The landscape ecology of bees visiting squash in a heavily forested temperate region

Christine Urbanowicz

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Approved by:

Aaron Moody, Ph.D.

Conghe Song, Ph.D.

Peter White, Ph.D.

ABSTRACT

CHRISTINE URBANOWICZ: The landscape ecology of bees visiting squash in a heavily forested temperate region
(Under the direction of Dr. Aaron Moody)

There is increasing interest to understand how to conserve bees that pollinate crops. My research examined local and landscape-scale effects on the diversity and abundance of bees visiting yellow squash and zucchini flowers in the piedmont of North Carolina. Explanatory models were constructed using variables related to field-level floral resources, landscape composition, and landscape configuration. Bee diversity, measured as species richness, was positively correlated with the abundance of flowers in a field and the clumpiness of wooded land and was negatively correlated with proportion of developed area around a field. The abundance of bees visiting zucchini, measured as visitation rate, was negatively correlated with the proportion of wooded land around a field, but no models could explain variation in visitation rate for yellow squash. This research demonstrates that efforts to conserve bee diversity need to consider the importance of land-management decisions made within a field and across a landscape.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

Table

LIST OF FIGURES

Figure

CHAPTER 1

INTRODUCTION

Efforts to conserve biodiversity are increasingly looking beyond protected areas and targeting working landscapes (Polasky et al. 2003, Vandermeer & Perfecto 2007). Given that 46% of the land in the United States is managed for crops and agroforestry (Lubowski et al. 2006) and 2.6% of the land is urban, it is important to understand the role of these landscapes in conserving biodiversity - particularly groups of species that provide ecosystem services. One such service is animal-mediated pollination, which is required for approximately one third of US crops and dependent on healthy bee populations (Greenleaf & Kremen 2006, McGregor 1976). Bees, like many organisms, are threatened by land-use change, which influences individual behavior, population dynamics, and community composition (Bommarco 2010, Kremen et al. 2007). In this study, I examined how the local environment on fields and the land cover around fields affect the diversity and visitation rate of native bees visiting squash flowers. Studying the response of bees to the landscape context of fields is particularly important because pollination is a mobile ecosystem service (Kremen et al. 2007), affected not only by land-use decisions made within a field but also decisions made across a landscape.

Native bees and crop pollination

Pollination occurs when bees are foraging for nectar or pollen and transfer pollen from a flower's stamen, where pollen is produced, to a flower's stigma (Richards 2001). This

process is a vital component of sustaining food production; in the United States, one third of crops depend on animal pollination while another third benefit by producing larger and healthier fruits (McGregor 1976). Although often overshadowed by the European honey bee, native bees greatly contribute to food production. Some crops, such as blueberries, are most effectively pollinated by native bees (Tuell et al. 2009). Furthermore, many farmers depend solely on native bees if they do not have managed honey bee populations. Native bees may even provide the majority of pollination services on farms that have managed honey bees (Winfree 2008).

Bees represent a diverse taxon: there are over 20,000 bee species worldwide (Kremen et al. 2003). Rather than focusing on select species, conserving a diversity of bees is important for crop pollination for several reasons. First, a diversity of bees may enhance pollination services due to species-specific niche partitioning (Hoehn et al. 2008). Bees emerge and are most active at different times of the growing season, causing a great turnover in pollinator communities between spring and fall (Oertli et al. 2005). Temporal turnover also occurs within the time frame of single day because bees vary in their diurnal activity (Hoehn et al. 2008, Tepedino 1981). This temporal complementarity can facilitate the pollination of a diversity of crops that open their flowers at different times and may also lead to higher fruit set within a single crop (Hoehn et al. 2008). Bees also have varying preferences for flower sizes and morphologies (Heard 1999). While most bees are not dependent on a single plant species, these preferences result in some degree of specialization between plants and their pollinators. For example, Winfree et al. (2008) found that bees had crop-specific floral preferences that resulted in watermelon and tomato having distinct sets of pollinators.

In addition to diversity, the redundancy of bees within a community may increase the resilience of a crop pollination system to disturbance (Peterson et al. 1998, Winfree et al. 2007a). Functional redundancy helps ensure that a loss of one species will not lead to the collapse of a pollination network. Much of the recent research on bees has been motivated by the possibility that native bees may be viable substitutes for declining populations of European honey bees (*Apis mellifera*; Lonsdorf et al. 2009, National Research Council of the National Academies 2006, Winfree et al. 2007a). Some native bee species are also showing patterns of widespread decline, including several bumble bee (*Bombus*) species in North America (Cameron et al. 2011). These declines have been linked to disease, reduced genetic diversity, and environmental change. Local declines in bee abundance and diversity are also widely reported, especially in areas with high anthropogenic disturbance where the need for crop pollination is great (Winfree et al. 2009). Given these declines, there is increasing interest in understanding how to conserve and promote native bee populations and their vital ecosystem service.

Maintaining bee populations in human-dominated landscapes

To maintain populations of any species, their habitats have to be conserved. In the case of bees, like many species, there are two habitat types to consider: nesting substrate and foraging resources (Westrich 1996). Nesting habitats vary by bee species but are usually in relatively undisturbed areas where bees excavate nests in wood or bare ground or use preexisting underground cavities such as abandoned insect burrows or rodent nests (Cane 2001). Unfortunately, specific habitat requirements are still unknown for many species due to the challenge of locating and surveying nesting sites. Compared to nesting habitat, much more is known about floral resources used by bees for pollen, nectar, oils, and resins. As

discussed, bees differ in their preferences for foraging habitat based on flower structure, size, and bloom time (Kremen et al. 2007).

By influencing the quality, availability, and accessibility of foraging and nesting resources, land-use decisions in and around fields should indirectly affect the diversity and abundance of bees visiting crops (Roulston & Goodell 2011). I first focus on field-level foraging resources. Then, I discuss how bees may respond to the composition and configuration of the landscape around fields.

Field-level foraging resources

While agricultural fields may not provide suitable nesting habitat due to irrigation and ground disturbance (Kim et al. 2006), flowering crops and wildflowers growing between rows and in the field margin can provide bees with foraging resources (Winfree et al. 2008). In some landscapes, crops may be particularly important because they bloom after many forest species, thus creating a continuity of foraging resources (Kremen et al. 2007). Previous research has shown that increased flower abundance has a positive effect on bee diversity (Holzschuh et al. 2007, Kohler et al. 2008) and abundance (Rundolf et al. 2007). Through experimental manipulation of the landscape, Kohler et al. (2008) found that pollinators ignored scattered flowers in agricultural landscapes in favor of larger quantities in natural areas. Both large and small-bodied bees may be attracted to areas where flowers are more abundant because the energy spent traveling from one floral patch to the next is reduced. Gathmann and Tscharntke (2002) found that bee foraging time, and therefore presumably foraging energy, declined in areas with an abundance and diversity of food resources. Bees may also return to resource-rich patches rather than search for new patches (Osborne et al. 1999), further reducing energy requirements.

In addition to flower abundance, flower diversity is also important to consider. Because bees exhibit preferences for certain flowers, a field with a diverse flower population may attract a diversity of bees. Many studies have found a positive relationship between local flower diversity and bee diversity (Biesmeijer et al. 2006, Pontin et al. 2007, Potts et al. 2003), suggesting that increased floral diversity alleviates competition between species through niche partitioning.

Landscape effects

Kremen et al. (2007) described pollination as a mobile ecosystem service because bees travel across the landscape to pollinate crops in a field. Equally important, the dispersal of bees across a landscape maintains genetic diversity within populations and may potentially rescue sink populations close to a field site (Kim et al. 2006). It is therefore expected that the landscape context of a field is an important determinant of bee diversity and abundance. The composition of land cover around a field may be related to the abundance and quality of nesting and foraging resources. The spatial configuration of land cover may further influence the accessibility of these resources.

Landscape composition

To my knowledge, all studies on landscape composition and bee diversity or abundance have considered forested areas to be natural or semi-natural habitat (Kremen et al. 2004, Lonsdorf et al. 2007, Ricketts 2004, Steffan-Dewenter et al. 2002, Watson et al. 2011, Winfree 2008). Forests provide nesting habitat to wood-nesting bees and may be utilized by ground-nesting bees if the forest floor is relatively undisturbed or if bees prefer to nest under forest canopy (Winfree 2007). In addition, trees and understory plants in forested areas may

provide bees with foraging resources. Owing to differences in bloom time, woodlands also help to ensure that foraging resources are available throughout the summer. For example, flowers in Pennsylvanian woodlands bloom before crops (Winfree et al. 2007b). This continuity is especially important for social bees, which have flight seasons that are longer than the blooming period of any one crop. Like forests, fields in a landscape may support bees, especially if the fields are uncultivated or if cultivated fields have flowering crops (Lonsdorf et al. 2007, Steffan-Dewenter 2006).

Fahrig (2003) reviewed extensive evidence that a reduction in total habitat area reduces population growth rates, alters species interactions, and reduces the number of specialist species, ultimately leading to reduced population sizes and species richness. Many studies have found a positive relationship between forested area and the diversity or abundance of bees visiting crops, suggesting that bees are sensitive to habitat loss around a field (Ricketts et al. 2004, Watson et al. 2011). Similarly, Kremen et al. (2004) found a positive linear relationship between the area of nesting habitat around farms and pollen deposition. Bees may be differentially affected by total habitat area; large-bodied bees demand more resources than smaller bees and are therefore believed to be most sensitive to the loss of foraging habitat (Larsen et al. 2005).

Developed area around a field may negatively influence bee diversity and abundance because it is inversely related to habitat loss. Furthermore, developed areas may be associated with physical changes to the local environment, such as herbicide and pesticide use, atmospheric pollution, the heat island effect, high numbers of exotic species, and soil compaction (McIntyre et al. 2001, McKinney 2002). These changes may affect the quality of nesting and foraging habitat and may make developed areas inhospitable to particularly

sensitive species. Some studies, however, have found that development can have a positive influence on bee species richness or abundance (Winfree 2007, Cane et al. 2006).

Configuration

A large body of literature in landscape ecology investigates whether the spatial configuration of habitat, independent of habitat composition, is important in maintaining persistent populations (Fahrig 2003). In general, habitat loss alone can have negative consequences for populations, whether that loss is concentrated in one area or spread across a landscape. Fragmentation, independent of composition, may have positive, negative, or no effect on populations (Fahrig 2003).

Bee foraging behavior is the most often-cited reason for why landscape configuration may influence bee diversity and abundance (Cane 2001). Bees are central-place foragers, meaning that they continually return to their nesting habitat after foraging (Ricketts et al. 2008). The optimal foraging theory dictates that bees will minimize their energy expenditure by selecting foraging habitats that are close to nesting habitats (Pyke 1984). These foraging limitations may explain why foraging frequency has been shown to decrease exponentially with distance from nesting habitat (Cresswall et al. 2000). A similar negative relationship may be expected for bee diversity because maximum foraging distance varies with bee size, and only the largest bee species can travel far from nesting habitat (Greenleaf et al. 2007). For example, Ratti et al. (2008) found that large-bodied bumble bees were found across a large cranberry field, but small-bodied *Lasioglossum* spp. only foraged on cranberries along the field edge.

Not only must bees travel daily to forage, but individuals must also disperse to mate and establish nests. Long distances between patches could reduce gene flow and

7

recolonization rates among fragments, negatively influencing the persistence of populations and possible meta-populations (Zayed et al. 2005). Therefore, nesting habitat patches that are well connected may help maintain viable bee populations and sufficient pollination services (Neal and Kremen 2007). In addition to bee abundance, bee diversity may also respond to fragmentation because species vary in their dispersal capacity (Kremen et al. 2007). Little research has been conducted on landscape effects of long-distance dispersal. However, Kim et al. (2006) hypothesized that the observed relationship between bee abundance and proximity to natural habitat was due to metapopulation dynamics, whereby bee individuals from natural habitats would 'rescue' sink populations nesting in unsuitable field habitats.

Some research has shown that the species-area relationship may help explain a loss of bee diversity with increasing fragmentation (Kremen et al. 2004). The relationship predicts that an increase in patch area will lead to an increase in biodiversity (McGuinness 1984). In general, a large patch has greater habitat heterogeneity than a small patch, thus fulfilling the niche requirements of a greater number of species. In addition, a large patch may provide a buffer for edge-sensitive species, especially some ground-nesting species that prefer to nest in relatively undisturbed forest interiors and avoid habitat edges (Ricketts 2001, Rickets et al. 2004).

Most of the studies showing a negative influence of fragmentation on the diversity or abundance of bees visiting crops were conducted in areas of extreme habitat loss where natural or semi-natural habitat composed less than five percent of the landscape. In areas with a large proportion of natural habitat, the effects of fragmentation may be positive. A fragmented landscape may provide a greater area of edge habitats, which may be preferred by some species. Svensson et al. (2000) observed bumble bees nesting in forest edge more

frequently than forest interiors, potentially because the edges have little undergrowth and shelter bees from the sun and wind. Other species prefer nesting in open ground on fields but may only find suitable habitat in field edges where the ground is not plowed, treated with pesticides, or irrigated (Kim et al. 2006).

Fragmentation in highly forested landscapes may also facilitate foraging. Bommarco (2010) showed that small forest patches in Europe were preferred by habitat generalists, which benefitted from the complementary resources around the patch edge. Likewise, Winfree et al. (2008) found that bee diversity and abundance were greater in forest fragments within agricultural and developed areas than in extensive forests. The researchers concluded that the fields and gardens surrounding the forest fragments probably provided foraging resources that were easily accessible. Solitary bees, which have short flight seasons and may solely depend on flowering crops, may particularly benefit from having small fragments of natural habitat within an agricultural field.

Research needs

Little research on bee diversity and crop pollination services has been conducted in temperate landscapes where there are large proportions of natural or semi-natural habitat. The research that has been conducted in this setting has shown that results from highly modified agricultural landscapes may not be applicable to all landscapes. Moreover, due to the bias in the literature, studies that take into account landscape configuration are generally limited to measuring the distance between a field and the nearest semi-natural habitat patch. Where numerous habitat patches are dispersed across the landscape, other measures of fragmentation are necessary. These measures may provide better insight into how landscape configuration influences the diversity or abundance of bees visiting crops.

Objectives

My research examined how the local environment and landscape context of crop fields influence bee diversity and crop visitation rate. Crop visitation rate is a widely-used estimate of pollination services and is related to bee abundance (Vázquez et al. 2005). My first objective was to characterize and compare the diversity and visitation rate of bees visiting yellow squash and zucchini. My second objective was to determine how these variables respond to 1) field-level floral resource availability, 2) landscape composition, which describes the proportion of different land covers around a field, and 3) landscape configuration, which describes the spatial arrangement of these land covers. I tested the following sets of hypotheses:

H1. Bee diversity and visitation rate will increase with an increase in the cover of wildflowers and flowering crops, which attract bees to fields by providing concentrated foraging resources. Furthermore, given that bees exhibit floral preferences, bee diversity will be highest on fields with high floral diversity.

H2. Bee diversity and crop visitation rate will be negatively related to the proportion of developed area and positively related to the proportion of land cover types that provide foraging and nesting resources, such as woodlands.

H3. Given that the fragmentation of foraging and nesting resources can be beneficial in highly forested landscapes, bee diversity and crop visitation rate will be highest in the most fragmented landscapes. In addition, bee diversity and visitation rate will be highest at field sites close to woodland edges, as predicted by the optimum foraging theory.

CHAPTER 2

METHODS

Study area

      The study was conducted in the northeast piedmont of North Carolina (Figure 1). The natural vegetation largely consists of mixed oak and oak-hickory-pine forests, many of which are secondary forests that developed on abandoned agricultural fields (Christensen & Peet 1984, Griffith et al. 2002). The dominant land uses are pine plantations, pasture, and urban and surburban development (Griffith et al. 2002). The climate is warm and humid with a mean annual temperature of 59.1° Fahrenheit (15.1° Celsius) and a mean annual rainfall of 46.95 inches (119.3 cm) (NOAA 2011). In June and July 2011, when the fieldwork was conducted, the average daily temperature was 76.7° F (24.8° C), and the average maximum temperature was 80.1° F (26.7° C). Small farms and large community gardens are abundant and are scattered across forested and developed areas, providing ideal field sites for this research.

Site selection

      Twenty field sites, 18 growing yellow squash and 14 growing zucchini, were selected. These crops were selected because they require pollination by bees and are commonly grown by farmers in the area. I included but did not distinguish between crookneck and straightneck yellow squash varieties and dark green zucchini varieties. All the field sites had less than one acre of cultivated land. Each field site had to be at least 3 km

away from all other sites to limit any possible overlap in bee populations. Of the 20 field sites, five had managed honey bees, and at least another three were neighboring fields that were known to have managed honey bee colonies. Producers at twelve field sites claimed to use organic or natural farming practices.

Field survey – bee visitation rate and richness

Each site was surveyed once between June 14 and July 14, 2010 when both male and female flowers were blooming. To ensure that bees were counted when they were most active, surveying began at 0700 under bright overcast to sunny conditions when temperatures were less than 75º F (29º C). For each crop, a transect was established down the entire length of a randomly chosen row and divided into six equal segments. At a randomly chosen point within each segment, bee visits were counted for five minutes by observing as many flowers that could be simultaneously viewed. This stratified random sampling design allowed for various field sizes to be surveyed for a total observation time of 30 minutes, which is greater than or equal to the length of time used in similar surveys (Winfree et al. 2008). A visit was considered to be any time a bee entered and touched the interior of a flower. To expedite the process, half of the points in each row were videotaped using a black point-and-shoot camera placed approximately 0.6 meters from the flowers, and the visits were later counted. The final visitation rate was calculated as the total number of bees observed in the six five-minute observation periods divided by the total number of flowers. While recording, bees were distinguished based on size and social behavior into the following functional groups: honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), small solitary bees (< 10 mm long), and large solitary bees (> 10 mm).

Following the crop visitation survey, bees were netted so that specimens could later be identified. Netting was chosen over passive sampling methods, such as pan traps, so that only bees visiting squash flowers were included in the diversity count. In-field identifications were not possible because many species are not distinguishable using morphological features that can be seen with the naked eye (Cane 2001). For each crop, bees that were active amongst the squash flowers were hand-netted for thirty minutes by continually walking up and down the randomly chosen crop row. This length of netting time was chosen based on methods in similar studies (Winfree et al. 2008). I did all of the netting in order to avoid biases introduced by differences in netting experience or technique. Each specimen was later identified to the species level except for species in the genus *Lasioglossum*, which are difficult to separate using taxonomic keys. Specimens representing *Lasioglossum* were collected at 12 field sites, and no more than 4 specimens were collected from each crop. I saw no morphological differences between specimens from the same field site, thus giving some indication that they represented the same species. Given that netted samples are biased towards over-representing the abundance of large bees relative to the abundance of small bees (Cane 2001), diversity was calculated as species richness rather than a metric that accounts for abundance. Furthermore, species richness is the diversity metric of choice in similar studies (Greenleaf and Kremen 2006, Winfree et al. 2008, Ricketts et al. 2008). Although bees in the genus *Lassioglossum* were not identified to species level, the term species richness is used for the sake of simplicity.

Field survey – floral resources

Both the abundance and diversity of local floral resources were surveyed. Following Winfree et al. (2008), the row length of all crops flowering during the survey was measured,

and the diversity of flowering crops was calculated as species richness. In addition, bee-attractive flowering plants growing between rows and in the field margins were surveyed using a stratified random sampling procedure. One point was randomly selected within every 10 m interval along the field margins and along four randomly selected rows. At each point, a 1 m x 1 m quadrat, which was divided into a grid of 100 cells, was used to estimate combined wildflower cover. For each species in a quadrat, I counted the number of cells containing flowering heads and summed these counts for each quadrat. Combined wildflower cover was then averaged across all quadrats from the field margins and between the crop rows. Wildflower species richness was also calculated for each field.

Landscape analysis - classification

Given that bees respond to the landscape at a small spatial scale and that relatively small features in a landscape, such as hedgerows, may support bee populations, it was necessary to classify the landscape at a high spatial resolution (Londsdorf et al. 2010). I obtained freely available three-band (red, green, and blue) orthoimagery with a 6-inch (approximately 15 cm) pixel resolution from the NC Emergency Management, Geospatial & Technology Management Office. The images of my study area, collected in February 2010 on an aircraft flying at an altitude of 5000 feet, were geometrically corrected and adjusted for topographic relief, lens distortion, and camera tilt.

I resampled the original imagery to a spatial resolution of 2 m, which reduced noise and computational requirements while maintaining a spatial scale relevant to bees. ENVI EX (Version 4.8) was used for object-based image analysis (OBIA). OBIA segments an image into objects based on spectral information and then classifies those objects based on spectral and spatial attributes. After several trials of combining the scale and merge levels, the best

14

segmentation results were obtained with a scale level of 30 and a merge level of 80. I used rule-based classification, which produces a more accurate classification compared to supervised methods (Exelisvis 2011). My rules described 22 different object classes that represented hedgrows, evergreen patches, deciduous patches, isolated trees, buildings, pavement, lawns, fields with bare soil, fields with cover crops, pastures, water bodies, and shadows on these different surfaces. After classification, I merged these classes into five final land-use-land-cover classes: water, developed areas, deciduous wooded areas, evergreen wooded areas, and fields/grassy areas. The term "wooded areas" was chosen over "forests" because the former term encompasses small patches of trees, hedgerows, and shrubby natural areas. Ancillary data of roads and water bodies from the 2011 US Census Bureau's MAF / TIGER database were added to the classified image. I buffered the road line segments to a width of 9 m for local roads, 18 m for major roads, and 36 m for interstates.

I evaluated the accuracy of my classified image by generating 1000 random points across the image and classifying them by visually inspecting the original orthoimage. Based on these reference data, the overall accuracy was 86.29%, and the Kappa coefficient was 0.8052. The largest source of error came from confusing deciduous and evergreen wooded areas (Table 1). Also, 22% of developed pixels and 24% of water pixels were incorrectly classified as fields/grassy areas. The edges of roads and small ponds are often adjacent to grassy areas and may have been segmented into the wrong object, hence producing these errors. Overall, the classified image was considered to be very good and was used to quantify the composition and configuration of the landscape.

Landscape analysis - metrics

I quantified both the composition and configuration of the landscape surrounding each field. Composition refers to the proportion of land in each land cover class, and configuration describes how these land covers are arranged across space (Fahrig 2003). Following the methodology of Watson et al. (2011), Winfree (2007), and Steffan Dewenter (2003), I calculated landscape metrics for areas within nested buffer distances (radii) from the center of each surveyed crop row: 500, 1000, 2000, 3000, 4000, and 5000 m. Later, during the statistical analysis, I determined at which buffer the landscape metrics most correlated with bee richness and visitation rate. This exploratory approach was taken because little is known about how far bees can disperse and therefore what spatial extent they will most respond to (Steffan Dewenter 2003). The areas of each land cover class were calculated using Python and ArcGIS 10 and converted to proportions.

Three metrics were used to describe landscape configuration. In similar studies, the most widely used configuration metric – and many times the only metric – is distance to nearest forest patch (Greenleaf and Kremen 2006, Winfree et al. 2008, Ricketts et al. 2008). I measured the Euclidian distance to the nearest edge of a wooded patch that contained at least one core pixel. Thus, the minimum possible wooded patch size was 6 m x 6 m and was not a single isolated tree. The spatial pattern analysis program FRAGSTATS (version 3.4) was used to quantify wooded area contagion and interspersion withthe clumpiness index. The index varies from -1 to 1, returning a value of 1 when a land cover is maximally aggregated. Values less than zero indicate greater disaggregation than expected under a spatially random distribution. This metric was chosen over other contagion metrics because it provides a measure of fragmentation that is not confounded by the total area of wooded land (McGarigal

et al. 2002, Neel et al. 2004). Lastly, I used FRAGSTATS to find the total perimeter length of all fields and grassy areas. This metric reflects the availability of field edge, which may provide more suitable nesting habitat than field interiors (Steffan Dewenter 2002).

Statistical analysis

To analyze differences in native bee diversity and visitation rate between yellow squash and zucchini, I used Wilcoxon sum-rank tests. For each crop, a Wilcoxon sum-rank test was also used to compare visitation rate between honey bees and native bees, while a two-tailed Kruskal Wallis test was used to compare visitation rates between the three bee functional groups (bumble bees, large solitary bees, and small solitary bees). Honey bee visits were excluded from the remaining analyses so as to focus on the native bees visiting crops.

Non-metric dimensional scaling was used to test for a difference in the communities of bee species visiting yellow squash and zucchini (R CRAN version 2.14.1, "vegan" package). Field sites were ordinated using the Bray-Curtis similarity coefficient. The null hypothesis of no difference in bee communities was then tested by means of a multi-response permutation procedure (MRPP). The returned agreement statistic (A) describes within-group homogeneity and is a measure of effect size independent of sample size (McCune and Grace 2002).

Prior to modeling the effects of landscape on bee diversity and visitation rate, I identified the spatial extent (i.e., buffer) at which each landscape metric had the most explanatory power. To do so, I regressed the response variables against the landscape variables quantified at each nested spatial extent (500 m – 5000 m), and I chose the spatial extent that produced the best fitting model according to the Akaike information criterion

corrected for small sample size (AICc) (Johnson and Omland 2004). During this preliminary analysis, I found that combining the proportions of deciduous and evergreen classes into one class, "wooded area", produced a stronger model than considering each class separately. I therefore used their combined proportions for all of the regression analyses.

I used separate models to assess the responses of bee diversity and visitation rate to field-level variables, landscape composition, and landscape configuration. I initially generated full generalized linear models based on the following factors that could potentially influence bee diversity and visitation rate:

- **Field-level model:** Log row length of flowering crops, wildflower cover, flowering crop diversity (bee diversity model only), wildflower diversity (bee diversity model only)
- **Landscape composition model:** Proportion developed, proportion wooded area
- **Landscape configuration model:** Distance to nearest wooded area, wooded area clumpiness, and total perimeter of fields and grassy areas

The proportion of fields/grassy areas was not included in the landscape composition model due to issues of multicollinearity. Because bee diversity (number of species) and visitation rate (visits/flower/5 min) were count data, I tested Poisson and negative binomial distribution functions and selected the models with the lowest AICc. Poisson models were selected for bee diversity, and negative binomial models were selected for visitation rate. For the latter, the response variable was the log number of visits, and the offset was the log number of flowers observed. After fitting the initial models, a backwards stepwise regression procedure was used to remove insignificant variables and arrive at final models describing

the effects of field-level variables, landscape composition, and landscape configuration. These final models were compared using the model AICc values.

CHAPTER 3

RESULTS

In total, 1261 visits to crop flowers were counted, of which 986 were visits by native bees and 275 were visits by honey bees. Across all field sites, I collected 525 specimens representing 20 species. Of these species, seventeen were ground- or cavity-nesting bees and three were wood-nesting.

When comparing yellow squash and zucchini, there were no significant differences in bee diversity (W = 117, P = 0.52) and native bee visitation rate (W = 1407, P = 0.18) (Figure 2a). There were significantly more visits by native bees than honey bees for yellow squash (W = 37.5, n = 18, P < 0.001) and zucchini (W = 25.5, n = 14, P < 0.001) (Figure 2b). Of the field sites that had managed honey bee colonies, only one had a greater visitation rate by honey bees than native bees. At this site, there were 1.88 honey bee visits per yellow squash flower per five minutes compared to 0.22 native bee visits. There were also significant differences in the visitation rates of bee functional groups, with more visits by large solitary bees than bumble bees or small solitary bees (yellow squash: Kruskal-Wallis χ^2 = 12.9192, df = 2, p-value = 0.002; zucchini: χ^2 = 12.1975, df = 2, p-value = 0.002) (Figure 2c).

According to the MRPP analysis, the community compositions of bees visiting yellow squash and zucchini were not significantly different (A: -0.005256, p-value = 0.77). The r^2 value for the NMS ordination (Figure 3), which measures the linear fit between the fitted values (the Bray-Curtis similarity coefficients) and the ordination distances was 0.82.

There were no significant interactions between variables describing field-level factors, landscape composition, or landscape configuration, and so these interactions were dropped. Backwards stepwise regression allowed me to continue to remove insignificant effects from all models (Table 2). The spatial extent at which each landscape metric had the most explanatory power varied by metric and crop type (Table 2).

For each crop, I produced three final models to explain bee diversity, each of which had one significant explanatory variable ($P < 0.05$) (Tables 3 & 4). The significant field-level variable varied by crop; the row length of flowering crops was positively correlated with the diversity of bees visiting yellow squash (Figure 4), and wildflower cover was positively correlated with the diversity of bees visiting zucchini (Figure 5). For both crops, the proportion of developed area was negatively correlated with bee diversity (Figure 6). It should be noted, however, that this negative relationship for zucchini was largely driven by two points. Upon removing those points, there was no significant relationship ($P > 0.05$). The clumpiness of wooded areas was positively correlated with bee diversity for both crops (Figure 7). Figure 8 shows examples of landscapes and their corresponding wooded area clumpiness index values. For both crops, the landscape configuration model was the best fitting model (lowest AICc), followed by landscape composition and field-level models (Tables 3 & 4).

None of the variables could significantly explain the variance in visitation rate for yellow squash. For zucchini, the proportion of wooded area was significantly negatively correlated with visitation rate (Figure 9) (IRR = 0.986 +- 0.006, P = 0.027, AICc =123.89). However, when analyzed separately, the visitation rate of each functional group was not significantly related to the proportion of wooded area ($P > 0.1$) (Figure 10).

21

CHAPTER 4

DISCUSSION

Yellow squash and zucchini

The diversity, visitation rate, and community of bees visiting yellow squash and zucchini were not significantly different. Given that the squash plants are within the same species (*Cucurbita pepo*) and have similar corolla tube length, flower size, flower color, and timing of flower opening, it is not surprising that they had similar pollinator communities and levels of visitation. From the demonstrated similarities, I would expect the regression model results to be consistent across crops; this was the case for the landscape-level models but not the field-level models. I first review the models explaining bee diversity and then discuss the lack of significant models for explaining visitation rate.

Field-level effects on bee diversity

The variable driving a positive relationship between flower abundance and bee diversity differed between yellow squash and zucchini. For yellow squash, bee richness was highest in fields that had a large number (measured in row length) of flowering crop plants. For zucchini, bee richness was related to the cover of wildflowers but not the row length of flowering crops. Similar relationships between flower abundance and bee diversity have been found by Holzschuh et al. (2007) and Kohler et al. (2008). Both large and small-bodied bees may be attracted to areas where flowers are more abundant because the time and energy spent traveling from one floral patch to the next is reduced (Gathmann & Tscharntke 2002).

I considered the possibility that small fields, where flowering crop plants were less abundant, were in the most developed areas and that the landscape context, rather than local floral abundance, could be driving the observed relationship for yellow squash. However, while the farm in the most urban environment was also the one with the lowest row length of flowering crops, there was only a weak negative relationship between row length and developed area ($r^2 = 0.26$, $P = 0.022$). Furthermore, there was no relationship between wildflower cover and developed or wooded area. It should be noted that the relationship between bee diversity and the row length of flowering crops may not continue to hold for greater crop abundances. The fields in my study were all less than or equal to one acre. Larger fields, which can grow more flowering crops, may have a negative effect on bee diversity by representing barriers to movement (Ricketts 2004, Tuell et al. 2009). The inconsistent results between yellow squash and zucchini makes the effect of flower abundance – whether wildflowers or crop flowers – on bee diversity questionable. It is possible that the positive effect of flower abundance may be countered by increased competition between crops and other flowers for pollination (Kremen et al. 2007).

In contrast to floral abundance, bee diversity was not related to floral diversity. The landscapes around my field sites may be providing additional foraging resources for bees, thus diminishing any effect field-level floral diversity may have on bee diversity (Tscharntke et al. 2005). This reasoning was used by Winfree et al. (2008), who also conducted a study in highly forested landscapes and found no relationship between bee and floral diversity. However, I did find evidence that some flowers, such as small white flowers of *Galium aparine*, attracted a large number of small solitary bee species. Local flowers may affect bee diversity, but redundancy in floral traits between species, especially species in the same

genus, may result in not finding a pattern using species richness as a measure of floral diversity. It is also possible that the flowers attracting a high diversity of bees may draw bees away from squash. For example, small solitary bees may prefer small flowers, when available, over the relatively large squash flower (Heard 1999).

Landscape effects – spatial extent

All of the landscape-scale variables were most explanatory at spatial extents of 1 and 2 km. Other pollination studies that quantified landscapes around fields have done so at the same spatial extents (Holzschuh 2007, Kremen et al. 2004, Watson et al. 201, Winfree et al. 2008). The explanatory power of these spatial extents fits well with the home ranges of most species (Cane 2011). Furthermore, although home range and dispersal ability are not well separated in the literature (Hagen et al. 2011), the dispersal ability of most bees may also be within 1 and 2 km. Some larger bees that are capable of flying longer distances, such as bumble bees, may travel as far as 5 km when mating or establishing a nest (Lepais et al. 2010). Small solitary species that travel less than 1 km to forage (Gathmann & Tscharntke 2002) may still have a dispersal ability equal to or beyond 1 km (e.g., *Halictus rubicundus* [Potts and Willmer 1997]). Therefore, the reported effects of landscape context on bee diversity and visitation rate may not only be a function of habitat availability and foraging behavior but also long-distance dispersal. The dispersal of bees within 1 or 2 km of a field site may be maintaining genetic diversity within populations or may be rescuing sink populations close to a field site (Kim et al. 2006).

Landscape composition effects on bee diversity

As predicted, the proportion of developed area had a negative effect on bee diversity. Furthermore, this relationship appeared to exhibit a potential threshold response, with

diversity declining in field sites with more than 5% developed area. A negative response of bee diversity to developed land has been found by a number of papers reviewed by Hernandez et al. (2009) and Henson et al. (2005), while a threshold response has been found for other taxa, such as birds (Melles et al. 2003), stream invertebrate (Hilderbrand et al. 2010), and small mammals (Henson et al. 2005).

In contrast to my findings, other research has shown that bees may be more diverse in developed areas (Cane et al. 2006, Winfree et al. 2007a). These studies have either hypothesized or shown that bees use grassy areas bordering roads, backyard gardens, and lawns. In my study, however, these features were classified as fields/grassy areas, not development. Given the 2-m spatial resolution of my land cover data, the proportion of developed land was largely based on the area of the built environment, including buildings, roads, and other paved surfaces. With the exception of gravel or dirt roads that may be used by ground-nesting bees and wooden buildings that may be used by the three wood-nesting bee species, the developed pixels represent land with little habitat value.

There are several mechanisms that may be underlying the negative developed area - bee diversity relationship. First, habitat resources in developed areas may be of lesser quality than resources in rural areas. Urban and suburban lawns were in the same class as fields in more rural areas, but may provide less diverse and less abundant floral resources (Bates et al. 2011). Developed areas may also be associated with physical and potentially harmful changes to the local environment, such as herbicide and pesticide use, pollution, the heat island effect, and soil compaction (McKinney 2002). These factors may influence the quality of habitat and cause particularly sensitive species to avoid developed areas all together.

An increase in developed area can also be translated as loss of semi-natural habitat associated with fields or wooded areas (Lonsdorf et al. 2009). However, while not analyzed during stepwise regression due to issues of multicollinearity, the proportion of fields was not independently correlated with bee diversity. In addition, bee diversity was not related to the proportion of wooded area. This was a surprising result given that woodlands can provide bees with foraging resources - both flowering trees and understory plants – that are available before crops blooms. Bees with long flight seasons, such as *Bombus* spp. and *Lassioglossum* spp., could utilize these resources. Also, three other species could nest in the wood, and some ground and cavity nesting bees may prefer to nest under closed canopies or along forest edges rather than open areas (Winfree 2008).

Other studies also have found that semi-natural habitat area did not predict bee diversity (Londsdorf et al. 2009, Winfree 2007). The authors of these studies considered the possibility that small scattered patches of land cover types could not be separated with 30 m spatial resolution data. This problem of scale was not an issue with my data, as the 2 m resolution allowed me to classify small land cover patches that bees may detect while foraging and dispersing. Another explanation is that the positive relationship between habitat area and bee diversity may only hold true for areas of extreme habitat loss, defined by Winfree (2008) as areas with less than or equal to 5% natural habitat cover. In my study, the most developed landscape was 45% wooded area and 25% fields and grassy areas. Assuming that these land covers provided habitat to bees, foraging and nesting resources may have not been limiting.

Because the proportions of wooded area or fields could not explain variation in bee diversity, the effect of development on bee diversity may not be driven by habitat loss but by

habitat fragmentation or habitat quality. The potential effects of habitat fragmentation are discussed below.

Landscape configuration effects on bee diversity

For both yellow squash and zucchini, the final model based on the clumpiness of wooded areas was stronger than the models based on developed area or local floral resources. I hypothesized that fragmentation would benefit bee diversity due to an increase in edge habitats as well as a dispersion of complementary habitat resources throughout the landscape. Contrary to my expectations, the clumpiness of wooded land was positively correlated with bee diversity. The clumpiness index was not correlated with the proportion of wooded area but was significantly negatively correlated with the proportion of developed area ($P = 0.013$), suggesting that developed land is at least partly responsible for the fragmentation of wooded areas.

There are several reasons why wooded area fragmentation may result in a decline in bee diversity rather than the expected increase. First, developed areas may represent physical barriers to movement. Few studies have been conducted on potential barriers to bee movement, although other researchers have posited that buildings in urban areas may impede bee mobility (Matteson et al. 2008). Furthermore, roads may be avoided by bees and lead to increased mortality. Bhattacharya et al. (2003) found that bees prefer to avoid any barrier, including road barriers, but Hopwood (2008), studying roadside bee diversity and abundance, found no influence of road width or traffic. If roads are a barrier to movement, they may disproportionately affect larger bees that have to forage over greater areas to fulfill energy requirements (Bommarco et al. 2010). My data cannot provide a good test of this hypothesis,

but it may explain why the largest bee species were absent in the most fragmented landscapes.

The distance between wooded area fragments, regardless of the land cover between these fragments, may in itself represent a barrier to movement. Small bees that prefer to nest in the shade, bees with long flight seasons that forage in wooded areas during the spring, and wood-nesting bees would be most influenced by this distance effect. However, bumble bees and bees in the genus *Lassioglossum*, which have a long flight season, and the small wood-nesting bee *Augolora pura* were present in landscapes with a wide range of fragmentation levels. Therefore, is likely that the distance between wooded areas was not a barrier to movement.

Bee diversity was not significantly correlated with the distance between a field site and the nearest woodland patch, providing further evidence for a lack of a distance effect. While both Gariboldi et al. (2011) and Ricketts et al. (2008) report negative effects of isolation on bee diversity, these effects were shown to be strongest at isolation distances between 0.6 and 1.5 km. These long distances can filter out smaller-bodied bees that have limited flight ability. In contrast, the maximum distance between the surveyed crop row and a wooded area patch in my study was 65 m, which is within the foraging distance of the bees in my study (Gathmann & Tscharntke 2002, Zurbuchen et al. 2010). Winfree et al. (2008) similarly found no effect of distance to nearest woodland patch, potentially because the maximum distance of 343 m in their study also did not represent a barrier to foraging bees of any size.

Diversity may also be influenced by qualitative differences in wooded area patches of different size. More contiguous wooded areas may provide more ideal or diverse nesting

and foraging resources than smaller fragments. For example, relatively large patches may be natural forests that have native floral resources and undisturbed ground. In contrast, small patches, especially those in more developed areas, may be isolated trees or wooded lawns with few floral resources and disturbed ground. It is important to note, however, that other small patches of wooded land, such as hedgrows, may provide important bee habitat on agricultural fields (Hannon and Sisk 2009).

I also considered the possibility that a large proportion of small natural woodland patches may be unsuitable for ground nesting bees due to edge effects, such as desiccation (Aizen and Feinsinger 2003). However, bees are generally thought to benefit from woodland edges, which can provide shelter from sun and wind and access to foraging resources both in the woodlands and surrounding fields (Svensson et al. 2000). Moreover, there were no species in my study that are edge sensitive and require core forested habitat. One bee species, *Auglora pura,* has been found to be abundant in extensive forested areas, but it is not strictly a forest-associated bee because it is also abundant in open habitats (Winfree 2008).

Despite confounding factors that may be underlying the clumpiness index – diversity relationship, the relationship was consistent across crops and points to an overall negative effect of fragmented wooded areas. This negative effect is most likely a result of developed areas acting as barriers to movement and the low habitat quality of small wooded area patches.

Visitation rate

Visitation rate was negatively correlated with the proportion of wooded land, and this relationship was only significant for zucchini. While this relationship was not significant when analyzed for each functional group, the large solitary functional group appeared to be

29

driving the overall negative relationship. Although not recorded, the dominant species visiting squash was the large solitary bee *Peponapis pruinosa*, which specializes on cucurbits. This bee could benefit from decreased forest cover given its preference for nesting in open ground and dependence on squash (Julier and Roulston 2009). Because wild cucurbits are rare in the piedmont of North Carolina, *Peponapis pruinosa* populations will most likely only persist in agricultural areas where cucurbits are cultivated. Moreover, this squash specialist bee was present in even the most developed field sites, suggesting that it is largely insensitive to developed land and can readily disperse across fragmented landscapes.

Knowing that large solitary bees accounted for 58% of the total visits and that *Peponapis pruinosa* was by far the dominant large solitary bee, it is not surprising that other models failed to explain overall visitation rate. Landscape-level models may have not been significant because squash bees often nest directly under the squash plants (Julier and Roulsten 2009), minimizing any effect the landscape context may have on foraging behavior. Aside from cucurbits, which the squash bee specializes on, field-level floral resources would also have little effect on squash bee populations. Visits by bumble bees and small solitary bees, which accounted for 42% total visits, did not drive any model towards significance. One possible reason for this outcome was that visitation rate was not a good reflection of population size. The squash bee is a strong competitor for squash nectar and pollen and may have forced bees to forage on other crops.

Limitations

During analysis, I only used five land cover classes and ignored any variation within these classes. Other analyses have used similar thematic resolutions, thus allowing me to compare my results to the literature (Londsdorf et al. 2009; Ricketts 2004). Also, my

statistical analysis showed there may be some validity in my approach: The more parsimonious models that grouped deciduous and evergreen wooded areas into one class were stronger models than those that included both classes separately. However, within the field and wooded area classes, there is great variability in soil characteristics, human disturbance, and vegetation structure and composition that could greatly influence the availability and quality of bee habitat (Kim et al. 2006, Londsdorf et al. 2009).

This study could be made more rigorous with repeated sampling. Species turnover during the course of the season may have affected my results, as the flight seasons of many bees are less than the one-month duration of my fieldwork (Oertli et al. 2005). However, I did find that species diversity and visitation rate were not correlated with sampling date. Oertli et al. (2005), who surveyed bees in the Swiss Alps, also found that the abundance of bees can vary substantially between years, although the drivers of this variation may be large-scale climatic conditions that may affect all field sites equally.

There were several confounding factors that were not controlled for in this study. Pesticide and herbicide use may have a negative influence on bee diversity and abundance (Steffan – Dewenter et al. 2005), although there were no significant differences in bee diversity (yellow squash: $W = 42$, $P = 0.33$; zucchini: $W = 19$, $P = 0.74$) or native bee visitation rate (yellow squash: $W = 29$, $p = 0.77$; zucchini: $W = 27$, $P = 0.60$) between organic and non-organic fields. Other potentially confounding factors, such as ground tilling practices and crop rotation, may also influence bees visiting crops, particularly squash bees that nest under squash plants.

Given that bee communities and crop visitation rates vary between crops (Winfree et al. 2008), the findings reported here may not be readily transferred to all crops. In some

regards, squash provides a unique case because two squash bees, *Peponapis pruinosa* and *Xenoglossa strenua*, specialize on the crop.

Conservation implications

The overall dominance of native bees compared to honey bees in my results demonstrates their importance for crop pollination. Only six visits by bees to a squash flower are required for successful fruit set (Blaire et al. 2008), a requirement that was met and frequently exceeded during 30 total minutes of observations in all of my field sites. Squash bees accounted for a large proportion of the visits made by bees in the large solitary functional group. In particular, the squash bee *Peponapis pruinosa* was present at every field site, including those in more developed areas. Providing habitat for these specialist bees in the form of undisturbed open ground close to squash plants can help guarantee successful squash pollination (Julier and Roulston 2009). It should be noted, however, that undisturbed ground in a field may also provide habitat for agricultural pests and lead to increased weed growth.

In addition to *Peponapis pruiosa*, 18 other native bee species were observed visiting squash flowers. Although not tested in my research, other studies have found that such diversity will confer resilience to the pollination system and lead to greater fruit set (Klein et al. 2003). Field-level management decisions, such as allowing wildflowers to grow along rows and around fields, may have a significant positive influence on bee diversity. However, this research has also shown that the landscape context of a field matters. In general, the study area was a mosaic of scattered fields, developed areas, and abundant wooded areas. Maintaining this heterogeneous landscape will benefit bees and their pollination services, as it provides complementary foraging and nesting resources that are within close proximity to

each other. Nonetheless, conservation efforts for bee diversity should target areas in the most fragmented landscapes, especially those areas that are fragmented by development. These areas have the potential to support higher diversities by increasing the quality and availability of foraging and nesting resources. Recommendations on providing bee habitat are made by Vaughan et al. (2007).

Conclusions

The diversity of bees visiting squash was positively related to the clumpiness of wooded areas around a field, providing evidence that bee diversity declines in more fragmented landscapes. Field-level flower abundance and the composition of the landscape may also influence bee diversity. There was a lack of significant models explaining visitation rate, potentially because squash visits were dominated by a squash flower specialist. This research has implications for conserving bees and their vital ecosystem service. Given that bees travel across a landscape to disperse and forage, both field-level and landscape-level management decisions need to be considered. In particular, conservation efforts should be targeted at fragmented landscapes in developed areas.

Future research needs to continue investigating landscapes where there are large proportions of natural and semi-natural areas. Most research has been conducted in areas where there is extreme habitat loss, which may mask the effects of other factors that can be contributing to a reduction in bee diversity or abundance. Furthermore, it is possible that differences in landscape configuration are associated with differences in habitat quality, which may ultimately be influencing bee diversity. Studies on the availability of resources within small fragments of wooded areas would lend insight into mechanism driving the relationship between bee diversity and landscape context.

Table 1. Confusion matrix (in percent pixels) for the classified orthoimage. The matrix was based on 1000 reference pixels. The number of pixels in each class were as follows: 357 deciduous, 272 evergreen, 302 field/grassy area, 44 road, and 25 water.

	Reference pixels (percent)					
	Deciduous	Evergreen	Field/Grassy	Developed	Water	Total
Deciduous	91.7	11.2	8.7	14.8	8	39.1
Evergreen	1.6	87.1	2.2	1.9	0	25.1
Field/Grassy	5.4	0	84.9	22.2	24	28.9
Developed	1.3	1.7	4.2	61.1	0	5.3
Water	0	0	0	0	68	1.6
Total	100	100	100	100	100	100

Table 2. Initial regression models for bee diversity (species richness). The spatial extent that each landscape-scale level variable had the most explanatory value is shown for yellow squash (YS) and zucchini (Z). Incidence rate ratios (IRR) are exponentiated coefficients returned from a Poisson model with a log link and express the change in bee richness with a one unit increase in the independent variable. Yellow squash $n = 18$; Zucchini $n = 14$.

	Yellow squash		Zucchini	
Initial models	IRR (SE)	P	IRR (SE)	P
Field-level				
Flowering crop row length (m)	1.000 (<0.000)	0.026	1.000 (<0.000)	0.695
Wildflower cover (%)	1.042 (0.034)	0.230	1.060 (0.045)	0.200
Flowering crop diversity	0.994 (0.040)	0.880	1.003 (0.053)	0.955
Wildflower diversity	1.040 (0.055)	0.474	1.000 (0.056)	0.995
Landscape composition				
Proportion developed area (YS: 1000 m, Z: 1000 m)	0.999(<0.000)	0.026	0.999 (<0.000)	0.019
Proportion wooded area (YS: 1000 m, Z: 1000 m)	1.001(<0.000)	0.904	0.993 (<0.000)	0.221
Landscape configuration				
Forest clumpiness index (YS: 2000 m, Z: 2000 m)	1.101 (0.056)	0.086	1.176 (0.067)	0.015
Field perimeter (m) (YS: 2000 m, Z: 2000 m)	0.999 (0.011)	0.936	1.014 (0.013)	0.285
Distance to wooded patch	1.003 (0.008)	0.729	1.003 (0.010)	0.808

Table 3. Initial regression models for bee visitation rate (visits/flower/5 min). The spatial extent that each landscape-scale level variable had the most explanatory value is shown for yellow squash (YS) and zucchini (Z). Incidence rate ratios (IRR) are exponentiated coefficients returned from a negative bionomial model with a log link and express the change in visitation rate with a one unit increase in the independent variable. Yellow squash n = 18; Zucchini n = 14.

	Yellow squash		Zucchini	
Initial models	IRR (SE)	P	(SE)	P
Field-level				
Flowering crop row length (m)	1.000 (<0.000)	0.544	1.000 (<0.000)	0.288
Wildflower cover (%)	0.986 (0.054)	0.792	0.974 (0.051)	0.608
Landscape composition				
Proportion developed area (YS: 2000 m, Z: 500 m)	1.000 (<0.000)	0.840	1.000 (<0.000)	0.999
Proportion wooded area (YS: 2000 m, Z: 1000 m)	0.998 (0.002)	0.354	0.988 (<0.000)	0.039
Landscape configuration				
Forest clumpiness index (YS: 1000 m, Z: 2000 m)	1.075 (0.076)	0.341	0.963 (0.065)	0.561
Field perimeter (m) (YS: 1000 m, Z: 2000 m)	1.030 (0.052)	0.568	1.004 (0.013)	0.738
Distance to wooded patch	0.980 (0.016)	0.204	0.988 (0.011)	0.299

Table 4. Variables included in the final models for yellow squash bee diversity. Incidence rate ratios (IRR) are exponentiated coefficients returned from a Poisson model with a log link and express the change in bee richness with a one unit increase in the independent variable. Corrected Akaike information criterion (AICc) is a goodness-of-fit measure. N = 18.

Source of Variation	IRR (SE)	P	AICc
Field-level			
Flowering crop row length (m)	1.236 (0.076)	0.0107	74.57
Landscape composition			
Developed area (1000 m)	0.999 (<0.000)	0.0115	73.26
Landscape configuration			
Forest clumpiness index (2000 m)	1.110 (0.038)	0.0063	72.73

Table 5. Variables included in the final models for zucchini bee diversity. Incidence rate ratios (IRR) are exponentiated coefficients returned from a Poisson model with a log link and express the change in bee richness with a one unit increase in the independent variable. Corrected Akaike information criterion (AICc) is a goodness-of-fit measure. N = 14.

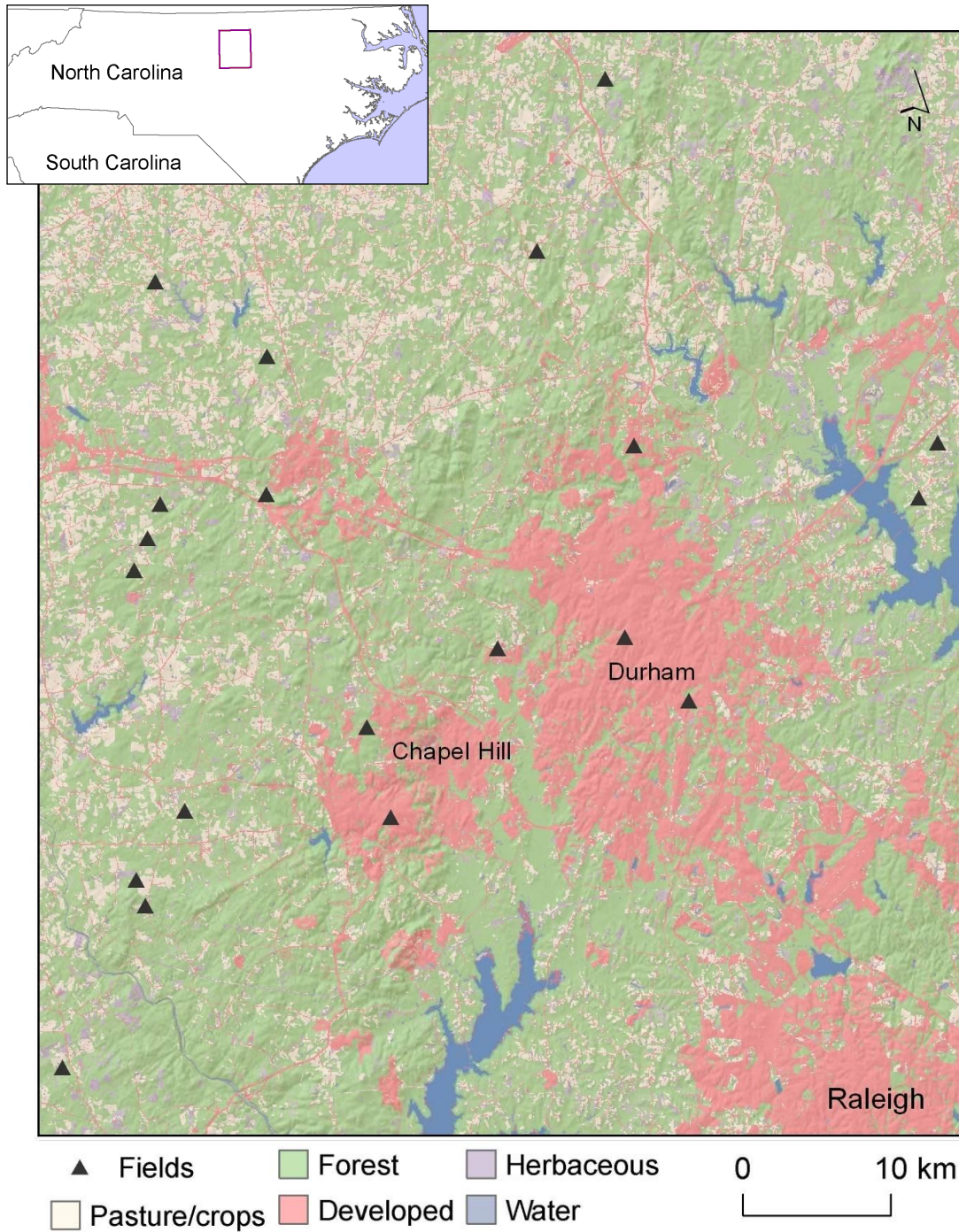| Source of Variation	IRR (SE)	P	AICc
Field-level			
Wildflower cover (%)	1.071 (0.033)	0.0384	63.21
Landscape Composition			
Developed area (1000 m)	0.999 (<0.000)	0.0316	61.47
Landscape configuration			
Forest clumpiness index (2000 m)	1.128 (0.049)	0.0149	60.45

Figure 1. Study area in the piedmont area of North Carolina. Land cover data were taken from the 2006 National Landcover Database (Fry et al. 2011).
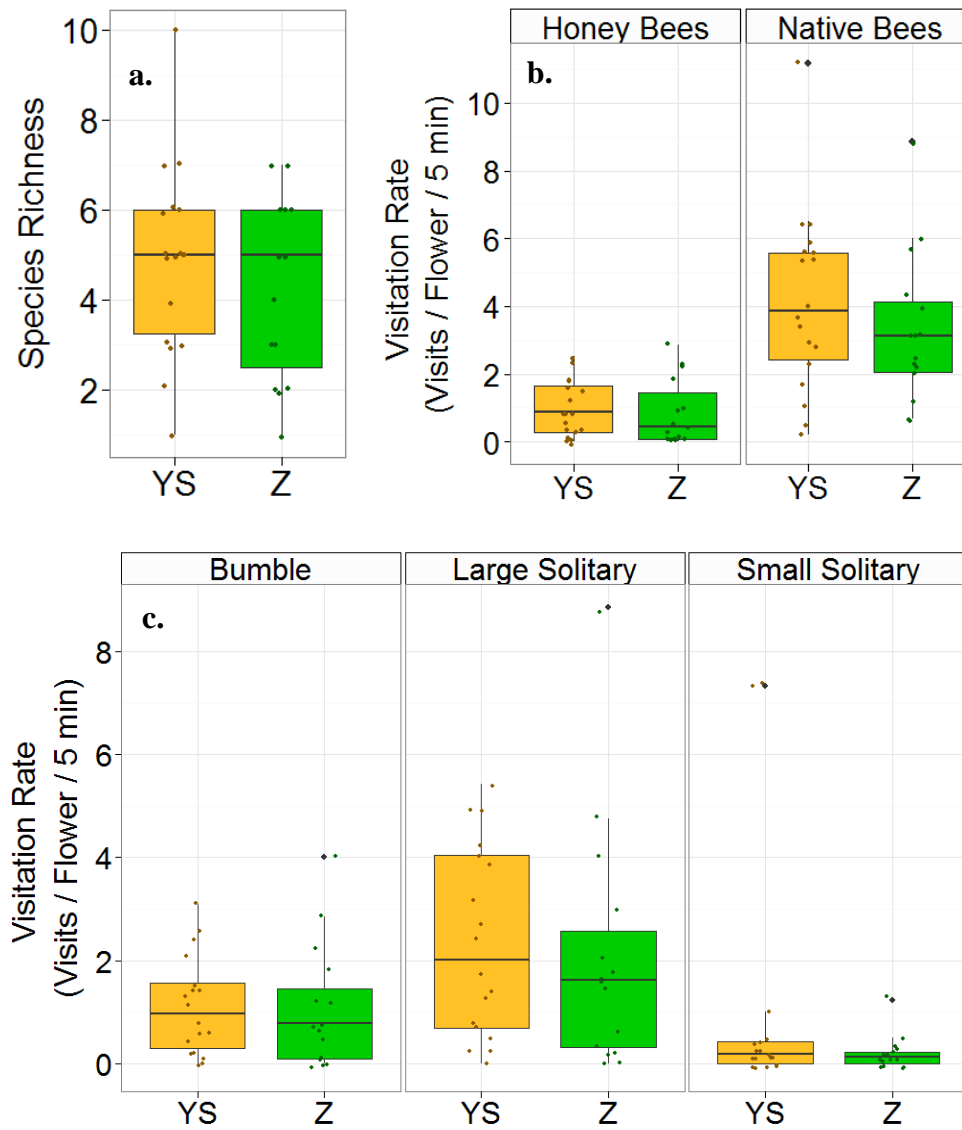
Figure 2. Bee species richness and visitation rate comparisons for yellow squash (YS) and zucchini (Z). a) Bee species richness; b) Visitation rate of honey bees and all native bees; c) Visitation rate of three functional groups.
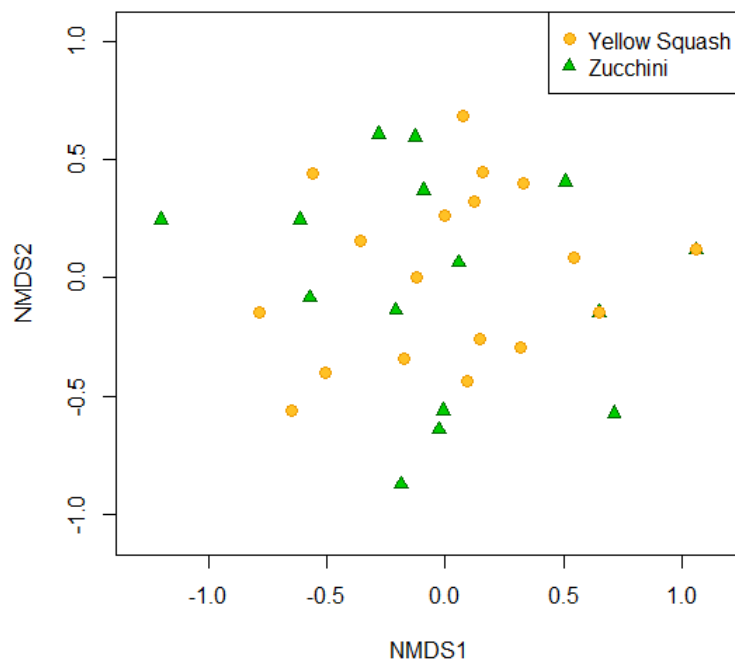
Figure 3. Non-metric multidimensional scaling ordination of field sites and crops according to bee species composition. The ordination is based on the Bray-Curtis dissimilarity index.
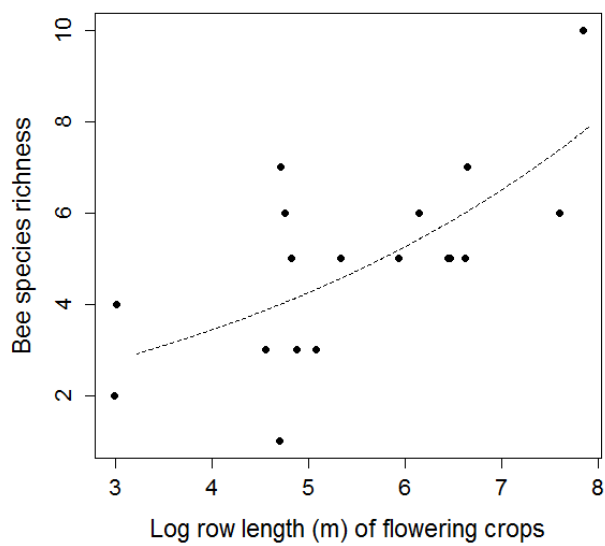

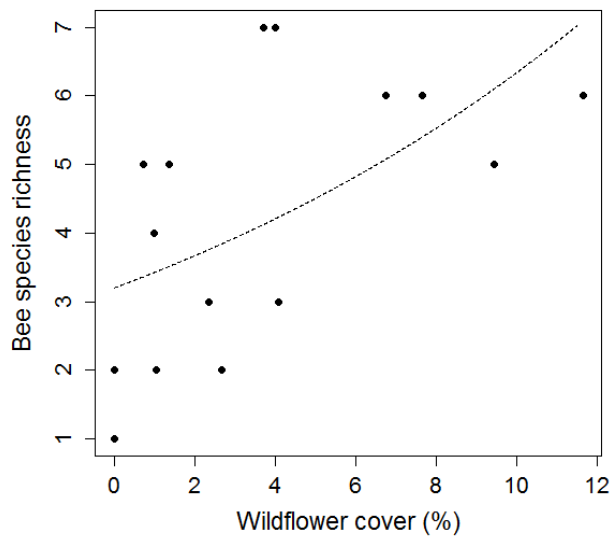**Figure 4.** Bee species richness and log row length (m) of flowering crops for yellow squash.

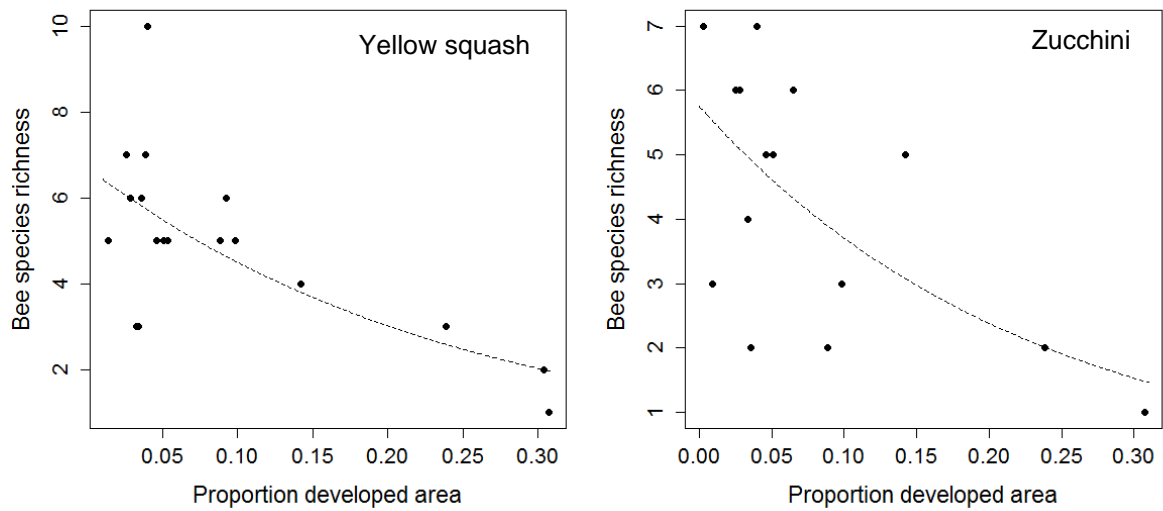**Figure 5.** Bee species richness and wildflower cover for zucchini.

Figure 6. Bee species richness and proportion developed area within 1000 m of each field site for yellow squash and zucchini.
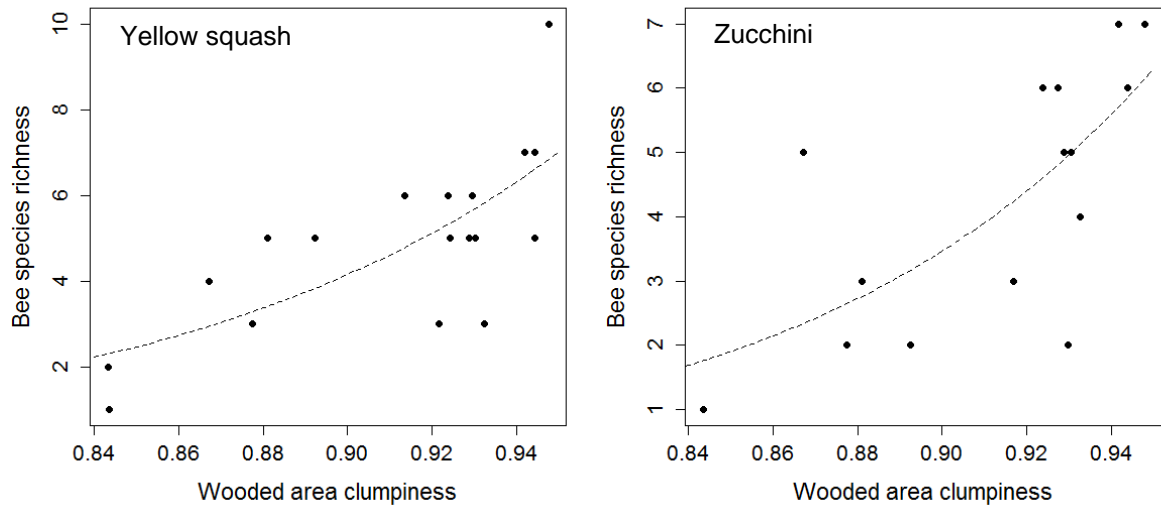
Figure 7. Bee species richness and the index of wooded area clumpiness within 2000 m of each site for yellow squash and zucchini. The clumpiness index is a cell-based measure of wooded area contagion and interspersion.
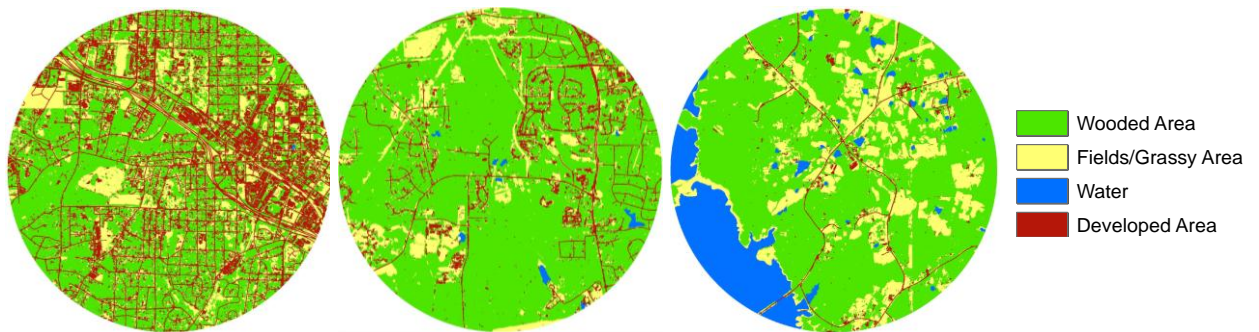

Figure 8. Examples of landscapes (2 km radius) with varying clumpiness index values. From left to right, the index values are 0.8432, 0.8924, and 0.9477.

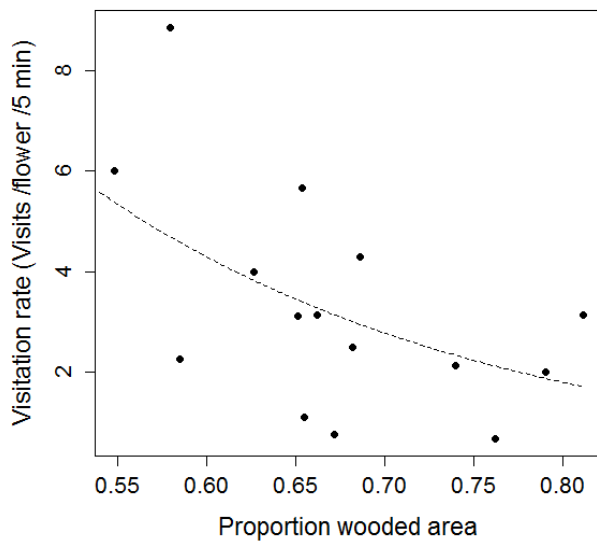**Figure 9.** Flower visitation rate (visits/flower/5min) and proportion wooded area within 1000 m of each site for zucchini.
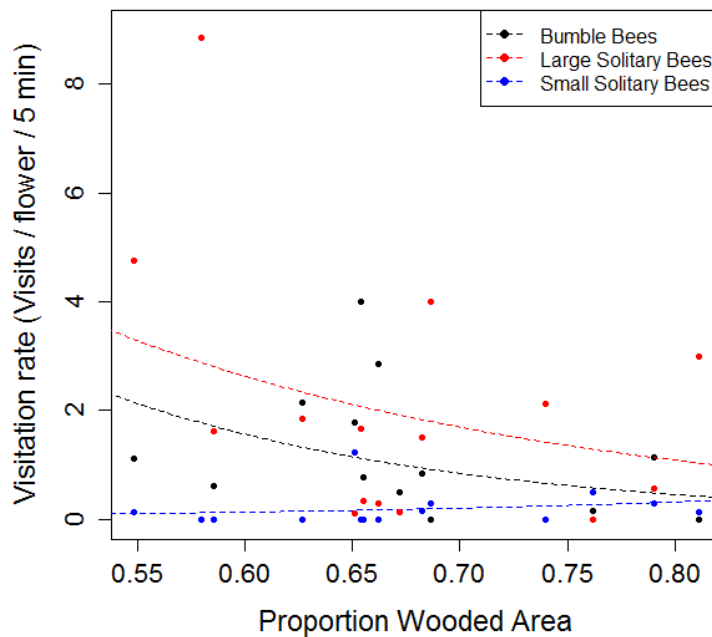

Figure 10. Flower visitation rate (visits/flower/5 min) and proportion wooded area within 1000 m of each site for 3 functional groups visiting zucchini. The relationship between visitation rate and proportion wooded area was not significant for any one group alone.

Table A1. Mean and standard deviation (SD) of each independent variable used in regression models.

Initial models	Yellow squash		Zucchini	
	Mean	SD	Mean	SD
Local variables				
Flowering crop row length (m)	514.94	691.73	636.00	834.65
Wildflower cover (%)	3.46	3.24	3.77	3.59
Flowering crop species richness	8.06	3.23	8.00	3.25
Wildflower species richness	3.94	2.24	5.20	3.36
Landscape composition				
Proportion developed area (YS: 1000 m, Z: 1000 m)	0.09	0.09	0.08	0.09
Proportion wooded area (YS: 1000 m, Z: 1000 m)	0.68	0.09	0.67	0.08
Landscape configuration				
Forest clumpiness index (YS: 2000 m, Z: 2000 m)	0.91	0.03	0.91	0.03
Field perimeter (m) (YS: 2000 m, Z: 2000 m)	255.58	91.42	249.94	75.32
Distance to wooded patch	30.50	12.59	31.80	14.55

Table A2. Total number of specimens caught and number of unique species in each functional group.

Species group	Total caught	Unique species
Bumble bees	209	5
Large solitary bees	166	5
Small solitary bees	113	9
Honey bees	37	1
Total	525	20

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