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Bee Visitation to Crops and other Flowers Planted as Bee Food

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To the Graduate Council:

I am submitting herewith a thesis written by Michael Edward Wilson entitled "Bee Visitation to Crops and other Flowers Planted as Bee Food." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Entomology and Plant Pathology.

John A. Skinner, Major Professor

We have read this thesis and recommend its acceptance:

Carl J. Jones, Annetee L. Wszelaki

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

Bee Visitation to Crops and other Flowers Planted as Bee Food

**A Thesis Presented for the
Master of Science
Degree
The University of Tennessee, Knoxville**

**Michael Edward Wilson
December 2011**

Dedication

I dedicate this work to my children; Jonas Michael and Summer Rose, and my wife Betsy. The enjoyment I receive from Jonas and Summer's fascination with nature through entomology far exceeds any other benefit from this work. Summer is the collector while Jonas is more interested in the biology, behavior, and making sure Summer takes good care of the subjects of study. Betsy's support throughout has been critical.

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Abstract

Farms that require insect pollination and reside in diverse landscapes benefit from pollination by native bees. However, populations of native bees and honey bees are generally in decline and this threatens food production. Documentation of crop pollination as an ecosystem service is needed to identify potential impacts from declining bee populations. This study identifies communities of bees providing pollination and how they vary across different crops and environmental conditions. Managing landscapes to provide additional food sources for bees may improve the health of wild and managed bees. This study also evaluated the attractiveness of bees to selected species of plants that could be used to provide food sources.

In 2008-09, bee visitation was measured on 10 different crops among 12 farms in Tennessee. On one of these farms, visitation was observed for 24 different flower species that could be used for supplemental bee forage. Bees visiting flowers were organized within a classification scheme of 10 taxonomic groups. Environmental data for each observation was recorded including the type of flower, the date, time, location, farm and plot size, if the farm was organic or conventional, and the number and sex of flowers when appropriate.

Nonmetric multidimensional scaling and linear models revealed that native bees are important visitors to crop flowers, but their abundance and composition depend on the type of flower. Within a flower type, other environmental effects can shift the community composition. Plants selected for habitat enhancement can be chosen based on the similarity of the community of bees which utilize them as compared to crops.

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File. Bee visitation abundance data at squash and pumpkin.....BeeAbundance.csv

Introduction

Ecological change, crops, and bees

Introduction

The annual value of honey bees to crop pollination in the United States is estimated to be \$14.6 billion (Morse and Calderone 2000). This dollar value alone may be insufficient to explain the total value of honey bees to crop pollination. Arguably, the real value of honey bees is more appropriately a deeply layered assessment of quality in life (Delaplane 2010). Most calories consumed by humans are from crops that do not depend on insect pollination (corn, wheat, etc.), but as countries develop, higher quality foods are desired which are often insect pollinated. As this trend occurred in U. S. history, native bees and crops, as well as imported bees and crops have been important in creating the modern U.S. food production system. A mini-review of changes in the ecological context of pollination in American agriculture follows.

In the New World, the earliest record of a honey bee is described as *Apis nearctica* by a single female specimen found in paper shale from the Middle Miocene in present day Nevada (Engel et al. 2009). Roughly 14 million years would pass before we have another record of the genus *Apis* appearing in the New World with the introduction of *Apis mellifera mellifera* in 1622 (Josselyn 1674). During that time important crops we now enjoy evolved both in the New World and the old and have been subjects of selection and improvement for food production. Managed and non-managed bees are essential to those crops which require or benefit from insect pollination.

Two crops native to North America and their pollinators

In North America, the origin and evolution of the five cultivated *Cucurbita* species; the squashes, pumpkins, and gourds, can be traced from a probable origin in Central America with *C. mixta*, *C. moschata*, and *C. pepo* being spread north with cultivation and trade by Native Americans (Whitaker and Bemis 1975). Requiring insects to move pollen between separate male and female flowers, a unique story unfolds with mutualisms involving humans, an oligolectic bee, and the spread north of *Cucurbita*. The only known pollen sources of squash bees (*Peponapis* and *Xenoglossa*) are the *Cucurbita* species; therefore, they were unlikely to exist in the Eastern U.S., north of Florida, before *Cucurbita* spread as a cultivated crop. With specialized pollen collecting structures and the ability to fly in low lighting and cool weather, they are well adapted to collect the large spined pollen grains in squash flowers, which are only open in the early morning (Hurd et al. 1971). However, with *Cucurbita* species being both wild and domestic, and squash bees being unmanaged pollinators, the story of their mutual spread is not so clear.

Two paths are proposed to explain the spread of *Peponapis pruinosa* into Eastern North America; one, in conjunction with the cultivation of *Cucurbita pepo* gourds associated with fishing technology along streams and rivers, and the other, as a non-human initiated spread of *Peponapis* in association with the wild buffalo gourd (*Cucurbita foetidissima*), as it progressed naturally through the Midwest (Bischoff et al. 2009). This second hypothesis hinges on whether or not buffalo gourd fragments found from the Middle Holocene were in fact growing wild or were traded into the Eastern

Woodland setting (Smith 1992). However, wing morphometry analysis suggests the latter hypothesis is more likely (Bischoff et al. 2009).

In a contemporary survey of cultivated *Cucurbita*, the National Squash Pollinators of the Americas Survey (SPAS) found that *Peponapis pruinosa* was abundant enough to provide sufficient pollination at 2/3 of 87 fields. This contribution to pollination is achieved in part by males of the species, something not possible with *Apis mellifera*. The close association with *Peponapis* and squash is not limited to food sources, but also includes their mate seeking behavior (Cane et al. 2011). Males are frequently observed seeking females in squash flowers and clearly increase bee traffic in their hunt for mates (personal observation). In the United States, 17.166 million pounds of squash and pumpkin were grown for fresh market and processing in 2010 (NASS 2011) and considering the SPAS findings, native squash bees likely contributed a substantial amount of the pollination. However, since 1/3 of fields across the Americas were without sufficient numbers for full pollination, supplementing with *Apis mellifera* is often warranted.

Squash and pumpkin are not the only important crops native to the Americas where native bees play an important role. The genus *Vaccinium* consists of 450 species, 25% of which are native to North America. Included in those are cultivated blueberries; southern rabbiteye (*Vaccinium ashei*), northern highbush (*Vaccinium corymbosum*) and lowbush blueberry (*Vaccinium angustifolium*). Perhaps the most dramatic example of a transition from a native, wild plant to a cultivated food crop occurs with lowbush

blueberry where Native Americans burned fields to improve production of wild blueberry stands in Maine. In modern times, through tree removal, limiting competition, and deterring diseases and pests; production of these native stands are further optimized (Kole 2011, USDA NRCS 2011, Bell et al. 2009a, Yarborough 2009). In established fields, few seedlings are successful under the canopy. Management practices attempt to maximize the yield of the resulting thick patchwork of genetic clones where pre-cultivation glacial events have left considerable genetic variation between clone patches and fields. For future selection and establishment of new fields, those clones which are most productive will be selected (Bell et al. 2009b, Bell et al. 2010).

Relying on insect pollination for seed set and high yields, even within self mating, native and introduced bees are important in blueberry production. At least eight native species of *Osmia* bees pollinate lowbush blueberry in Maine, but their abundance is limited by the number of nesting sites and below the level needed for full pollination. (Stubbs et al. 1997). Native bumble bees are more efficient at pollination of blueberry than honey bees, primarily due to their ability to ‘buzz pollinate’ or sonicate to release the pollen from the anthers (Free 1993). At least 14 species of *Bombus* have been recorded visiting lowbush blueberry (Finnamore and Neary 1978). Their abundance, however, is not sufficient to fully pollinate fields. Stocking with commercially reared *Bombus impatiens* is a suitable alternative to stocking with honey bees to achieve sufficient pollination (Stubbs and Drummond 2001). It is possible to determine if enough native bees are present in a field before supplemental stocking with honey bees, bumble bees, or

alfalfa leaf cutting bees. A field scouting method has been developed, and growers can calculate the quantity of bees needed to increase pollinator abundance to desired levels, or determine if the current level is sufficient (Drummond 2002, Yarborough and Drummond 2001).

The ecological context of lowbush blueberry in Maine has elements native to the system, including pollinators and the genetics resulting from the establishment of the crop. Higher yields have occurred as a result of increased management, which includes supplemental stocking of bees. This, however, does present several challenges related to bee populations. Pathogens present in commercially reared bumble bees are potentially being transmitted to wild native bees and managed honey bees (Colla et al. 2006, Genersch et al. 2006, Morkeski and Averill 2010). Beyond the pathogens possibly shared with native bees, problems with honey bees in this system abound, including but not limited to; pathogens, parasites, pesticides, landscape effects, and nutrition (Morse and Flottum 1997, Spivak and Le Conte 2010).

Increased awareness of problems in the beekeeping industry occurred when migratory beekeeper and lowbush blueberry pollinator Dave Hackenburg, found that 368 of 400 colonies lost their populations over a period of 3 weeks late in 2006 (Stokstad 2007). Although sudden losses of honey bees have occurred on occasion for over 100 years, the sudden loss Hackenburg observed was repeated for enough beekeepers in the U.S., with similarities abroad, that the general public, researchers, and congress took notice (Oldroyd 2007, Xerces Society 2008). This phenomenon was then termed Colony

Collapse Disorder (CCD), which describes a specific set of symptoms that differed from how colony losses had occurred in the past (vanEngelsdorp et al. 2009). The term CCD has since often been confused or equated to decline in bee populations in general (personal observation), and is only one aspect in a host of challenges to honey bee health.

Honey bees in the New World

As Europeans colonized and spread across the continent, Native Americans recognized the “white man’s fly”, or the honey bee, would precede settlers as this introduced species outpaced Europeans in its colonization of the continent (Jefferson 1787). As English and Spanish settlers came to North America, they brought with them their native honey bees *Apis mellifera mellifera* and *Apis mellifera iberica*, respectively (Sheppard 1989a, 1989b). Ruttner (1978) identified 20 geographically distinct populations of *A. mellifera*, in their native lands of the Western Old World and grouped them through principal components analysis based on 33 characters into four major groupings. At the extremes of these groupings are subspecies from Sub-Saharan Africa, in another group subspecies like *A. m. carnica* (present day Hungary, Yugoslavia, Bulgaria, and Rumania) and *A. m. ligustica* (Italy), and the third includes *A. m mellifera* and *A. m. iberica*. A fourth morphologically intermediate grouping from Turkey and Georgia includes *A. m. caucasica*. Ruttner’s groupings were later confirmed by Whitfield et al. (2006) using SNP genotyping. Representatives from each of these groups have been imported into the New World.

During a period of 63 years from 1859 to 1922, at least 8 honey bee races were introduced into the U. S. for sale and breeding (Sheppard 1989a, 1989b). Of these importations, the only ones considered overall successful were *A. m. mellifera*, *A. m. ligustica*, *A. m. carnica*, and *A. m. caucasica*. With trans-Atlantic trade of honey bees came concerns about transferring pathogens, parasites, and other un-desirable organisms. Importations were curtailed, when the Honey Bee Act of 1922 prohibited importation of honey bees into the U.S. due to a sudden collapse of colonies in Britain called Isle of Wight disease (Cale 1922). Still not fully explained, the malady caused 90% of the island's colonies to be lost between 1905 and 1915 (vanEngelsdorp and Meixner 2010).

Although unclear of the specific epidemiology of Isle of Wight disease, contemporaries discovered that the tracheal mite (*Acarapis woodi*) and a microsporidian (*Nosema apis*) were associated with diseased colonies (Hirst 1921, Fantham and Porter 1912). It would be 62 years after the import ban before *Acarapis woodi* was first established in the U.S. in 1984. It was first noticed in the New World in Columbia in 1980 (Mussen 2001). The arrival of *Nosema apis* to the U.S. predates the import ban and could have been present in honey bees at first arrival (White 1919). The tracheal mite proved to be particularly devastating to U.S. populations of honey bees, spreading to all major beekeeping states in less than five years, despite the destruction of 43,367 colonies by regulatory agencies to slow its spread (Mussen 2001). The carnage the tracheal mite left in its wake is somewhat clouded by the introduction of another bee mite into the U.S., the varroa mite (*Varroa destructor*). Losses from *Varroa destructor* could have occurred

as early as 1987 (National Research Council (NRC) 2007). In Figure 1, the honey bee colony losses in the U.S., just after 1989, are apparent. The dramatic drop after 1982 is due to changes in NASS survey methods. Between 1982 and 1985, NASS did not conduct the survey. Subsequent surveys excluded beekeepers with fewer than 5 colonies, when before 1982 they were included. It is understood that declines from 1989 to 1996 are generally attributed to tracheal mites and varroa mites. A 39% decline in U.S. bee populations has been recorded since 1981 (NRC 2007).

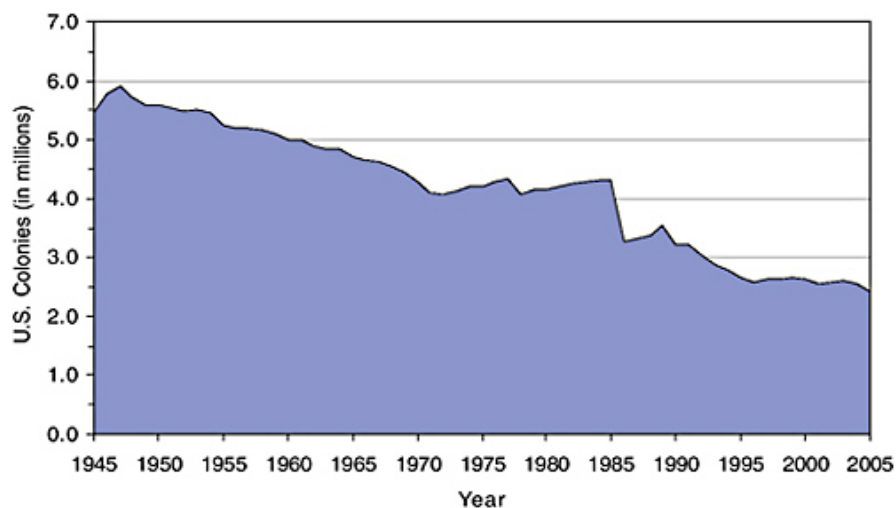


Figure 0.1. U. S. honey bee colonies, 1945 – 2005. Data compiled from USDA – NASS. From National Research Council (2007). Status of Pollinators in North America. Committee on the Status of Pollinators in North America. National Research Council. The National Academies Press. Washington, D.C. 322p.

Importation restrictions relaxed with amendments to the Honey Bee Act of 1922 until a 1976 regulation stopped importation of all stages of life including eggs and sperm

because of the release of *A. m. scutellata* into Brazil in 1956 (Kerr 1967, Sheppard 1988b). Termed Africanized bees, these bees originated from one of many subspecies originating in Sub-Saharan Africa (*A. m. scutellata*) and then hybridized with European honey bees in Brazil. Bees in this area retained the highly defensive behavior, genetic markers, and mitochondrial DNA of *A. m. scutellata* showing that honey bees of European lineage were primarily replaced in the American tropics (Guzman-Novoa and Page 1999, Muralidharan and Hall 1990).

The appearance of *A. m. scutellata* in the United States occurred 14 years later when it was discovered in Texas in 1990 (Hunter et al. 1993). The 1976 import ban did not stop all legal honey bee imports. Some documented importation has occurred since 1976, including bees from the Primorsky region of Russia, Australian package bees, and small amounts of *A. m. ligustica* and *A. m. carnica* germplasm for breeding programs (APHIS 2010, Rinderer 1997, Sheppard and Cobey 2011). Honey bee imports from Australia were banned late in 2010, due to the detection of an Asian honey bee, *Apis cerana*, in northern Australia and the risk of transferring this species and its associated exotic pests and viruses to the United States (APHIS 2010, Australian Government 2011, Harman 2011).

Schiff and Sheppard (1995, 1996) and Delaney et al. (2009) describe the resulting genetic characterization of honey bees widely used in the United States. They are mostly of *A. m. ligustica* and *A. m. carnica* origin. Bee samples collected in 2004 and 2005 had generally lost haplotypes from *A. m. mellifera* and the Iberian Peninsula, as compared to

samples from the early 1990's. This was probably due to selection on economic criteria and feral colony losses from mites. Although commercially traded U.S. honey bees are primarily similar to *A. m. ligustica* and *A. m. carnica*, genetic markers specific to Africanized bees are present and distributed by some commercial bee producers (Delaney et al. 2009, Whitfield et al. 2006).

Cucurbitaceae imported and floated into the New World

The Columbian Exchange refers to the exchange of organisms near after Columbus' voyages to the Americas. Crosby (1972) points out how the most important changes brought on by the Columbian voyages were biological in nature. Crosby (1972) also suggests that nothing can be understood apart from its own context. This context is applied to humans as a biological entity, where our dependence and effect on the environment defines our culture, reproduction, and survival. Included in early post 1492 biological exchanges were the Old World Cucurbitaceae and honey bees.

Cucurbitaceae is a family within the Cucurbitales clade of rosids with genera important as food crops including *Citrullus lanatus* (watermelon), *Cucumis spp.* (cucumber, melons, cantaloupe), and *Cucurbita spp.* (New World squash, pumpkin and gourds) (Smith 1977, Zhang et al. 2006). Old World melons were one of the first imported crops to do well in the West Indies with Columbus' second return in 1494 (Crosby 1972). The melons (*Cucumis melo*) most likely evolved in Asia along with cucumber (*Cucumis sativus*), which was imported and grown in North America by the

mid 16th century (Sauer 1993, Sebastian et al. 2010). Watermelon, originating in Swaziland and South Africa, was cultivated by the Spanish in Florida by 1567 (Dane and Liu 2007, Sauer 1993).

How Cucurbitaceae became 'native' in both the New World and the Old World is a result of long-distance dispersion (Schaefer et al. 2009). Based on global herbarium sampling for DNA sources, Cucurbitaceae is thought to have initially diversified in the Late Cretaceous, north of the Tethys zone in Asia. Five possible overseas dispersal events to the Americas, mostly from Africa to South America are thought to have occurred, probably by floating fruits. North American Cucurbitaceae then descended from seven expansions of Central and South American Cucurbitaceae, giving rise to cultivated *Cucurbita spp.* native to the New World (Schaefer et al. 2009).

Pollination requirements of Cucurbitaceae food crops, along with many other important food crops, are thoroughly reviewed in Delaplane and Mayer (2000). Recommendations for stocking of honey bees and managed non-*Apis* bees, as well as recommendations and contributions to pollination by non-managed bees are provided. For cantaloupe, the flower stigma must receive at least 400 pollen grains to produce marketable fruit. Recommended honey bee hive densities range from 0.1 to 5 colonies per acre or 3 bumble bee colonies per 1000 glasshouse plants. For cucumber, the recommended number of honey bee visits to a flower range from 6 to >18 to optimize fruit set. Recommended beehive densities range from 0.1 to > 7.4 hives per acre. In watermelon, bumble bees transfer more pollen resulting in good fruit in one visit while

honey bees need 6 visits. The recommended stocking rates for honey bees in watermelon range from 0.2 to 12.5 hives per acre, or 1 honey bee per 100 flowers in all parts of the field (Delaplane and Mayer 2000).

Honey

The most important role of honey bees is their pollination of widely available, nutritious crops (Aizen et al. 2009, Delaplane 2010, Morse and Calderone 2000). However, honey is often the driving force behind their management in developing nations. Honey bees (*Apis spp.*) are the only genus of bees that produce combs of harvestable honey (Michener 2000). In American history, particularly after the period between 1851 and 1873 when the moveable frame hive, wax comb foundation, centrifugal honey extractor, and the bellows smoker were invented, honey production was the driving force behind the management and trade of honey bees. This is also true before the mid-1800's when bee gums, skeps, and wild hives were raided for honey and beeswax by colonists and Native Americans. Honey bee populations spread across the continent by wild propagation and by human transportation for honey production (Horn 2005).

Honey bee populations sometimes spread with the expansion of non-native plants like sweet clover (*Melilotus spp.*). In the early 1900's sweet clover transformed the landscape, cattle production, and honey production. One of North Dakota's first major economic booms came with sweet clover, which provided forage for cattle and abundant

nectar that honey bees converted to honey. Clover seed set requires insect pollination, so the simultaneous effort of honey production and clover production for pasture mutually benefited both commodities. In the early 1900's, the pollination industry found its beginnings in California, where many orchards and vine crops needed supplemental bee stocking. However, the pollination industry did not greatly expand until the mid 1900's when the U.S. became a global supplier of insect pollinated crops like almonds (Horn 2005).

In developing countries, honey production closely tracks with human population increase. FAO data shows that honey bee colony numbers are increasing in developing countries, while decreasing in the U. S. The primary reason for the increase in developing countries is probably honey production. In the U. S., with the availability of low cost imported honey, many beekeepers have left honey production as a business and instead have concentrated on renting their colonies for pollination. The price of honey likely drives down further the number of managed U.S. colonies as some beekeepers do not enter the pollination industry. In developing countries, the growth in insect pollinated crops is outpacing the growth in honey bee colonies despite their increased numbers. As these countries become global suppliers of food crops, sufficient pollination may be a limiting factor (Aizen and Harder 2009).

In closing, over 240,000 species of the world's flowering plants rely on animal pollinators for reproduction. Bee pollination is critical to agriculture for fruits, vegetables, berries, seed production, fiber, drugs, and forage for agricultural animals. However, the

ecological context of insect pollinated crops is constantly changing. Declines in many bee species are evident with honey bees clearly in decline in North America. To address this, monitoring, habitat improvement, and increasing public awareness are needed to ensure these changes occur in a way that can sustain food production and other biological necessities (NASS 2007).

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Part 1

Native bee and honey bee visitation across a variety of agricultural crops

Abstract

The importance of native bees in crop pollination is well documented through studies that either examine a single agricultural crop or conduct separate analyses on observations per flower type. This study uses bee visitation on ten agricultural crops to represent the importance of native bees in crop pollination. Separate analyses per crop are used to generate mean proportions of bee visitation organized by categories of bees. This shows that native bee visits often occur as frequently, or in greater proportions than honey bee visits. Visitation across multiple crops is then analyzed together with nonmetric multidimensional scaling to show how the communities of bees that provide crop pollination change depending on the crop. Within squash and pumpkin plantings, continuous and discrete factors can further explain shifts in the community composition of flower visitors. Results suggest that developing pollinator conservation for farms that grow a wide variety of crops will likely require a wide variety of conservation strategies. Farms that concentrate on a single crop may be able to tailor conservation practices towards the most important bees in their system.

Introduction

The large scale production of insect pollinated crops is made possible by commercial management of the western honey bee (*Apis mellifera*). Beekeepers generally contract with fruit and vegetable growers to ensure populations of pollinating bees are at a level high enough to provide the desired crop yield (Delaplane and Mayer 2000).

Recent losses in managed honey bee colonies due to diseases, pests, and pesticides have underscored how integral bees are to our way of life (National Research Council 2007). Declines are not only reported in honey bees, but also in scores of the 3,509 species of bees present in the United States (Spivak et al. 2011, Ascher and Pickering 2011). Large scale declines in native bees would not go unnoticed by many food producers (Klein et al. 2007). Although honey bees are the main pollinator of many large scale fruit and vegetable farms, native bees still provide, or can provide, a substantial amount of pollination to those fields. Losey and Vaughan (2006) calculated that non-*Apis* bees provided the pollination to 3.074 billion dollars worth of crops annually during 2001-2003. In New Jersey and Pennsylvania, it was determined that native bees alone were abundant enough to provide greater than 90% of the pollination needed in watermelon fields (Winfree et al. 2007). On squash and pumpkin farms in Virginia, West Virginia, and Maryland, the native squash bee (*Peponapis pruinosa*) was the most abundant pollinator (Shuler et al. 2005). In the Squash Pollinators of the Americas Survey, *Peponapis pruinosa* was abundant enough to provide sufficient pollination at 2/3 of 87 squash fields (Cane et al. 2011).

Non-*Apis* bees' contribution to pollination will vary based on landscape level effects, such as the scale of commercial agriculture. In California's Central Valley, crop pollination by native bees is positively related to habitat, with more intensive agricultural areas lacking native bees (Kremen et al. 2004). In Maine's lowbush blueberry fields, there are numerous *Osmia spp.* bees that provide pollination. However, their abundance

is limited and not sufficient to provide full pollination, possibly due to lack of nesting sites (Stubbs et al. 1997, 1992). Isaacs and Kirk (2010) found that agricultural intensification strongly affects the level of pollination contributed by non-*Apis* bees. Ricketts et al. (2008) used results from 23 studies to find exponential declines in pollinator richness and native bee visitation rate related to increased distance of the target crop from natural habitat.

Measuring the contribution of non-*Apis* bees to pollination often utilizes flower visitation adjusted with pollination efficiency ratios. Some bees are more efficient pollinators than others (Delaplane and Mayer 2000), so interpretation of visitation should be tempered by the bee's efficiency. Smaller bees generally have a smaller foraging range and may move less pollen than larger bees (Greenleaf et al. 2007). Oligolectic bees, such as the squash bee, which specialize their foraging on a few closely related species, may be more efficient pollinators than generalist honey bees (Canto-Aguilar and Parra-Tabla 2000). However, Tepedino (1981) found their efficiencies to be nearly equal. In blueberry, *Bombus spp.*, *Andrena spp.*, and the oligolectic bee *Habropoda laboriosa* are more efficient pollinators than *Apis mellifera* (Javorek et al. 2002, Cane 1997).

To measure efficiencies in the field, various methods can be employed. Flowers are often bagged before opening. Then, once the flower is open; the bag is removed and observed until a single bee visits the flower. The flower is then either removed to count the number of pollen grains deposited or removed by the bee or the flower is re-bagged and the resulting seed-set recorded. Other measures include counting pollen grains on

visitors, visitation rate combined with monitoring fruit and seed set, and methods that incorporate other characteristics of the plant, like period of stigma receptivity and occurrence of self pollination (Dafni et al. 2005).

These methods are labor intensive and often are more appropriate for studies that concentrate on single plant species. Results from single plant species are informative and can be repeated for each species of interest. However, to investigate the contribution to pollination by non-*Apis* bees across numerous crops simultaneously, incorporating pollination efficiency is cumbersome. Pollination efficiency ratios from previous studies could be used to adjust visitation data in a new study, but this may not be necessary to develop a general understanding of the relative importance of non-*Apis* bees. Vazquez et al. (2005) showed that the most frequent animal mutualists usually contribute the most to plant reproduction. Using pollinator effectiveness as measured by pollen removal, deposition, or seed set in previous studies, they showed that the most abundant pollinators were not necessarily the most efficient ones. However, when considering the total effect of the species on pollination, the most abundant species contribute the most to pollination. Therefore, visitation alone is an informative measure, although not as precise as measures that take into account pollination efficiency.

The average farm size in Tennessee is 138 acres. Vegetable and fruit production is ranked nationally at 26th and 44th respectively (NASS 2007). Lacking large scale agriculture, East Tennessee should receive a significant benefit by native bee pollination, but documentation is not available. The objectives of this study are to 1) measure the

abundance of native bees visiting crop flowers and compare their abundance to that of honey bees and 2) examine how the community of bees at crops change depending on the type of crop, location based factors, temporal effects, and flower sex in squash and pumpkin. Different crops may benefit from different groups of bees and understanding what various groups of bees are providing pollination is needed to develop management practices that address their specific needs.

Materials and methods

Study sites

The study sites were fruit and/or vegetable farms in Tennessee, USA. Ten were located in the East Tennessee Valley (Anderson, Grainger, Jefferson, and Knox Counties), and one was located in Lawrence County. Farms grew between 1 and 15 crops, with less than 100 cultivated acres. Study plots within these farms were plots of single crops that require insect pollination; rabbiteye and highbush blueberry (*Vaccinium ashei* and *Vaccinium corymbosum*), cantaloupe (*Cucumis melo*), cucumber (*Cucumis sativus*), eggplant (*Solanum melongena*), pumpkin (*Cucurbita spp.*), squash (*Cucurbita pepo*), sunflower (*Helianthus annuus*), and watermelon (*Citrullus lanatus*), a crop that benefits from pollination by increased yield; okra (*Abelmoschus esculentus*), and a crop where the effect of bee pollination is unclear; pole beans (*Phaseolus vulgaris*) (Al-Ghzawi et al. 2003, Delaplane and Mayer 2000, Gemmill-Herren and Ochieng 2008,

McGregor 1976). To provide pollination, some farmers had hives of honey bees placed on their farms, while 3 relied on bees already present in the landscape. Individual vegetable and blueberry plots were between a few hundred square feet and 20 acres. Research was conducted at three sites in 2008 from June till August. In 2009 research was conducted at these sites and at 8 additional farms from April until September.

Bee visitation

Within each location, a transect was chosen per vegetable plot to be a representative sampling of the plot. Transects avoided edges when possible and would cross multiple rows when numerous rows were present. Transect length varied relative to the size of the plot, with a range of 60 to 1200 feet. The same transect was walked multiple times of day and multiple days to sample bee visitation over a period of days and at different times of day. All observations were made starting near sun rise (700 hrs.) and ending by 1300 hrs with the exception of blueberry, where observations were made until 1600 hrs since this crop flowers early in the year when morning temperatures are low enough to affect pollinator flight.

The response variable was recorded as the number of bees, organized into 10 categories, visiting crop flowers along a transect. The bee categories followed a taxonomic sufficiency approach (Terlizzi et al. 2003) of identifying bees in the field instead of collecting bees and later identifying them in the lab. This was done to avoid destructive sampling and to allow for the collection of more data. Voucher specimens

(596 bees) were collected by netting at flowers and by fluorescent yellow, blue, and white painted pan traps with soapy water (Droege 2010). Voucher specimens were identified to genus and organized into the 10 categories to ensure field identifications could be related to specific genera of bees (see appendix).

The categories are *Agapostemon*, *Andrena*, *Apis* (*Apis mellifera*), *Bombus*, Megachilidae (*Osmia* and *Megachile*), Panurginae and *Halictus* (*Calliopsis*, *Protandrena*, and *Halictus*), *Peponapis*, small Halictidae (*Augochloropsis*, *Augochlora*, *Augochlorella*, *Lassioglossum*, and *Sphecodes*), uncommon bees (*Ceratina*, *Eucera*, *Hylaeus*, *Melissodes*, *Nomada*, *Perdita*, *Svastra*, and *Triepeolus*), and *Xylocopa* (*Xylocopa virginica*). The bee's identification occurred in the field, by sight, by one observer (Michael Wilson) with the exception of the observations at the blueberry plot in Lawrence County (Dan Eiser). With blueberry, visitation was recorded for bees both visiting the flower legitimately, thought to provide pollination, or robbing nectar through slits and, therefore, not clearly providing pollination (Dedej and Delaplane 2004, Sampson et al. 2004). Other variables include: the number of flowers (except in blueberry), flower sex in squash and pumpkin, the date, time of day, size of the farm (small, < 3 acres in cultivation; medium, 3- 25 acres; large, > 25 acres), size of the plots (small, < 1 acre plot; large, > 1 acre), and whether the farm was conventional or organic. Data was only collected on days when conditions were conducive to bee visitation and when flowers were near peak bloom. Avoided were rainy or overcast days and unseasonably cold days when bees were clearly absent due to the cool temperature.

Data analysis

To account for differences in sampling effort from transects of various lengths, observation counts were equalized to the shortest transect length (60ft). After equalization, any observation with less than 4 total bees was removed, being considered insufficient for representative visitation. The counts were then transformed to proportions of bees for each category. For analysis that concentrated on squash and pumpkin flowers only, data was transformed to bees per flower as the response variable.

Linear mixed models in SAS (Version 9.2) were used to develop uni-variate, least square means to estimate proportions of bee categories responsible for the total visitation. The linear models were calculated with the SAS MMAOV macro, mixed model analysis of variance (Saxton 1998), using log transformation and the provided diagnostics for normality testing. Bee category was used as a fixed effect, while a random variable accounted for variance of location interaction with bee category. When all observations for a flower type occurred at a single transect, the date of the observation interacting with bee category was used as a random effect. For each flower type, some bee categories were combined into 'other bees' when the response deviated too far from normality to function in the linear model.

For multi-variate analysis, nonmetric multidimensional scaling (NMDS) in the Vegan package for R (Version 1.17-4) was used with Bray-Curtis rank similarity.

Permutation testing, weighted average confidence intervals, vector fitting, and thin plate regression splines allowed for significance testing and graphics to describe differences in environmental factors on the NMDS ordinations. For the NMDS of all crops, Megachilidae was combined with uncommon bees due to their low abundance. For the NMDS of squash and pumpkin *Agapostemon*, *Andrena*, *Megachilidae*, Panurginae and *Halictus*, uncommon bees, and *Xylocopa* were combined into 'other bees' due to their low abundance or absence.

Results and discussion

Considering that interaction frequency can be used as a surrogate for the total effect of pollination contribution (Vazquez et al. 2005), the mean proportion of various bee categories at crop flowers indicates that native bees are providing significant pollination services to farms (Table 1.1 and Table 1.2). The least square means for visitors to squash and pumpkin show that honey bees are among the most significant visitors. However, other bee categories are equally significant. Honey bees only represented about $15.1\% \pm 3.1$ of the total visitors to squash and pumpkin. Results are similar for watermelon (Table 1.2) where honey bees represent about $16.5\% \pm 5.5$ of the visitors and do not statistically differ from the proportion of bumble bees. Except with watermelon, the small Halictidae category represents a significantly larger proportion of the total bee visitors with $46.4\% \pm 13.1$.

Table 1.1. Mean proportion of visiting bee categories to squash and pumpkin on ten farms.

Bee category*	Mean proportion (se)	LSD**
<i>Bombus</i>	0.243 (0.046)	A
<i>Peponapis</i>	0.188 (0.037)	A
<i>Apis</i>	0.151 (0.031)	A
Small Halictidae	0.020 (0.011)	B
Other bees	0.007 (0.009)	B

*From a total of 8,825 bees counted in 144 observations.

**Least square means separation after accounting for random effect of location interaction with bee category. Fixed effect of bee category was significant ($P = 0.0075$).

Table 1.2. Mean proportion of visiting bee categories to crops on three farms.

Crop	Bee Category	Mean proportion (SE)	LSD*	Bee category effect
Watermelon				$P < 0.001$
	Small Halictidae	0.464 (0.131)	A	
	<i>Apis</i>	0.165 (0.055)	B	
	<i>Bombus</i>	0.069 (0.030)	BC	
	<i>Agapostemon</i>	0.012 (0.016)	CD	
	Other-bees	0.009 (0.015)	CD	
	Panurginae and <i>Halictus</i>	0.004 (0.014)	D	
Peponapis	0.002 (0.013)	D		
Cantaloupe				$P = 0.004$
	<i>Apis</i>	0.560 (0.186)	A	
	Small Halictidae	0.087 (0.042)	B	
	<i>Bombus</i>	0.085 (0.041)	B	
Cucumber				$P = 0.358$
	<i>Apis</i>	0.241 (0.154)	A	
	Small Halictidae	0.195 (0.130)	A	
	<i>Bombus</i>	0.168 (0.116)	A	
Blueberry				$P < 0.0001$
	<i>Bombus</i>	0.553 (0.201)	A	
	<i>Apis</i>	0.059 (0.036)	B	
	<i>Andrena</i>	0.040 (0.030)	B	

Other bees	0.025 (0.025)	B
Watermelon had 32 observations with 2,162 bees counted, cantaloupe 20 observations with 1,327 bees, cucumber 17 observations with 762 bees, and blueberry (legitimate visits only) 13 observations with 1,042 bees. Each crop was present on three farms, but not necessarily the same three farms.		

* Least square means separation after accounting for random effect of location interaction with bee category.

For other crops where observations occurred on at least three farms, the proportion of bees that were honey bees varied depending on the crop (Table 1.2). Significance testing across crops was not possible with the linear models; instead each crop was analyzed separately. Considering cantaloupe visitors, we can see that honey bees were the most significant group visiting, representing $56\% \pm 18.6$ of the total visitors. The categories of bees visiting cucumber did not significantly differ from one another, while on blueberry, bumble bees were the most dominant visitors.

Observations for eggplant, pole beans, and okra only occurred on one farm. Honey bee colonies were placed on this farm and honey bee visitation to flowers was frequent to other crops at this farm (combined in data above). However, for these three crops, honey bees were so infrequent that their numbers were combined with other bee categories. Carpenter bees (*Xylocopa*) visited these crops and appeared to be providing pollination, since they were not robbing nectar from slits cut in the sides. None of the 136 bees on eggplant were honey bees. The most significant visitor on eggplant was *Bombus* ($72.4\% \pm 35.8$, $P = 0.047$). The only other groups present, *Xylocopa* ($8\% \pm 6$) and Small Halictidae ($6.5\% \pm 5.3$), did not significantly differ from each other. On pole beans (297 bees visiting), *Bombus* ($46.6\% \pm 8.2$) and *Xylocopa* ($46.8\% \pm 8.2$) were equally the most

significant visitors ($P < 0.0001$), while small Halictidae ($2.1\% \pm 1.1$) and other bees ($0.3\% \pm 0.8$) were less frequent and statistically equal in their visitation. Bees occurred very infrequently on okra (67 bees). The most significant group on okra was *Bombus* ($71.6\% \pm 21.7$, $P = 0.0003$), while the only other bee groups visiting, small Halictidae ($8.0\% \pm 3.7$) and *Xylocopa* ($7.7\% \pm 3.6$), were fewer and statistically equal in their visitation. On sunflower, 215 bees were observed. Means for sunflower are not reported because observations were not normally distributed.

The linear models used to generate these means did not make comparisons among crops, but the numbers indicate that different crops may benefit from different categories of bees. To investigate this further, we examined the bee community composition with NMDS ordination, using bee categories as a substitute for species. In Figure 1.1, ellipses representing a 95% confidence interval for the average observation for a given crop are shown for 7 crops grown at the same location. Pole beans, eggplant, and okra have a distinctly different community of bees than any other crop. The ellipses for squash and cantaloupe overlap, showing that observations on these crops are similar to each other. Observations on squash, however, are much different than watermelon and cucumber. Using permutation testing, we see that the type of crop clearly influences the ordination ($P < 0.001$). Other factors, such as time of day also have a significant effect ($P < 0.001$). Vector fitting and regression splines on Figure 1.1 appear to echo the direction of some of the ellipses, suggesting a change in bee community composition for some of the crops throughout the day. For example, the ellipse for watermelon stretches towards the small

Halictidae category, parallel to the vector for time of day. This indicates an increase in the proportion of small Halictidae present later in the day. The ellipse for okra is orthogonal to the time of day vector because bees only occurred on this crop late in the day.

If we include data for other crops and locations in the NMDS ordination, we lose the ability to identify other factors that may influence the ordination, such as time of day and location. This is because the experimental design lacks balance since some crops occurred at single locations and some locations had a single crop. However, we can still apply the type of crop as a class factor and examine differences in community composition based on the type of crop (Figure 1.2). The similarity of observations for squash and pumpkin are not surprising, since some varieties of pumpkin are the same species as summer squash. With an increased amount of observations, there is a clear distinction between the average observation of squash and cantaloupe, as compared to Figure 1.1 where squash and cantaloupe did not statistically differ. In Figure 1.2, the average observation for cucumber and cantaloupe are very similar, which is not surprising since they are both Old World Cucurbitaceae and have similar flowers. However, the average observation for watermelon, another Old World Cucurbitaceae, does not overlap cucumber and is considerably closer to the small Halictidae bee type, their most frequent visitor. For blueberry, observations are graphed for all bees visiting blueberries, and only those bees that are legitimately visiting the flowers. These ellipses form on a gradient between *Apis* and *Bombus*, and are not pulled towards *Xylocopa*. *Xylocopa* perforated the flowers, initiating nectar larceny, allowing the flowers to be

robbed by *Apis* (Dedej and Delaplane 2004), but *Xylocopa* bees were not abundant on blueberry and, therefore, have little effect on these ellipses. Again, we see a strong effect from the type of crop on the ordination ($P < 0.001$).

Within a single flower type, we can examine location based class factors on the ordination without interference from effects of different flower types. We can also examine effects from continuous factors: time of day, date, and female flower ratio. Squash and pumpkin have separate male and female flowers. Honey bees prefer female flowers, while squash bees prefer pollen producing male flowers (Tepedino 1981); therefore, a higher ratio of female flowers in a field may shift the composition of bees providing visitation.

Figure 1.3 shows the effect of three different class factors on the NMDS ordination of visitors to squash and pumpkin. There is a significant difference between the average observation at organic farms ($n=2$) and conventional farms ($n=8$), however this difference could be due to the low number of farm replication or factors specific to the farms, such as farm size. The average observation at medium sized farms ($n=4$) is significantly different than farms large in size ($n=4$) in nearly the same way as the ellipses identifying organic vs. conventional. The ellipses for these two different factors overlap each other on the ordination. Similarly, if we compare the average observation for the size of the plot, farms with small plots ($n=6$) differ from farms with large plots ($n=4$) and their ellipses again overlap organic farms and conventional farms, respectively. It is therefore impossible to determine what location based factors are responsible for a

shift in community composition in this study, but it is clear that location does affect the ordination ($P = 0.001$). Figure 1.4 shows effects from continuous variables on the ordination. Regression splines show a non-linear effect for female flower ratio ($P = 0.001$). Effects from time of day ($P = 0.016$) and date ($P = 0.001$) were more linear in the direction of their respective vectors.

Native bees from the surrounding environment make up a significant proportion of bees providing visitation to crops in the study area as compared to managed honey bees. The linear models rarely showed honey bees being more frequent than some of the other categories of bees. Therefore, non-*Apis* bee losses in the study area would likely reduce total bee visitation to crops or require higher stocking of honey bees, and therefore, increase costs. Crops less attractive to honey bees, or frequently visited by native bees unique to that crop, could be more sensitive to non-*Apis* bee losses. From the ordination Figures 1.1 and 1.2, we can clearly see that some bee groups favor specific crops, even when those crops are grown at the same location. Conservation strategies to benefit pollinators on diverse farms will likely need to address a variety of needs for the various bees important on those farms. On farms growing a single crop that is dominated by a single group of bees, like *Bombus* in blueberry, targeting conservation strategies for the bees most important in pollinating that crop would be most beneficial.

Factors beyond flower type, which can effect non-*Apis* bee populations warrant further investigation. Ordination may be a useful numerical tool to analyze information generated by more complex studies investigating factors that affect bee populations

(Figure 1.3). Understanding temporal and flower preference effects (Figure 1.4) will also be necessary to conduct studies that accurately measure bee communities at flowers.

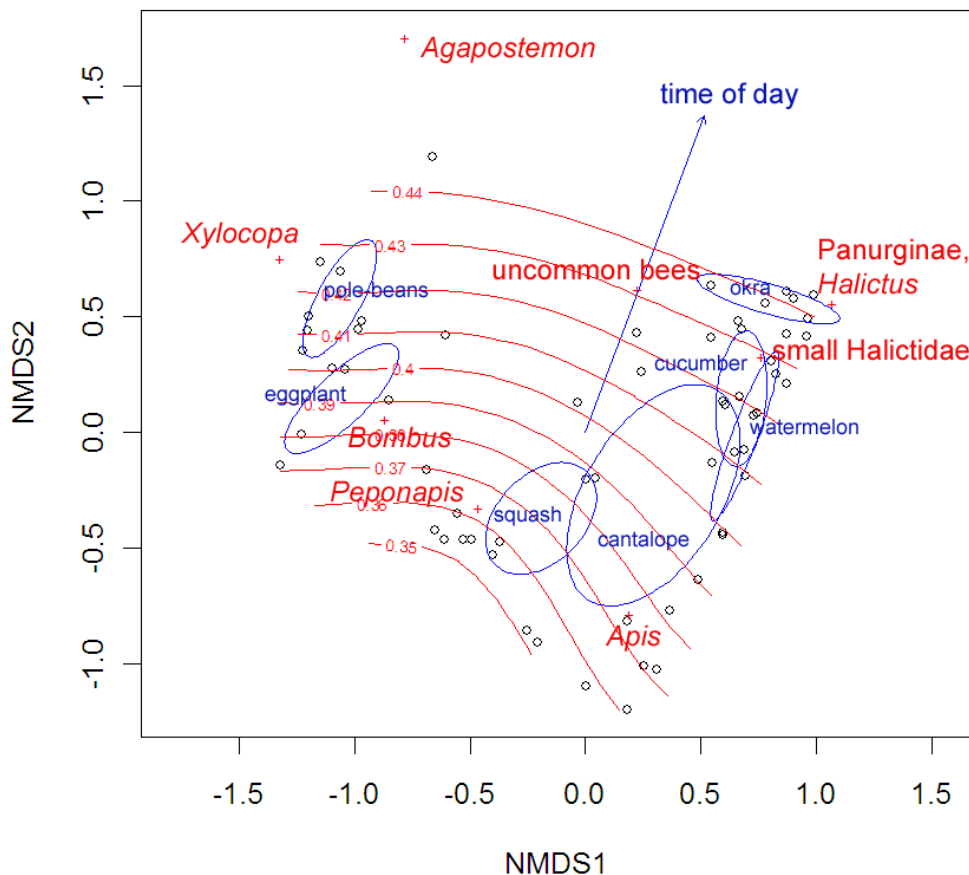


Figure 1.1: Bee visitation on one East Tennessee farm represented by nonmetric multidimensional scaling (NMDS) ordination. Unlabeled points represent transect observations. Labeled crosses represent bee category scores. Ellipses are the class factor of flower type and 95% confidence intervals of the standard deviation of their weighted averages. Permutation testing of flower type within day shows this factor is significant ($P < 0.001$). A vector fitted to the time of day within flower type is significant ($P < 0.001$). Thin plate regression splines further show the effect of time of day on the ordination using a generalized additive model with family = quasipoisson.

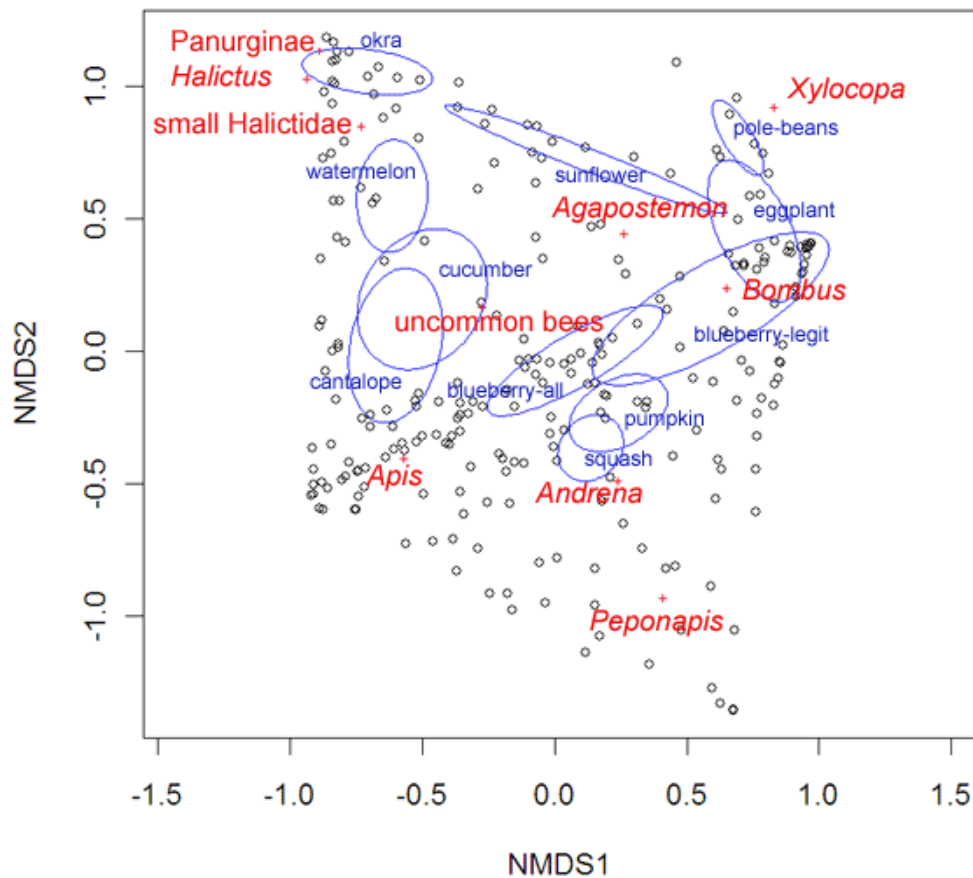


Figure 1.2: Bee visitation to 10 crops across 11 Tennessee farms represented by NMDS ordination. Unlabeled points represent transect observations. Labeled crosses represent bee category scores. Ellipses are the class factor of flower type and 95% confidence intervals of the standard deviation of their weighted averages. Permutation testing of flower type shows the factor is significant ($P < 0.001$).

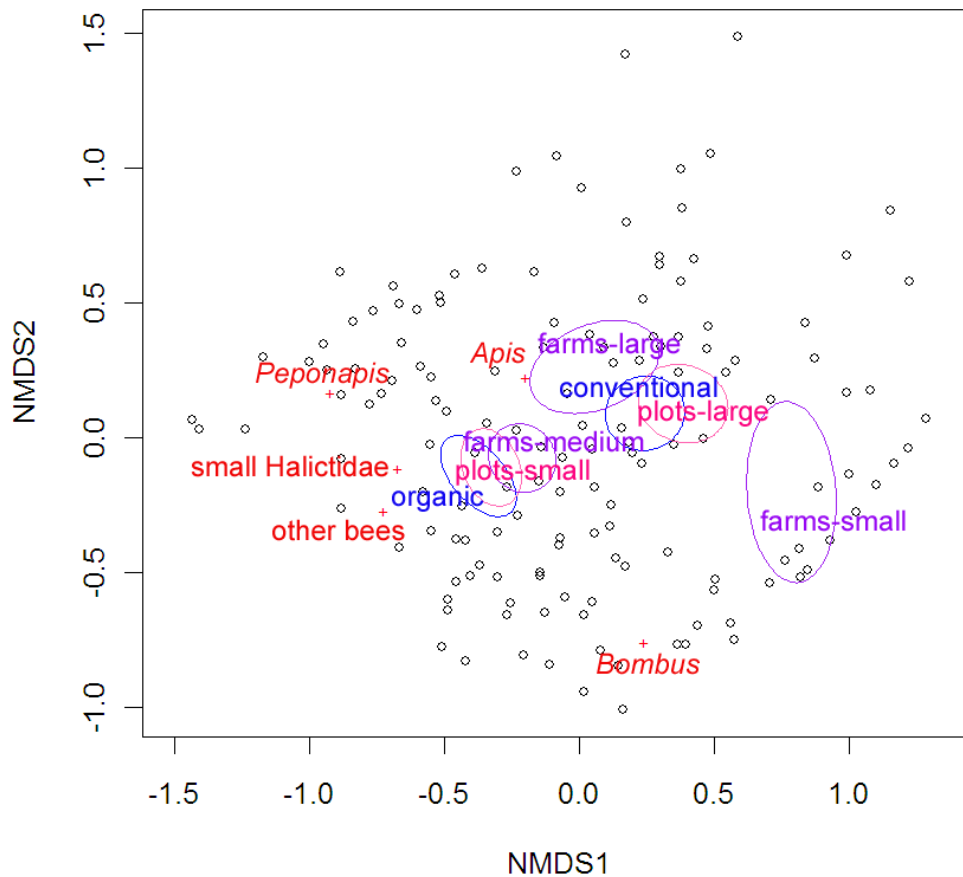


Figure 1.3: Bee visitation to squash and pumpkin across 10 East Tennessee farms represented by NMDS ordination. Unlabeled points represent transect observations. Labeled crosses represent bee category scores. Ellipses are the class factors and 95% confidence intervals of the standard deviation of their weighted averages. Class factors are farm size ($P = 0.001$), plot size ($P = 0.001$), and organic practices ($P = 0.001$).

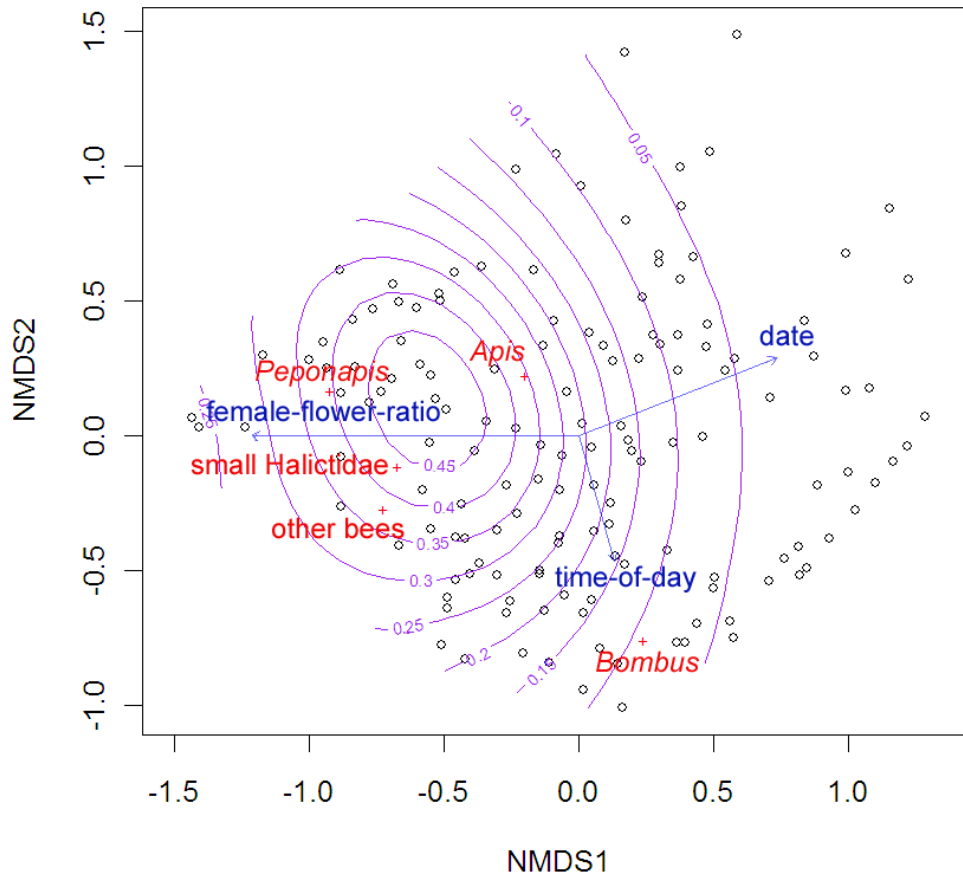


Figure 1.4: Bee visitation to squash and pumpkin across 10 East Tennessee farms represented by NMDS ordination, with environmental vectors and regression splines for time of day. Unlabeled points represent transect observations. Permutation testing within transect specified as strata shows the vectors are significant for date ($P < 0.001$), time of day ($P = 0.018$), and female flower ratio ($P < 0.001$).

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Part 2

Visitation to flowers used as food sources for bees important in crop pollination

Abstract

Flower plantings can improve habitat for bees on farms by providing pesticide free and resource rich food sources. Evaluation of potential plants to use in bee food plots is needed to ensure that plantings effectively provide food for bees important in crop pollination. At a single farm, bee visitation was observed for 24 flowering species that could be used in bee food plantings along with four vegetable crops. Permutational ANOVA of distance matrices showed that the composition of bees visiting flowers is consistent across multiple transects of the same flower or flower mix at a single location, but differ among flowers and seed mixes. Using nonmetric multidimensional scaling, differences in the composition of bees showed that a few flowers can be selected to target feeding only honey bees and bumble bees, two of the most important bees in crop pollination. However, other bees are providing pollination to crops at the study site and providing food for them would be missed by selecting only these flowers. To provide supplemental food for all bees providing pollination services, it will likely be necessary to plant a diverse set of flower species.

Introduction

Eighty-seven of the 115 leading global food crops are dependent on animal mediated pollination and threatened by agricultural intensification (Klein et al. 2007). Many important pollinators are in decline, but conservation and restoration practices can provide mitigation (National Research Council 2007). In the U.S., conservation

provisions through the National Resources Conservation Service (NRCS) have been highly successful in establishing habitat to provide resources for bees (Spivak et al. 2011). Honey bees (*Apis mellifera*) are considered the most important pollinator of agricultural crops, but many other non-*Apis* bees are highly important in crop pollination and can benefit from habitat conservation and restoration (Delaplane and Mayer 2000).

Pollination services provided by non-*Apis* bees require natural or semi-natural habitat patches be near the target crops (Garibaldi et al. 2011, Ricketts et al. 2008). The health and effectiveness of managed honey bees also benefit from nutritious, pesticide-free pollen sources (Brodshneider and Crailsheim 2010). Extensive efforts are underway to provide these sources through “bee pastures” (Decourtye et al. 2010). Beyond floral resources, habitat conservation can provide undisturbed nesting sites for ground nesting bees. Ground nesting bees are an important resource for agriculture (Cane 1997) and their presence can be influenced by habitat proximity (Kim et al. 2006). However, floral resources are likely to be the limiting factor for bee populations (Roulston and Goodell 2011), and, therefore, possibly the easiest to utilize and improve.

Benefits from restoration of habitat can be understood by differences observed in areas of natural habitat gradients. In California’s Central Valley, Kremen et al. (2004) showed that pollination services by native bees was positively related to natural habitat, but none of the other factors examined, including farm type, insecticide usage, field size, and abundance of honey bees. Contrasting this with areas such as New Jersey and Pennsylvania, habitat gradients are not as dramatic. Native bee visitation in these areas is

consistently high across locations (Winfree et al. 2007). Using meta analysis to review the results from 54 studies, Winfree et al. (2009) showed that habitat loss and fragmentation significantly negatively affected bee abundance and species richness, but only in areas where little natural habitat existed. When the landscape is structurally rich, the species richness and abundance of wild bees is greater than in landscapes with fewer habitat patches. However, not all bee species are affected equally. Bumble bees, which are social bees with distant foraging ranges, are not always significantly affected by landscape context (Steffan-Dewenter et al. 2002).

Establishing new, flower rich habitat is unlikely to increase bee diversity and abundance, unless new establishments are in close proximity to pre-existing flower-rich habitat (Kohler et al. 2008). Lacking sufficient habitat nearby could explain why an urban garden could fail to increase insect richness (Matteson and Langellotto 2011). However, even in areas with minimum natural habitat, improvements in bee populations should occur with restoration. Independent of natural habitat proximity, the abundance of important social bees capable of distant foraging ranges, like bumble bees, can be positively influenced by flowering resources, even flowers provided by commercial crops (Steffan-Dewenter et al. 2002, Westphal et al. 2003). Measuring functional effects of plant-pollinator networks instead of species richness and abundance can further show restoration of pollination services without contribution from adjacent, pre-existing natural habitat. Forup et al. (2008) examined pollination networks to show that visitation and movement of pollen was re-established on restored habitat, in this case western European

heathlands, by their most important pollinators (honey bees, bumble bees, and hover flies). Less common species were only found in ancient heathlands, a habitat characterized by ericaceous dwarf shrubs established over 250 years ago. In the complete absence of natural habitat, semi-natural habitat is often present in the form of pastureland, or some other land use capable of producing flowering plants or nesting sites. Morandin et al. (2007) showed that in these areas, a mosaic of intensive agriculture and pastureland produces a higher abundance of bumble bees in canola fields than in landscapes without pastureland.

To restore habitat or otherwise provide additional nectar and pollen resources for bees, it is important to understand flower preference of different bee groups. Bees may 'prefer' or by other means partition their presence at flowers, based on morphological characteristics of the flower. For example, long tongued bumble bees may utilize flowers with deep corollas, while bees with shorter tongues must search for resources that their mouthparts can reach (Inouye 1980). The native squash bees *Peponapis* and *Xenoglossa* only obtain pollen from *Cucurbita* species using pollen collecting structures specialized to their species and adapted specifically to accommodate the varying morphology of pollen grains within *Cucurbita* (Hurd et al. 1971).

To develop bee pastures on farms, it may be helpful to consider what bees are important in pollination of crops at farms to ensure bee pastures are providing additional sustenance for these bees. We can provide additional plants to benefit bumble bees (Carvell et al. 2004, Pywell et al. 2005, and Pywell et al. 2006), but the only way to

provide additional food for squash bees would be to grow more *Cucurbita*. Among flowers that do provide food for bees important as crop pollinators, differences in the abundance of bees attracted may also vary, explaining their effectiveness in providing bee food (Tuell et al. 2008).

The goal of this study was to determine the effectiveness of 3 commercially available flower mixes and 3 common field covers in providing food resources for bees. Observations of bee visitation was analyzed using nonmetric multidimensional scaling (NMDS) ordination to make comparisons based on bee abundance and preference among flower mixes and covers. Then, visitation was compared among individual bee food species and crops grown at the same location to determine if the bee food species were benefiting the same bees contributing to crop pollination at the study site.

Materials and methods

Study site and plots

The study site was located at the University of Tennessee, East Tennessee Ag Research and Education Center, Organic Crops Unit. This is a 100 acre experiment station with 21 acres in cultivation during 2009. Fourteen of the 21 acres are managed organically. In spring of 2008, three wildflower mixes were planted in a randomized block design. Each of the three plots within a block was 2 X 6 meters placed linearly in a row. This was repeated 3 times for 3 blocks. Before planting, a cover of wheat was

mowed down and the ground was thoroughly cultivated with a disk. As weeds began to emerge, a second cultivation with a disk was made to kill the weeds. Two drip irrigation lines were placed in the middle of each row, but water was only provided a few months after planting during the dry summer season of 2008. In early spring 2009, the flower mix plots were weeded. The only noticeable weed removed was wild sweet potato vine (*Ipomoea pandurata*).

Bee visitation was observed from May through August 2009, after the flower mixes were well established. In addition to the flower mixes, bee visitation was observed on other flowering plants at the Organic Crops Unit. These measurements were made in plots of; 3-4 acres in yellow sweet clover (*Melilotus officinalis*), buckwheat (*Fagopyrum esculentum*) planted between the rows of flower mixes as well as in other acre size plots, wild white dutch clover (*Trifolium repens*) densely growing in mowed areas around vegetable plots, and in plots of squash, pumpkin, watermelon, and cucumber that were less than 1/4 acre.

Flower mix composition

Seeds for the three flower mixes were purchased from American Meadows, Williston, VT. The first mix (southeast wildflower seed mix) included 26 species for southern region conditions (mix-ps); the second (dry area wildflower seed mix), included 25 species for dry areas (mix-dt); and the third (native southeast wildflower seed mix) included 17 species of native wildflowers (mix-n) (see Table A.2). The proportion of

seed per species in the mix was unknown. To determine the composition of plants in bloom where observations of bees would occur, a “hula” hoop (3,959 cm²) was thrown randomly three times per plot in each block on 7 occasions during the study period. For each hoop toss, the species of flowers in bloom within the hoop were recorded. Since there were 3 plots per flower mix and 3 hoop tosses per plot, a maximum score of 9 was possible for any species in flower for each date. The results were graphed in SigmaPlot (Version 9.0) to give a representation of the species in flower and their abundance, based on their hoop toss score. Data on the Y axis was arranged so that no columns would be hidden.

Bee visitation

Transects were established through all flowering plots to conduct visual counts of bees on flowers. In the wild flower mixes, counts included all bees visiting flowers within the 2 X 6 meter plot. For vegetable crops and field covers, transects were established that would cover a 2 meter wide area of the plot in flower to allow comparisons of observations made in the wild flower mixes. These transects were chosen to be a representative sampling of the plot and varied in length relative to the size of the plot, with a minimum length of 60ft. Transects avoided edges when possible and would cross multiple rows when numerous rows were present. The same transect was walked multiple times of day (from 07:20 hrs till 15:30 hrs) and multiple days (13 days from May 21st through August 19th) to sample bee visitation over a period of days and at different times

of day. Within field covers, there was one transect for yellow clover, 5 transects in buckwheat, and 3 transects in white dutch clover. The vegetable plots were represented by 1 transect each, except for squash which had 2 transects.

The response variable was recorded as the number of bees visiting flowers along a transect, organized into 10 easily recognized categories of bees. Many bees require examining microscopic characters to determine their species. Therefore, the bees were grouped into categories following a taxonomic sufficiency approach (Terlizzi et al. 2003) to identify bees in the field. This avoided destructive sampling and allowed the collection of more data. Voucher specimens (596 bees) were collected by netting at flowers and by fluorescent yellow, blue, and white painted pan traps with soapy water (Droege 2010). Voucher specimens were identified to genus and organized into the 10 categories to ensure that field identifications could be related to specific genera of bees (see appendix). The categories are: *Agapostemon*, *Andrena*, *Apis* (*Apis mellifera*), *Bombus*, Megachilidae (*Osmia* and *Megachile*), Panurginae and *Halictus* (*Calliopsis*, *Protandrena*, and *Halictus*), *Peponapis*, small Halictidae (*Augochloropsis*, *Augochlora*, *Augochlorella*, *Lassioglossum*, and *Sphecodes*), uncommon bees (*Ceratina*, *Eucera*, *Hylaeus*, *Melissodes*, *Nomada*, *Perdita*, *Svastra*, and *Triepeolus*), and *Xylocopa* (*Xylocopa virginica*). The species of plant the bees were observed on was also recorded. In partridge pea (*Chamaecrista fasciculata*) counts were organized into bees visiting the flower and bees visiting the nectaries found on the stem of the plant. For all other plants, bees were

only counted if they were on their flowers and appeared to be obtaining nectar or pollen. The date and time were also recorded.

Data analysis

Observations were organized into two data sets. The first set used flower type as a class factor with observations from mix-ps, mix-dt, mix-n, buckwheat, yellow clover, and white dutch clover. Each flower mix plot was 6 meters long; therefore, counts for field covers were equalized to 6 meter lengths to standardize sampling effort. After equalizing for transect length, observations with less than 9 total bees were removed being considered insufficient for representative bee visitation. *Andrena*, Megachilidae, *Peponapis*, and uncommon bees were combined into the 'other bees' category, due to low or zero visitation.

To measure the variance from multiple transects of a given flower type on the distance matrix, permutational multivariate analysis of variance using distance matrices was conducted with Adonis in the Vegan package of R (Version 1.17-4). Using method = Bray-Curtis and 999 permutations, the linear model identified the effect of transect within the flower type and flower type as explanatory variables. Then, nonmetric multidimensional scaling (NMDS) in Vegan was used with Bray-Curtis rank similarity, permutation testing, and weighted average confidence intervals to graphically illustrate differences in visitors based on flower type.

For analysis of the second data set, the individual flower species, instead of mixes, was used as the explanatory factor and observations from the vegetable plots were added. Observations of flowers within the three mixes combined all blocks into a single transect, because some flowers were low in abundance. This made the flower mix transects 18 meters long, therefore, counts for field covers were equalized to 18 meter lengths to standardize sampling effort. After equalization, observations with less than 4 total bees were considered insufficient for representative bee visitation. Four was used instead of 9 to preserve observations for flower species with few visitors, or flower species low in abundance. Counts for bee categories were converted to proportion of total bee counts in the observation then subjected to NMDS with Bray-Curtis rank similarity, permutation testing, and weighted average confidence intervals. The original ten categories of bees were preserved in the NMDS ordination.

Results and discussion

The study period was during the second year after establishment of the flower mix plots. This study does not measure the performance of the flower mixes over the 2 years past their establishment. Instead, the study examines the composition of bees occurring on the different flowers during the 4 month study period. To understand differences in the bees recorded among different flower mixes, it is important to understand what flower species in the mixes were blooming at that time. Figures 2.1, 2.2, and 2.3 describe the composition of flowers blooming in the 3 plots of mixed flowers. Within each mix, some

species occurred that were not in the original seed mix, likely due to seeds drifting during the previous season. Also, flowering plants that were not a part of any mix were found, likely from seeds drifting from nearby plots. These flowers' presence and visitation of bees to them is included in the results. During the study period, the number of flower species within each mix was 17, 13, and 12 in mix-ps, mix-dt, and mix-n, respectively. Twenty-one unique flower species occurred among all three mixes.

For the first data set of visitation to the flowering plants, Adonis analysis indicated the variance from multiple transects within a flower type did not have a significant effect on the distance matrix ($P = 0.129$). However, the flower type did have a significant effect ($P = 0.001$). It is possible that the same flowers or flower mix should attract the same groups of bees at a single location. Multiple transects within a flower type could then be omitted in NMDS analysis. In the experimental design of similar future studies, multiple transects of the same flower type at the same location may be unnecessary.

Results from NMDS analysis is shown in the ordination Figure 2.4. Ellipses represent 95% confidence intervals identifying the average observation among flower types in relation to each other. Ellipses for mix-ps and mix-dt are not statistically different from each other but are different from all other flower types. The communities of bees visiting these mixes are similar to each other. If deciding between these two mixes, the bees they attract are the same and not a consideration. However, if selecting future plantings among all the flower types, the group of bees that will be fed varies among the available options. For example, yellow clover ordines directly on top of

Apis, since it was predominantly visited by honey bees. White clover and buckwheat both ordinate between *Bombus* and *Apis*, showing how these two bee categories were nearly equally frequent visitors. Mix-n received more visitation from *Bombus* than any other bees, as reflected in the ordination.

A decision on which flowers to plant as bee food on farms could be based on what bees are important for pollination of crops grown on these farms. In part 1 of this thesis, we showed that native bees are important crop pollinators, but their importance and composition varies among different crops. For example, since bumble bees provided 55% \pm 20 of visitation to blueberry, farms only growing blueberry may want to concentrate on feeding bumble bees. Most of the bumble bees visiting blueberry in that study were queens (personal observation) that must have overwintered nearby from the previous season. Overwintered queens establish a new nest in spring that will produce workers and then change later in the season to produce queens for overwintering and establishment of the following year's nests (Heinrich 1979). Therefore, their abundance during blueberry bloom for the following year is dependent on their ability to produce queens after blueberry bloom ceases. Planting flowers selected to feed bumble bees after blueberry bloom stops may improve their success for the next year's blueberry bloom.

In the second data set, we compare the composition of bees visiting flower species that could be used in a bee food plot and vegetable flowers at the same location. Observations of bees on several flower species were removed from this data set due to the low abundance threshold. In Figure 2.5, white clover and buckwheat flower types

again fall between *Apis* and *Bombus*, but this time observations previously combined into mix-n are now related to the individual flower species. From that mix, bee balm (*Monarda citriodora*) and hairy vetch (*Vicia villiosa*) were dominated by *Bombus* visitors as well as the flowers from partridge pea (*Chamaecrista fasciculata*), labeled Chamecrista-f. Observations on partridge pea extra-floral nectaries (Chamecrista-n) were different and ordinate near *Apis*, their most frequent visitor. Observations on watermelon, squash, and pumpkin ordinate outside of this gradient between *Apis* and *Bombus* indicating a more diverse set of bees are visiting these flowers, primarily *Peponapis* and small Halictidae. Other bee food flowers *Rudbeckia spp.*, *Cosmos bipinnatus*, and *Coreopsis lanceolata* ordinate away from *Bombus* and *Apis* showing less utilization by these bees. However, considerable variation in *Bombus* visitation to *Cosmos bipinnatus* and *Coreopsis lanceolata* exists as seen in Figure 2.5, where the ellipses extend towards *Bombus*. Due to the importance of honey bees and bumble bees in crop pollination (Delaplane and Mayer 2000), selecting only these last four flowers in a bee food plot could miss providing food for some of the most important crop pollinators, since *Bombus* and *Apis* were not consistently utilizing these flowers. However, selecting only bee food plants between the gradient of *Apis* and *Bombus* could miss providing food for other bees important in pollination of vegetable crops, since the vegetable plots ordinate outside of the gradient between *Apis* and *Bombus*.

A diverse set of flowers for bee food plots will be necessary to provide supplemental food for the diverse species of bees providing pollination on farms. Yet,

even diverse food plots are unlikely to provide food for all bees important in crop pollination. The native squash bee *Peponapis* is an important pollinator of squash and pumpkin (Cane et al. 2011), but was not present on any of the bee food flowers. It is oligolectic to squash and pumpkin (Hurd et al. 1974), therefore, methods to conserve this bee will need to utilize other strategies such as reduced tillage practices (Shuler et al. 2005) and ensuring that pesticides do not negatively impact their populations.

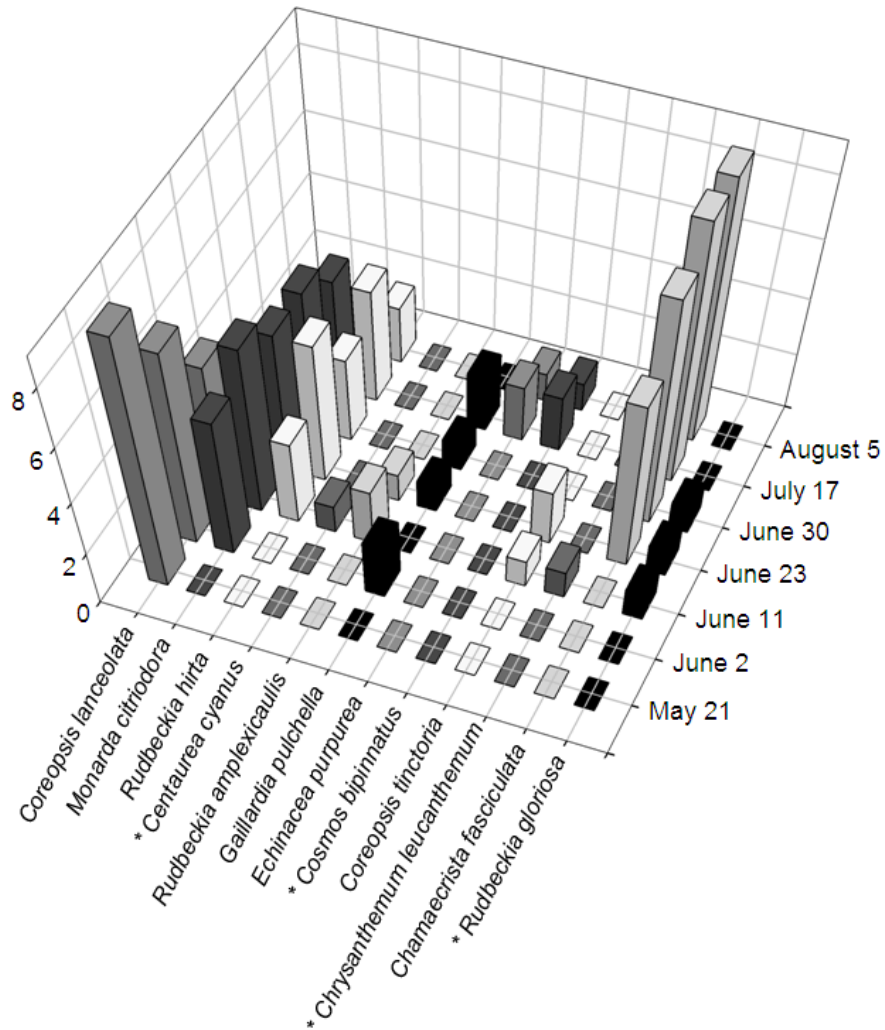


Figure 2.1: Flower mix-n species in flower from May 21st to August 5th, 2009. The maximum possible score for each species per sampling date is 9. Each score was determined by 3 hoop tosses for each of the 3 blocks. Species were arranged so no columns would be hidden. Species marked with an asterisk (*) were not listed in the original seed mix.

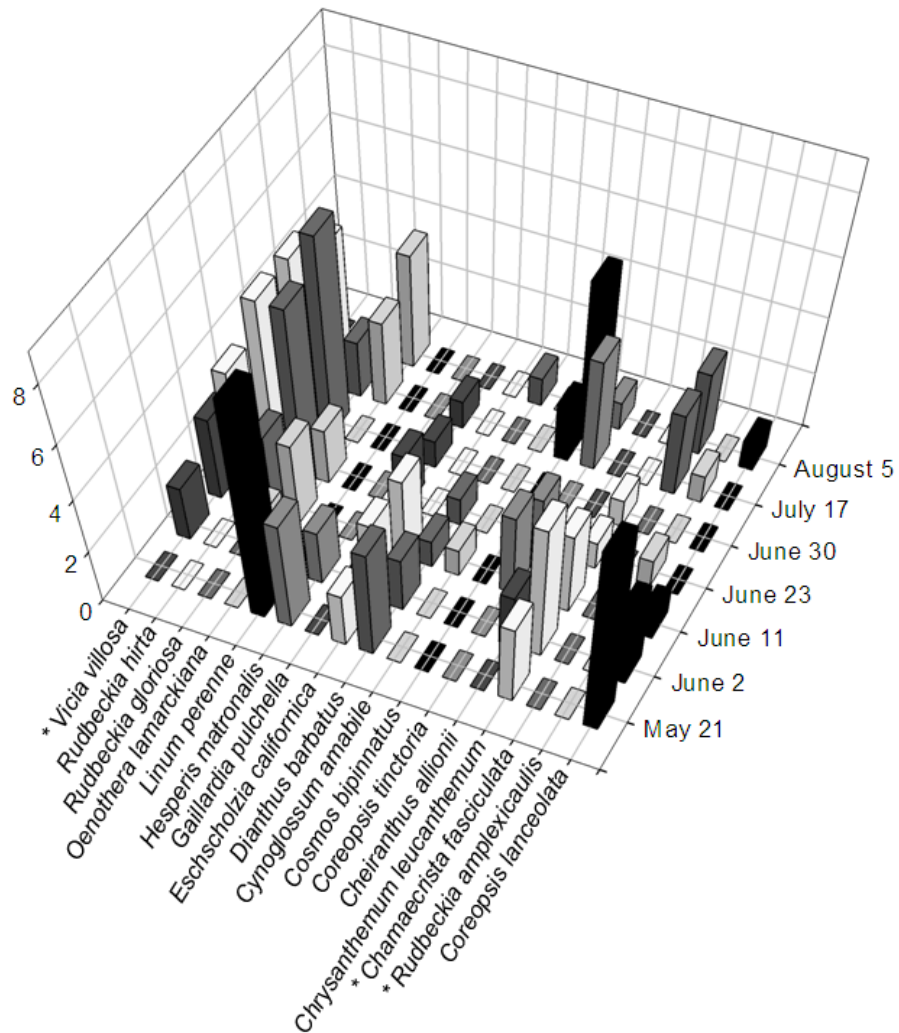


Figure 2.2: Flower mix-ps species in flower from May 21st to August 5th, 2009. The maximum possible score for each species per sampling date is 9. Each score was determined by 3 hoop tosses for each of the 3 blocks. Species were arranged so no columns would be hidden. Species marked with an asterisk (*) were not listed in the original seed mix.

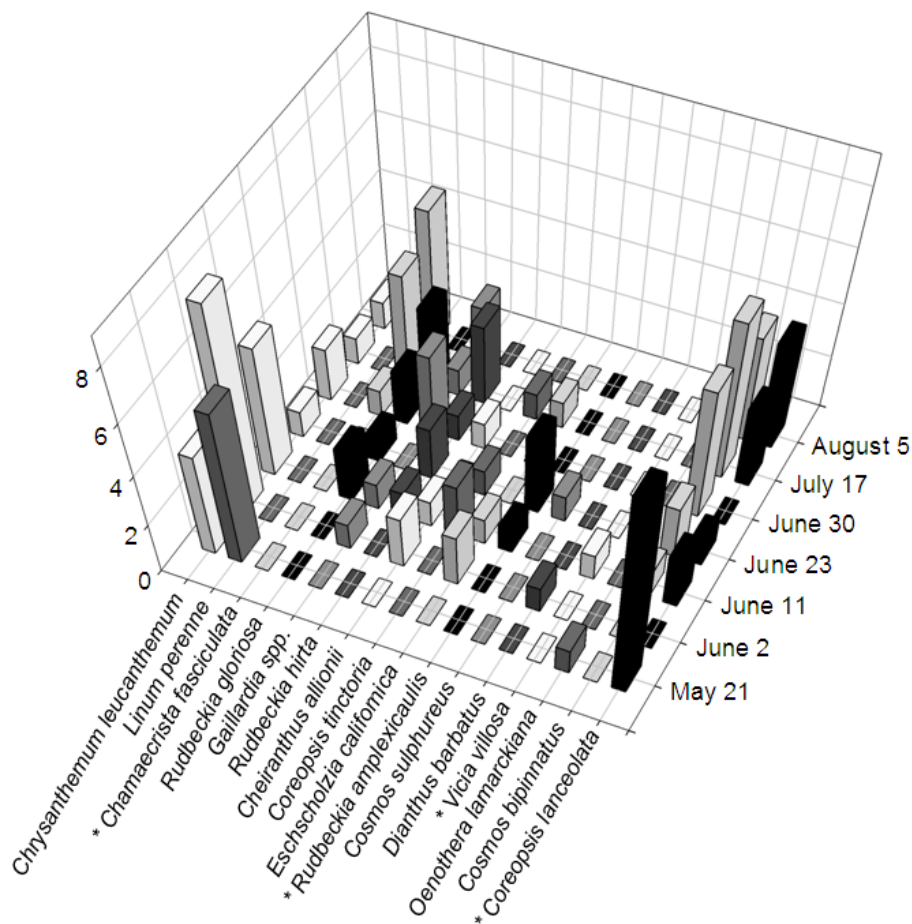


Figure 2.3: Flower mix-dt species in flower from May 21st to August 5th, 2009. The maximum possible score for each species per sampling date is 9. Each score was determined by 3 hoop tosses for each of the 3 blocks. Species were arranged so no columns would be hidden. Species marked with an asterisk (*) were not listed in the original seed mix.

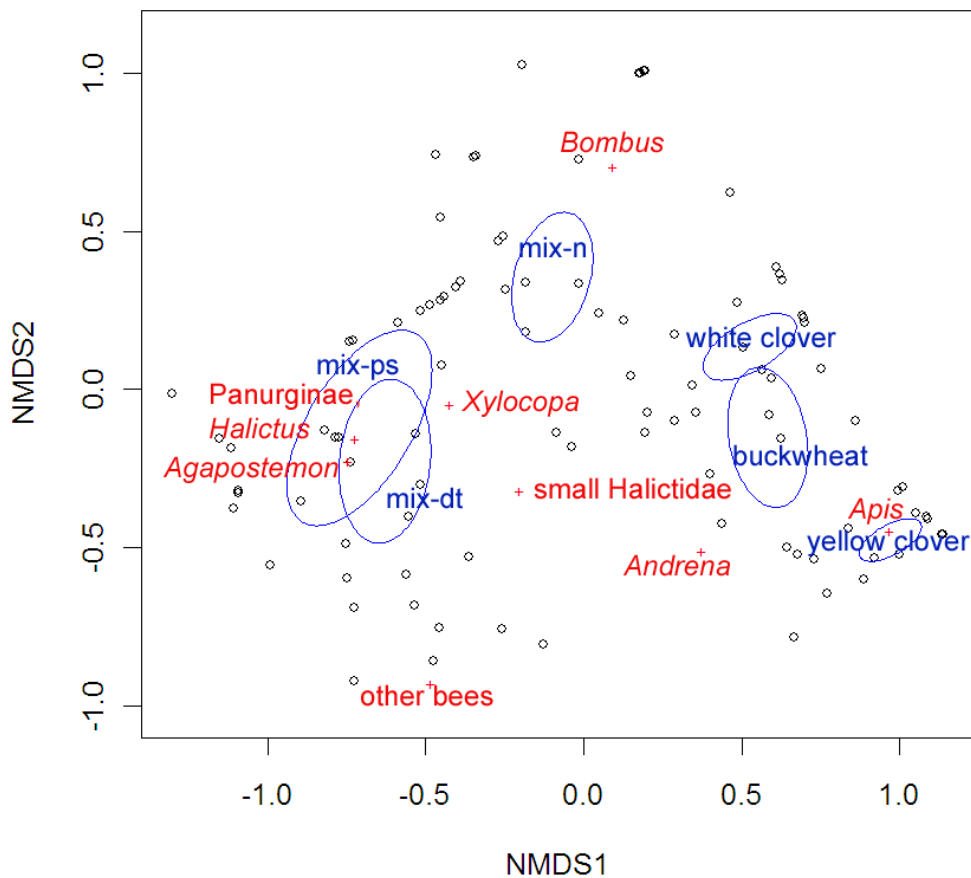


Figure 2.4: Bee visitation to 3 flower mixes, white clover, buckwheat, and yellow clover represented by non-metric multidimensional scaling (NMDS) ordination. Unlabeled points represent transect observations. Labeled crosses represent bee category scores. Ellipses are the class factor of flower type and 95% confidence intervals of the standard deviation of their weighted averages. Effect of flower type on the ordination is significant ($P < 0.001$).

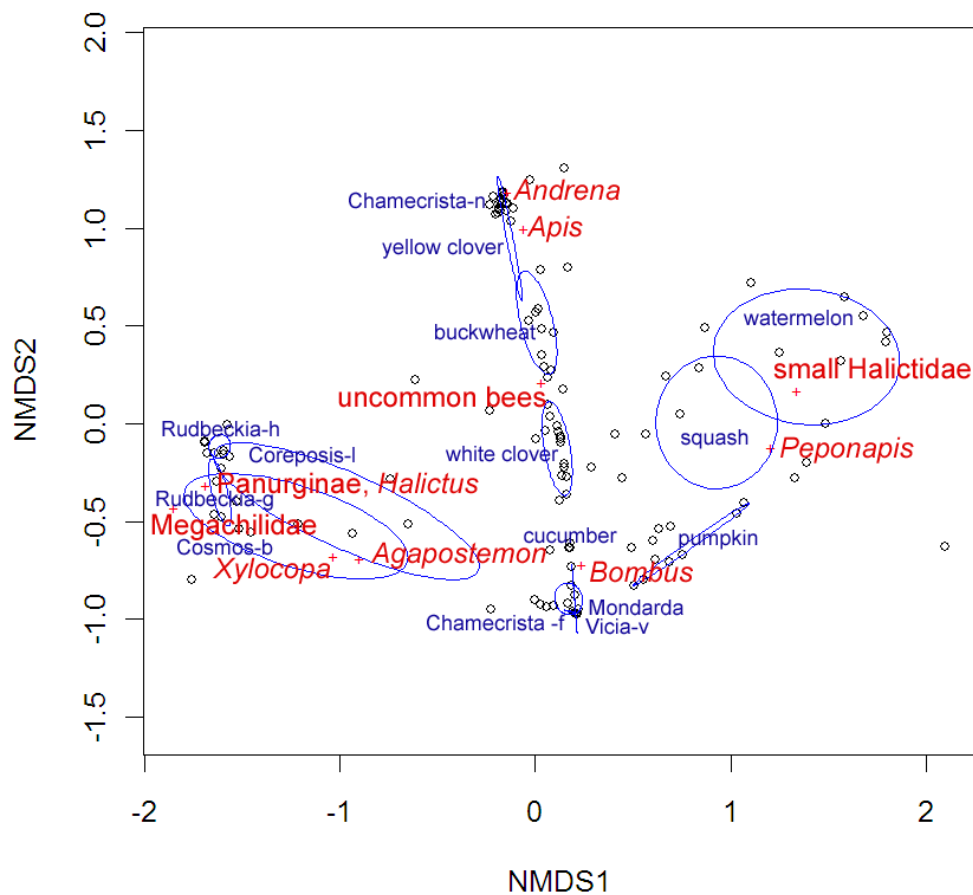


Figure 2.5: Bee visitation to crops and other flowering species represented by NMDS ordination. Unlabeled points represent transect observations. Labeled crosses represent bee category scores. Ellipses are the class factor of flower type and 95% confidence intervals of the standard deviation of their weighted averages. Effect of flower type on the ordination is significant ($P = 0.001$).

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Conclusions

Honey bees are clearly critical to the production of many food crops in both large and small scale production systems. Within small production systems like those encountered in this study, we see how food production relies at times quite heavily on the health of the surrounding ecosystem. Non-managed bees present in the landscape are providing large proportions of the total bee visits to these crops. We cannot predict for certain what would happen at these study sites if either honey bees or key non-*Apis* bees were removed from the system. However, we can look to large scale agriculture in areas like California's Central Valley, where non-*Apis* bees are more rare visitors to crops for comparison. Those systems are more dependent on managed honey bees as pollinators and are more sensitive to the instability in supply and health of managed honey bees.

This study represents a picture in time of the contribution of the surrounding ecosystem to crop pollination. Since similar work in the study area has not occurred before, and is not going on now, we do not know how or if the contribution of native bees to crop pollination is changing over time. The groupings of non-*Apis* bees observed in this study may represent only a small amount of the diversity that may have been present in the recent past. For example, the native southern blueberry bee *Habropoda laboriosa* is among the most important pollinators of blueberry in the south. However, it was not observed at any of the three blueberry study sites. It could be that the study sites are outside of its natural range, or that we have lost this important, efficient pollinator of blueberry. Without long term studies occurring both in the past and in the future, we simply do not know. The native squash bee was present at all sites growing squash and/or

pumpkin in the study area, but in numbers unlikely to provide full pollination (personal observation). Through the Squash Pollinators of the Americas Survey, we see that in other areas full pollination without honey bees can occur due to the abundance of squash bees. In 2009, the study area experienced heavy rains that may have affected the abundance of this ground nesting bee. Or, it may be that the recent, widespread introduction of the neonicotinoid class of systemic pesticides now used in squash and pumpkin production have reduced their numbers. Or still, it may be that this area does not support large numbers of native squash bees for some other reason and their abundance in 2009 was normal. Long term studies are needed to monitor these important pollinators. For this reason, abundance data for squash and pumpkin is included as an attachment to this thesis, see comma separated file (.csv), BeeAbundance.csv. The .csv can be opened in spreadsheet software like OpenOffice CALC or Microsoft Excel.

If major native bee losses occur in the area, and crop yields decrease, the fact that pollinators are insufficient may not be immediately evident. And, without knowing more about the non-*Apis* bees capable of functioning within this system and providing crop pollination, their presence will be even that much harder to restore if losses occur. There is an existing ecology behind food production that is defined by historical and evolutionary events. We can examine this ecology, but as outlined in the introduction of this thesis, it changes constantly. It is our responsibility to ensure that changes occur in the best interest of sustaining food production and other biological necessities.

Habitat restoration and improvement for bees has widespread interest and activity through planting food for bees. Lists of plants to use exist, and sources of seed are abundant, although not always affordable to many land owners and land managers. Literature is lacking that clearly shows economic benefits to investing in restoration for pollination. But, we can indirectly imply through logic, that bees require food and if the landscape does not have sufficient food to support the necessary abundance and diversity of bees, then providing supplemental food sources should help. What else is lacking, but probably more useful to improve upon, is the widespread knowledge of what flower species provide food for what bees, and if those same bees are important in crop pollination. Then, we need to know what flowers are the most efficient to grow and produce the most nectar and pollen with an optimal nutritional profile for these bees to thrive. In conjunction with this, we need to have some idea of the area requirements of habitat, which could vary per combinations of plants and bee species, which an ecosystem requires to provide pollination. This all seems very complicated and one might be inclined to instead count on crop pollination through the use of *Apis mellifera*, a bee proven to be a requirement for the large scale production of nutritious foods. But, clearly the challenges with honey bees that have been presented within recent years through reliance on this single species for most crop pollination should inform us to not forget the stability and requirement for diversity in food production.

Appendix

Table A.1. Voucher bee specimens organized into 10 categories easily recognizable in the field.

Category designation	Geuns or species	Number collected
<i>Agapostemon</i>	<i>Agapostemon</i>	31
<i>Andrena</i>	<i>Andrena</i>	33
<i>Apis</i>	<i>Apis mellifera</i>	5
<i>Bombus</i>	<i>Bombus</i>	30
Megachilidae	<i>Megachile</i>	2
	<i>Osmia</i>	2
Panurginae and <i>Halictus</i>	<i>Protandrena</i>	11
	<i>Calliopsis</i>	3
	<i>Halictus</i>	60
<i>Peponapis</i>	<i>Peponapis</i>	6
Small Halictidae	<i>Augochloropsis</i>	1
	<i>Lassioglossum</i>	348
	<i>Augochlora</i>	1
	<i>Augochlorella</i>	10
	<i>Sphecodes</i>	4
	<i>Ceratina</i>	1
Uncommon bees	<i>Eucera</i>	6
	<i>Melissodes</i>	11
	<i>Svastra</i>	1
	<i>Perdita</i>	17
	<i>Triepeolus</i>	2
	<i>Nomada</i>	3
	<i>Hylaeus</i>	1
<i>Xylocopa</i>	<i>Xylocopa virginica</i>	7

Specimens are deposited at the University of Tennessee, Department of Entomology and Plant Pathology insect museum, Knoxville, TN.

Table A.2. Flower mixes planted in 2008.

Native southeast wildflower seed mix (mix-n)	
Botanical Name	Common Name
<i>Asclepias tuberosa</i>	Butterfly Weed
<i>Chamaecrista fasciculata</i>	Partridge Pea
<i>Coreopsis lanceolata</i>	Lance-Leaf Coreopsis
<i>Coreopsis tinctoria</i>	Plains Coreopsis
<i>Echinacea purpurea</i>	Purple Coneflower
<i>Eryngium yuccifolium</i>	Rattlesnake Master
<i>Gaillardia pulchella</i>	Indian Blanket
<i>Ipomopsis rubra</i>	Standing Cypress
<i>Liatris spicata</i>	Blazing Star
<i>Lupinus perennis</i>	Wild Blue Lupine
<i>Monarda citriodora</i>	Lemon Mint
<i>Phlox Drummondii</i>	Drummond Phlox
<i>Ratibida columnaris</i>	Mexican Hat
<i>Rudbeckia amplexicaulis</i>	Clasping Coneflower
<i>Rudbeckia hirta</i>	Black-eyed Susan
<i>Salvia coccinea</i>	Scarlet Sage
<i>Tradescantia ohiensis</i>	Spiderwort
Southeast wildflower seed mix(mix-ps)	
Botanical Name	Common Name
<i>Cheiranthus allionii</i>	Siberian Wallflower
<i>Chrysanthemum leucanthemum</i>	Ox-Eye Daisy
<i>Coreopsis lanceolata</i>	Lance-Leaf Coreopsis
<i>Coreopsis tinctoria</i>	Plains Coreopsis
<i>Cosmos bipinnatus</i>	Wild Cosmos
<i>Cynoglossum amabile</i>	Chinese Forget-Me-Not
<i>Dianthus barbatus</i>	Wild Sweet William
<i>Echinacea purpurea</i>	Purple Coneflower
<i>Eschscholzia californica</i>	California Poppy
<i>Gaillardia pulchella</i>	Indian Blanket
<i>Gysophila elegans</i>	Baby's Breath
<i>Hesperis matronalis</i>	Dame's Rocket
<i>Ipomopsis rubra</i>	Standing cypress
<i>Lavatera trimestris</i>	Rose Mallow
<i>Liatris spicata</i>	Dense Blazing Star
<i>Linum grandiflorum rubrum</i>	Scarlet Flax
<i>Linum perenne lewisii</i>	Blue Flax

<i>Lobularia maritima</i>	Wild Sweet Alyssum
<i>Lupinus perennis</i>	Wild Lupine
<i>Lupinus texensis</i>	Texas Bluebonnet
<i>Oenothera lamarckiana</i>	Evening Primrose
<i>Papaver rhoeas</i>	Red Poppy
<i>Phlox drummondii</i>	Drummond Phlox
<i>Rudbeckia hirta</i>	Black-eyed Susan
<i>Rudbeckia gloriosa</i>	Gloriosa Daisy
<i>Salvia coccinea</i>	Scarlet Sage

Dry area wildflower seed mix (mix-dt)

Botanical Name	Common Name
<i>Achillea millefolium</i>	White Yarrow
<i>Centaurea cyanus</i>	Cornflower
<i>Cheiranthus allionii</i>	Siberian Wallflower
<i>Chrysanthemum coronarium</i>	Garland Chrysanthemum
<i>Chrysanthemum leucanthemum</i>	Ox-Eye Daisy
<i>Coreopsis tinctoria</i>	Plains Coreopsis
<i>Cosmos bipinnatus</i>	Wild Cosmos
<i>Cosmos sulphureus</i>	Sulphur Cosmos
<i>Dianthus barbatus</i>	Sweet William
<i>Dimorphotheca sinuata</i>	African Daisy
<i>Eschscholzia californica</i>	California Poppy
<i>Gaillardia aristata</i>	Perennial Blanketflower
<i>Gaillardia pulchella</i>	Annual Indian Blanket
<i>Gypsophila elegans</i>	Annual Baby's Breath
<i>Linaria maroccana</i>	Baby Snapdragon
<i>Linum perenne lewisii</i>	Blue Flax
<i>Lobularia maritima</i>	Sweet Alyssum
<i>Lotus corniculatus</i>	Bird's Foot Trefoil
<i>Oenothera lamarckiana</i>	Evening Primrose
<i>Papaver rhoeas</i>	Red Poppy
<i>Penstemon strictus</i>	Rocky Mountain Penstemon
<i>Ratibida columnaris</i>	Yellow Prairie Coneflower
<i>Rudbeckia gloriosa</i>	Gloriosa Daisy
<i>Rudbeckia hirta</i>	Black-eyed Susan
<i>Silene armeria</i>	None-so-Pretty

Vita

Michael Wilson grew up in and around Clinton, Tennessee where he lives with his family today. He graduated from Clinton High School in 1993 then attended the University of Tennessee Knoxville to receive his Bachelor's of Fine Arts in 1998. Soon thereafter he found a career in information technology at the University of Tennessee. His skills in information technology have been utilized by the honey bee research and extension community as content manager for an eXtension.org Community of Practice in bees (a web based, educational outreach system). Working at a university helped provide the opportunity to periodically build on his academic history in science and education and enter a Master's program. Not only concerned with books and computers, his interest in biology and agriculture, along with his hands on creative streak, led him to become a beekeeper just before the turn of the century and build a part-time beekeeping business in the time between.