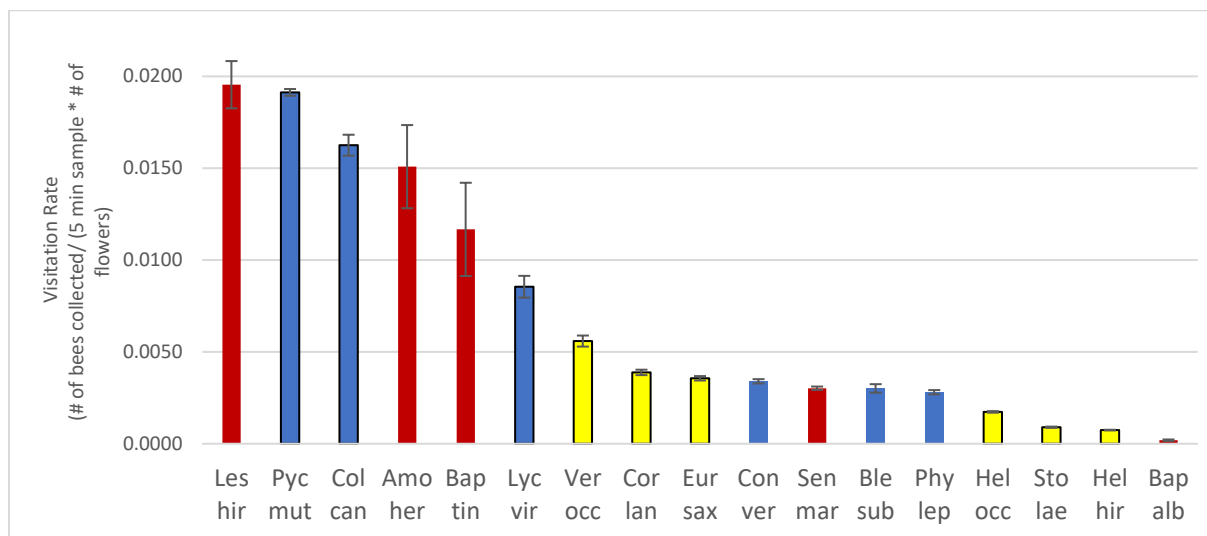


Figure 8b. Average Bee Visitation Rate Per Plant Species 2020

Calculated by the number of bees per unit floral area, per sample, averaged across all blocks and collections. Each plant species is labeled with an abbreviation of the first three letters from the genus and species name. The color of each bar represents each plant family; Asteraceae (yellow), Fabaceae (red), and Lamiaceae (blue). *Lespedeza hirta* had the highest visitation rate ($0.02. \pm 0.001$).

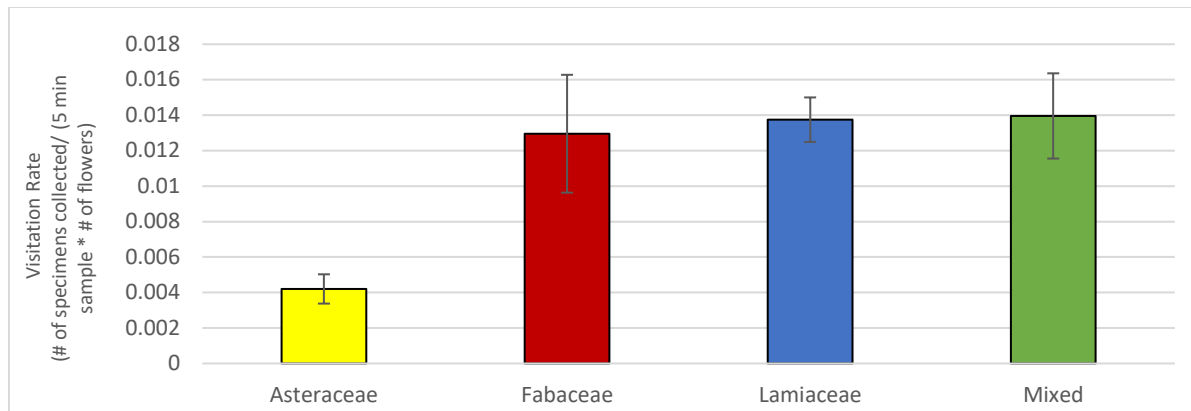


Figure 9. Average Visitation Rate Per Treatment 2020

Visitation rate from 2020 for each of the four treatments, across all blocks. Visitation rate was calculated by total pollinator abundance, divided by the average size of the inflorescences, multiplied by the number of inflorescences, per sample. The Mixed plot had the highest average visitation rate (0.014 ± 0.002), followed by Lamiaceae, (0.013 ± 0.001), Fabaceae (0.013 ± 0.003), and Asteraceae (0.004 ± 0.001).

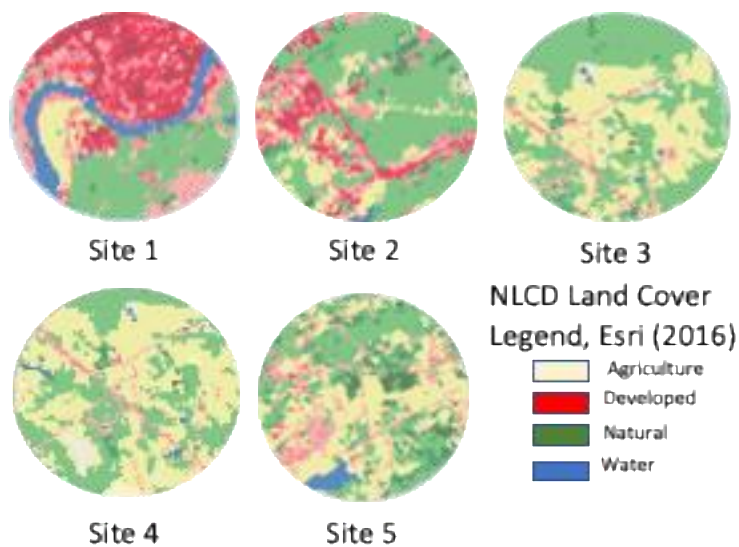


Figure 10. 2000m Buffer Analysis Using NLCD Layer (ESRI, 2016)

Using the NLCD layer, we classified the land cover types around in a 2000m radius with the Asteraceae plot at the center of each buffer for Site 1 (Urban Gardens), Site 2 (Arboretum), Site 3 (Cattle Pasture), Site 4 (Mixed Use Agriculture), and Site 5 (Organic Agriculture). Yellow indicates agriculture, red is developed, green is forested or natural cover, and blue indicates open water.

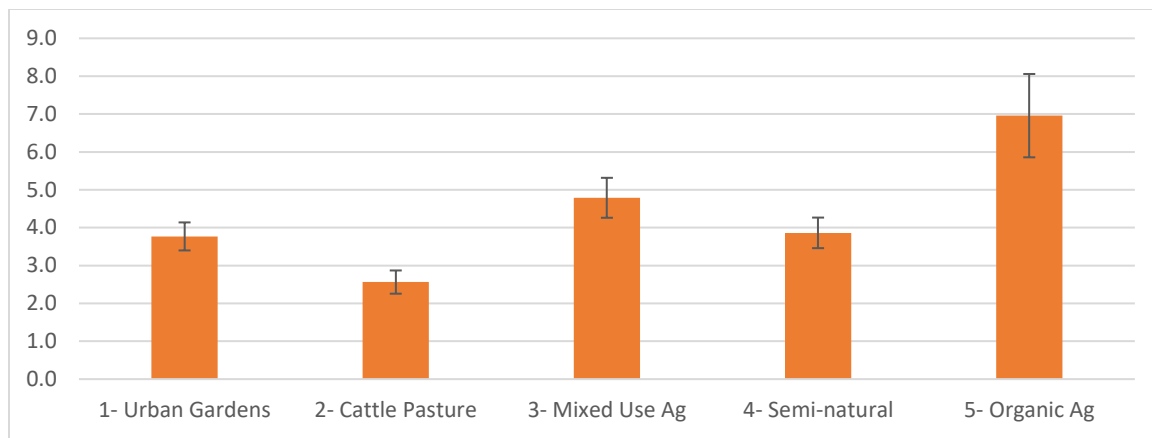


Figure 11. Average Bee Abundance per Site

This graph depicts the average number of bees collected per sample, per site for both years combined, 2019 and 2020. The Organic Agriculture block had the highest average bee abundance (7.0 ± 1.1), while the Cattle Pasture block had the lowest (2.6 ± 0.3).

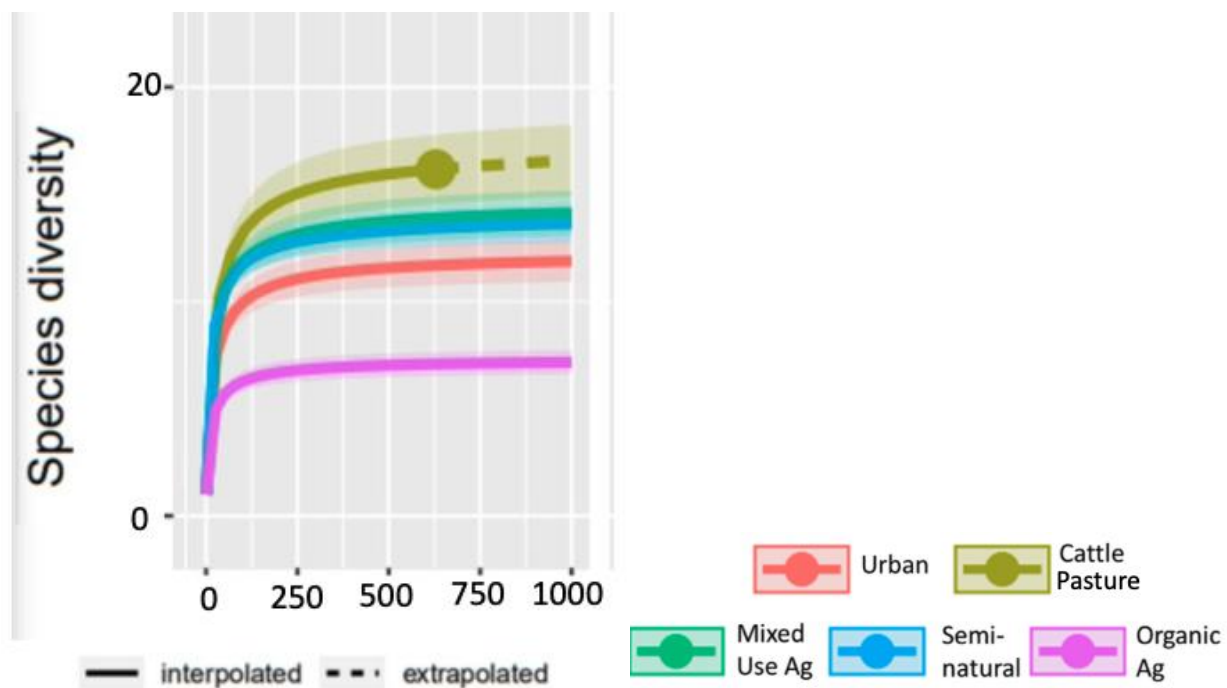


Figure 12. Shannon's Diversity Index per Site

Using the Shannon's Diversity Index, we calculated the bee species diversity for each site. The Cattle Forage block had the highest species diversity with an index of 16, followed by the Mixed Use Agriculture, Semi-natural, and Urban with indices of 12, and lastly the Organic Agriculture site with an index of 7.

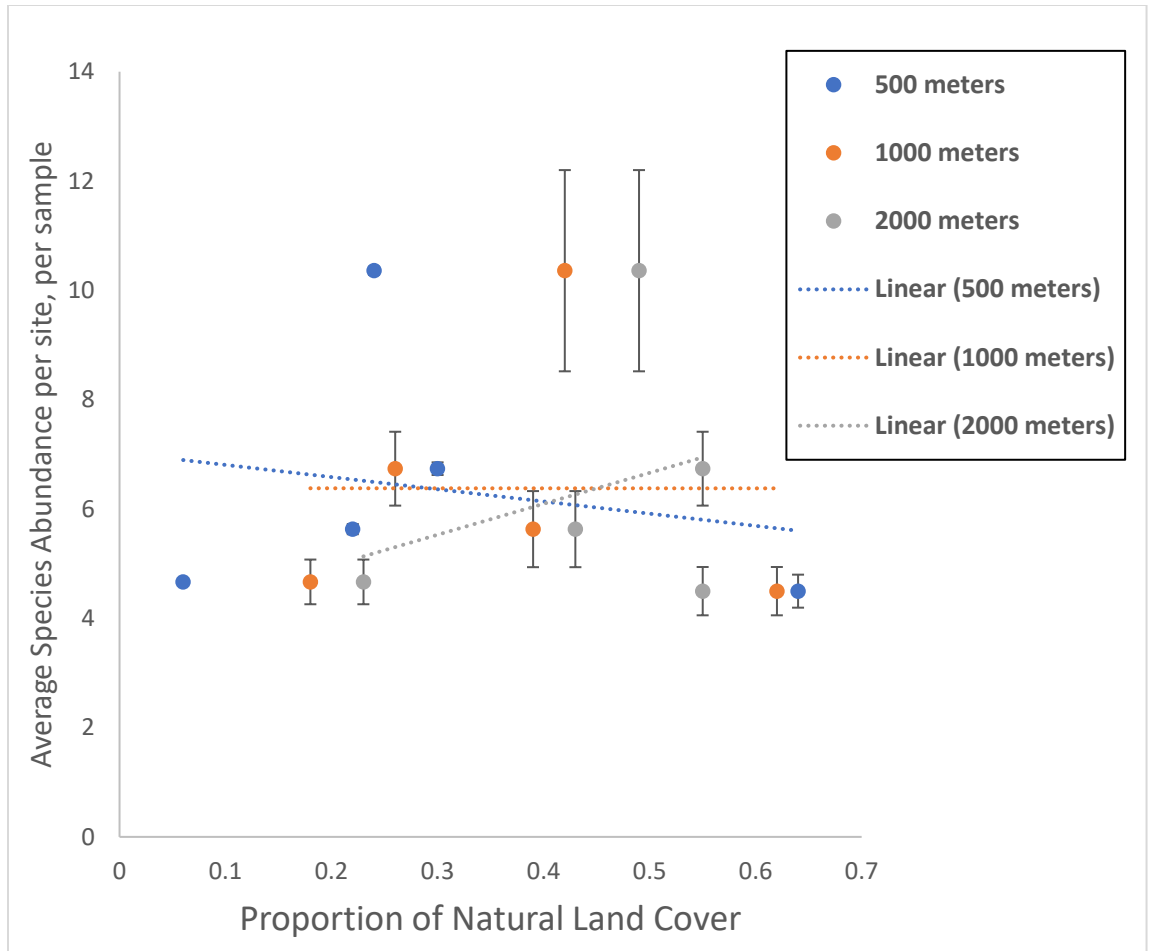


Figure 13. Comparison of Average Abundance and Proportion of Natural Land Cover at Selected Radii (500m, 1000m, 2000m)

Scatterplot depicting each site (dots) with the proportion of natural land cover on the x-axis and the average abundance per site, per sample on the y-axis at different radii: 500m (blue), 1000m (orange), 2000m (grey). For the 500m radius, $R^2 = 0.04$, 1000m radius, $R^2 < 0.01$, and for 2000m, $R^2 = 0.10$.

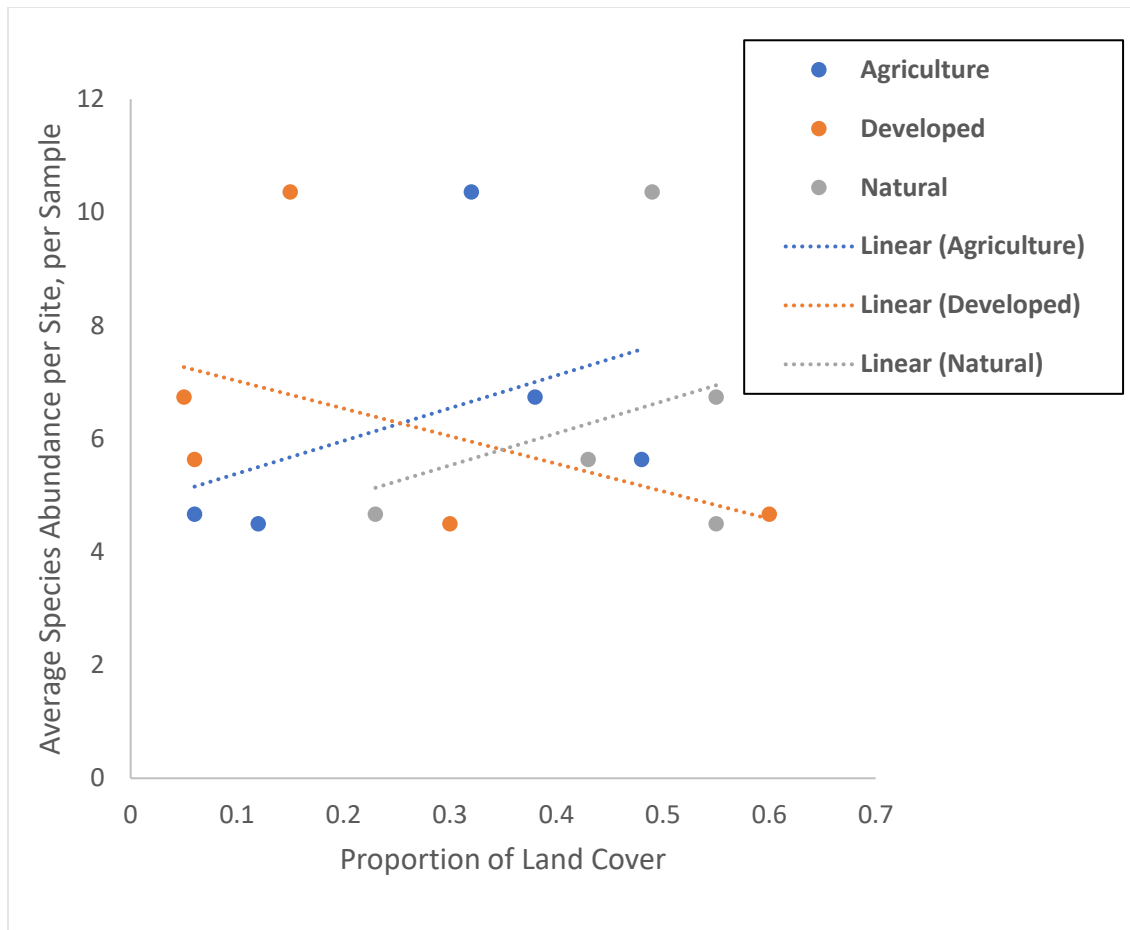


Figure 14. Comparison of Average Abundance Across Major Land Cover Classes at 2000m Radius

Scatterplot depicting each site (dot) and the proportion of land cover on the x-axis and the average abundance per site, per sample on the y-axis for different land cover types: agriculture (blue), developed (orange), and natural (grey). For agriculture, $R^2 = 0.18$, developed radius, $R^2 = 0.22$, and natural, $R^2 = 0.10$.

<i>Predictors</i>	log(Sp.Rich + 1)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	-0.84	-1.30 – -0.38	<0.001
X500.Nat	-0.61	-1.74 – 0.52	0.288
X1000.Nat	0.14	-1.08 – 1.36	0.823
X2000.Nat	1.27	0.14 – 2.40	0.028
Display [log]	0.22	0.20 – 0.23	<0.001
Random Effects			
σ^2	0.41		
τ_{00} Block	0.01		
ICC	0.02		
N _{Block}	5		
Observations	1216		
Marginal R ² / Conditional R ²	0.352 / 0.365		

Figure 15. Linear Model Summary Output, Species Richness and Natural Land Cover

The linear model included both floral display (log transformed) as a fixed effect and percentage of natural land cover for all three radii (500m, 1000m, and 2000m) and block as a random effect using the sjPlot package in R.

<i>Predictors</i>	log(Abundance + 1)		
	<i>Estimates</i>	<i>CI</i>	<i>p</i>
(Intercept)	-1.41	-2.27 – -0.55	0.001
X500.Nat	-1.29	-3.39 – 0.81	0.229
X1000.Nat	0.64	-1.63 – 2.90	0.581
X2000.Nat	1.84	-0.28 – 3.95	0.089
Display [log]	0.32	0.30 – 0.34	<0.001
Random Effects			
σ^2	0.80		
τ_{00} Block	0.03		
ICC	0.04		
N _{Block}	5		
Observations	1216		
Marginal R ² / Conditional R ²	0.373 / 0.397		

Figure 16. Linear Model Summary Output, Abundance and Natural Land Cover

The linear model included both floral display (log transformed) as a fixed effect and percentage of natural land cover for all three radii (500m, 1000m, and 2000m) and block as a random effect using the sjPlot package in R.

Table 1. Native Study Plants.

Asteraceae	Fabaceae	Lamiaceae	Mixed
<i>Helianthus occidentalis</i>	<i>Amorpha herbacea</i>	<i>Conradina verticillata</i>	<i>Helianthus occidentalis</i>
<i>Coreopsis lanceolata</i>	<i>Senna marilandica</i>	<i>Pycnanthemum muticum</i>	<i>Senna marilandica</i>
<i>Eurybia saxicastelli</i>	<i>Baptisia albescens</i>	<i>Lycopus virginicus</i>	<i>Conradina verticillata</i>
<i>Stokesia laevis</i>	<i>Lespedeza hirta</i>	<i>Physostegia leptophylla</i>	<i>Baptisia. albescens</i>
<i>Helianthus hirsutus</i>	<i>Baptisia tinctoria</i>	<i>Blephilia subnuda</i>	<i>Coreopsis lanceolata</i>
<i>Verbesina occidentalis</i>	<i>Thermopsis villosa</i>	<i>Collinsonia canadensis</i>	<i>Pycnanthemum muticum</i>

Table 2. Bee Specimens 2019 and 2020, Family, Genus, Species and Count

Family	Genus	Species	Count of Species
Andrenidae, n=15	<i>Andrena</i>	<i>personata</i>	3
		<i>placata</i>	1
		<i>near simplex*</i>	1
		<i>asteris*</i>	1
	<i>Calliopsis</i>	<i>andreniformis</i>	4
	<i>Pseudopanurgus</i>	<i>compositarum*</i>	3
		<i>labrosus</i>	1
		<i>rugosus</i>	1
Apidae, n=1,492	<i>Apis</i>	<i>melifera</i>	545
	<i>Bombus</i>	<i>impatiens</i>	331
		<i>bimaculatus*</i>	45
		<i>sp.</i>	20
		<i>griseocollis*</i>	13
		<i>pensylvanicus*</i>	7
		<i>citrinus*</i>	1
	<i>Ceratina</i>	<i>strenua</i>	261
		<i>calcarata</i>	118
		<i>dupla</i>	22
		<i>mikmaqi*</i>	15
		<i>sp</i>	12

“Table 2 Continued “

		<i>cockerelli</i>	6
	<i>Epeolus</i>	<i>bifasciatus</i>	5
	<i>Holcopasites</i>	<i>calliopsidis</i>	4
	<i>Melissodes</i>	<i>trinodis</i>	16
		<i>druriella</i>	12
		<i>denticulatus</i>	9
		<i>boltoniae</i>	3
		<i>sp A</i>	1
		<i>near boltoniae</i>	1
		<i>dentiventris</i>	1
		<i>comptoides</i>	1
		<i>bimaculatus*</i>	1
	<i>Melitoma*</i>	<i>taurea*</i>	1
	<i>Svastra*</i>	<i>obliqua*</i>	6
	<i>Triepeolus</i>	<i>remigatus</i>	2
	<i>Xylocopa</i>	<i>virginica</i>	33
Colletidae, n=11	<i>Hylaeus</i>	<i>affinis/modestus</i>	7
		<i>modestus*</i>	3
		<i>mesillae*</i>	1
Megachilidae, n=115	<i>Anthidium*</i>	<i>manicatum*</i>	4
		<i>oblongatum</i>	2
	<i>Coelioxys</i>	<i>modestus</i>	2
		<i>germana</i>	1
		<i>sayi*</i>	1
	<i>Heriades*</i>	<i>leavitti/variolosa*</i>	2
		<i>carinatus*</i>	1
	<i>Megachile</i>	<i>exilis</i>	29
		<i>mendica</i>	21
		<i>petulans</i>	17
		<i>rotundata</i>	13
		<i>pusilla*</i>	12
		<i>xylocopoides*</i>	1
		<i>sp</i>	1
		<i>concinna/pusilla</i>	1
		<i>brevis*</i>	1
	<i>Osmia*</i>	<i>georgica*</i>	1
		<i>sp*</i>	1
	<i>Paranthidium</i>	<i>jugatorium</i>	3
	<i>Stelis</i>	<i>louisae</i>	1
Halictidae, n=3475	<i>Agapostemon</i>	<i>virescens</i>	41
		<i>sericeus</i>	2

“Table 2 Continued “

Family	Genus	Species	Count of Species
Halictidae, n=3475	<i>Agapostemon</i>	<i>texanus*</i>	1
	<i>Augochlora</i>	<i>pura</i>	12
	<i>Augochlorella</i>	<i>aurata</i>	375
		<i>persimilis</i>	116
		<i>sp</i>	2
	<i>Augochloropsis</i>	<i>metallica</i>	185
	<i>Halictus</i>	<i>ligatus/poeyi</i>	921
		<i>confusus</i>	165
		<i>paralellus*</i>	6
		<i>sp</i>	2
		<i>rubicundus*</i>	2
	<i>Lasioglossum</i>	<i>sp</i>	947
		<i>apocyni</i>	154
		<i>imitatum</i>	149
		<i>callidum</i>	125
		<i>leucomum</i>	74
		<i>hitchensi</i>	56
		<i>trigeminum</i>	45
		<i>tegulare</i>	17
		<i>pilosum</i>	16
Halictidae	<i>Lasioglossum</i>	<i>admirandum*</i>	16
		<i>pectorale</i>	8
		<i>pruinatum</i>	6
		<i>platyparium*</i>	5
		<i>gotham*</i>	5
		<i>coriaceum</i>	4
		<i>zephyrum*</i>	3
		<i>versatum</i>	2
		<i>lustrans</i>	2
		<i>illinoense*</i>	2
		<i>rozeni</i>	1
		<i>paradmirandum</i>	1
		<i>lionotum*</i>	1
		<i>leucozonium*</i>	1
		<i>fuscipenne*</i>	1
		<i>coreopsis*</i>	1
		<i>cinctipes*</i>	1
	<i>Sphecodes</i>	<i>carolinus</i>	1
		<i>heraclei</i>	1

All bee specimens collected in 2019 and 2020. Asterisks (*) denote genera or species collected in 2020, not collected in 2019. This totals 99 bee species, representing 5 families.

Table 3. Non-Bee Specimens 2019, Order, Family, Percentage and Count

Order	Family	Percentage	Count
Coleoptera, n=162	Cantharidae	89.5%	145
	Chrysomelidae	3.7%	6
	Curculionidae	3.1%	5
	Coccinellidae	1.2%	2
	Mordellidae	1.2%	2
	Lampyridae	0.6%	1
	Scarabaeidae	0.6%	1
Diptera, n=78	Syrphidae	59%	46
	Tachinidae	10.9%	8
	Dolichopodidae	9%	7
	Unidentified	7.7%	6
	Conopidae	3.8%	3
	Sarcophagidae	2.6%	2
	Agromyzidae	2.3%	2
	Bombyliidae	1.3%	1
	Chironomidae	1.3%	1
	Chloropidae	1.3%	1
	Mycetophilidae	1.3%	1
Hemiptera, n= 86	Miridae	33.7%	29
	Cicadellidae	23.3%	20
	Pentatomidae	9.3%	8
	Unidentified	5.8%	5
	Rhopalidae	5.8%	5
	Geocoridae	4.7%	4
	Phymatinae	4.7%	4
	Thyreocoridae	4.7%	4
	Cydnidae	2.3%	2
	Rhyparochromidae	2.3%	2
	Acanaloniidae	1.2%	1
	Cercopidae	1.2%	1
	Tingidae	1.2%	1
Hymenoptera, n= 68	Vespididae	45.6%	31
	Scoliidae	22.1%	15
	Sphecidae	17.6%	12
	Braconidae	2.9%	2
	Chalcidoidea	2.9%	2
	Crabronidae	2.9%	2
	Unidentified	2.9%	2
	Ichneumonidae	1.5%	1
	Pompilidae	1.5%	1
Lepidoptera, n= 72	Hesperiidae	45.8%	33

“Table 3 Continued “

Order	Family	Percentage	Count
Lepidoptera	Nymphalidae	22.2%	16
	Unidentified	8.3%	6
	Erebidae	6.9%	5
	Pyrilidae	6.9%	5
	Yponomeutidae	5.6%	4
	Geometridae	2.8%	2
	Sphingidae	1.4%	1
Mecoptera, n= 1		100%	1

Non-bee specimens collected in 2019. Represents 6 orders and 34 families.

Table 4. Non-Bee Specimens 2020, Order, Family, Percentage and Count

Order	Family	Percentage	Count
Coleoptera, n=801	Cantharidae	87.1%	698
	Unidentified	3.6%	25
	Meloidae*	3.0%	24
	Mordellidae	2.9%	23
	Chrysomelidae	1.1%	9
	Curculionidae	1.1%	9
	Cerambycidae	0.6%	5
	Scarabaeidae	0.6%	5
	Coccinellidae	0.3%	2
	Lampyridae	0.1%	1
Diptera, n=305	Syrphidae	55.1%	168
	Unidentified	22.3%	68
	Conopidae	10.8%	33
	Tachinidae	8.5%	26
	Bombyliidae	2.0%	6
	Dolichopodidae	0.7%	2
	Stratiomyidae	0.3%	1
	Tephritidae*	0.3%	1
Hemiptera, n= 178	Pentatomidae	30.9%	55
	Cydnidae	20.79%	37
	Reduviidae	1.12%	2
	Cicadellidae	0.56%	1
	Geocoridae	0.56%	1
Hymenoptera, n = 188	Scoliidae	31.9%	60
	Sphecidae	20.7%	39
	Vespidae	18.1%	34

“Table 4 Continued “

Hymenoptera	Crabronidae	13.8%	26
	Parasitica	9.6%	18
	Unidentified	3.7%	7
	Pompilidae	1.6%	3
	Formicidae	0.5%	1
Lepidoptera, n= 247	Hesperiidae	55.1%	136
	Nymphalidae	14.6%	4
	Pieridae	13.0%	36
	Erebidae	8.5%	21
	Pyrilidae	2.8%	32
	Yponomeutidae	2.8%	7
	Lycaenidae	1.6%	4
	Unidentified	1.6%	7

Non-bee specimens collected in 2020. Totals 5 orders and 34 families.

Table 5. Landscape Analysis per Site, National Land Cover Database (ESRI, 2016)

	Land Cover Class	Radius (meters)		
		500m	1000m	2000m
Site 1, UT Gardens	Agriculture	0.9%	6%	8%
	Developed	69%	63%	66%
	Natural	6%	18%	23%
	Water	24%	12%	11%
Site 2, Arboretum	Agriculture	10%	40%	12%
	Developed	26%	18%	30%
	Natural	64%	42%	55%
	Water	-	-	3%
Site 3, Cattle Pasture	Agriculture	59%	47%	48%
	Developed	16%	12%	6%
	Natural	22%	39%	43%
	Water	2%	1%	1%
Site 4, Mixed Use Agriculture	Agriculture	64%	68%	38%
	Developed	5%	6%	6%
	Natural	30%	26%	55%
	Water	0.6%	1%	1%
Site 5, Organic Agriculture	Agriculture	64%	40%	32%
	Developed	11%	18%	15%
	Natural	24%	42%	49%
	Water	-	-	4%

Estimated percentages of land cover per classification at 500m, 1000m, and 2000m buffers at each site. The major land cover types are agriculture, developed, natural, and water.

VITA

Amani Khalil's passion for pollinators began as an undergraduate at George Mason University. Through various field courses and research opportunities, Amani uncovered an interest in agriculture work. She served as a Peace Corps Volunteer working in agriculture extension in rural South America, which gave her a glimpse into the diverse world of native bees. From there, she followed her curiosity to Dr. Laura Russo's native bee research at the University of Tennessee, Knoxville to obtain her Master of Science degree in Ecology & Evolutionary Biology. Upon graduating, Amani will be working with the USDA-ARS as an ORISE fellow researching dairy forage ecology in Madison, Wisconsin. Amani hopes to combine her pollinator expertise, with her love and appreciation for local food into career in holistic agriculture.