

Do bees matter to cranberry?

The effect of bees, landscape, and local management on cranberry yield

By

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For my buddy old pal, Becky.
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THESIS ABSTRACT

Native bees provide the majority of pollination services to wild and cultivated flowering plants. Unfortunately, as the area of modern agriculture expands, fragmenting and destroying natural habitat, the persistence of native bees and the pollination services they provide is threatened. With the current decline in managed bees, understanding how local management decisions and landscape factors influence native bees and their contribution to crop pollination becomes more urgent. Using Wisconsin cranberry as a model system, I examined the pollination requirements of cranberry, the contribution of bees to pollination, and the influence of local and landscape factors on native bees. I further investigated the barriers to farmer adoption of on-farm conservation programs for native bees. Contrary to previous studies, I found that non-biotic factors contribute significantly to cranberry pollination (chapter 1). My research demonstrates that, even in the absence of bees, cranberry is able to produce fruit. Fruit production was, however, increased when bees were present supporting the practice of using honey bees for pollination. At a farm scale, cranberry yield was positively correlated with an increasing stocking density of honey bee hives, but only at farms located in low-woodland landscapes (chapter 2). When honey bees were absent, all farms had significant yield, but those in high woodland landscapes had a marginally higher yield than farms in low woodland landscapes. Farms in high woodland landscapes also had a higher abundance and richness of native bees although there was only a weak relationship between native bees and yield (chapter 3). The contribution of bees to cranberry pollination increased with increasing flowering upright density, suggesting that local management can enhance the contribution

by bees. Additional results indicate that cranberry growers are interested in creating pollinator habitat on their farms but are limited by a lack of technical support and perceived time and financial commitments (chapter 4). This dissertation contributes to our understanding of cranberry pollination biology and how local and landscape factors influence bees and their contribution to yield. I provide practical guidelines for growers on pollination management for cranberry and for conservation professionals on increasing cranberry grower participation in federal pollinator conservation programs.

THESIS INTRODUCTION

The expansion of modern agriculture and human activity has led to the alteration and fragmentation of the landscape (Vitousek et al. 1997, Foley et al. 2005). The resulting loss of habitat has profound effects on the ability of organisms to persist (reviewed by Fahrig 2003) and the provisioning of ecosystem services (Luck et al. 2003). The response of species that directly influence ecosystem services such as pollination is of particular importance. Insect-derived ecosystem services alone are worth an estimated \$8 billion per year and directly impact human wellbeing (Losey and Vaughan 2006, Eilers et al. 2011).

Pollination is a particularly important service in agro-ecosystems as it is required by or benefits two-thirds of global crops (Klein et al. 2007). As honey bees continue to decline (Ellis et al. 2010), farmers may need to seek alternative ways to pollinate their crops. Native bees provide valuable crop pollination services (Losey and Vaughan 2006, Winfree et al. 2008) but are at risk of decline due to habitat loss and fragmentation, intensified agriculture, and agri-chemical exposure (Potts et al. 2010). Since bees are central place foragers and have limited flight distances (Greenleaf et al. 2007, Zurbuchen et al. 2010), they require readily accessible nesting and foraging resources throughout their entire flight season. Because of agricultural practices that disturb the soil (e.g., tilling), limit the abundance of flowering weedy species (e.g., use of herbicides), and cultivate crops as monocultures, modern agricultural landscapes provide poor habitat for bees.

One way for farmers to lessen the effects of modern agricultural practices on bees is through the adoption of on-farm habitat conservation programs. Providing habitat within agricultural landscapes could greatly enhance local resource availability and the ability of

bees to persist and provide pollination services within crop fields. Cost-share conservation programs through the United States Department of Agriculture Natural Resources Conservation Service (USDA NRCS) provide growers with financial incentives to install pollinator habitat. In addition, for farmers of pollinator-dependent crops, such as cranberries, the adoption of these programs could provide a direct economic return in the form of increased pollination services from native bees. In order for this strategy to be successful, however, growers must adopt these practices. Because of their dependence on pollinators, demonstrated commitment to environmental stewardship through the adoption of Integrated Pest Management (IPM) programs, and the availability of non-crop habitat on their farms, cranberry growers should be ideal candidates for adoption of federal on-farm conservation programs (Colquhoun and Johnson 2010).

Before we can determine the significance of pollinator decline to crop production, however, we need to understand the pollination requirements of the crop and determine how much bees contribute to its pollination. Therefore, the objective of this study was to gain a better understanding of the factors that affect pollination and native bees in the Wisconsin cranberry system.

Cranberry is generally considered a pollinator-dependent crop, although estimates of yield loss in the absence of bees vary greatly (Delaplane and Mayer 2000), suggesting that the pollination requirements are not clearly understood. Therefore, in Chapter 1, I designed complementary field and greenhouse experiments to test the contribution of both biotic and non-biotic factors to cranberry pollination. I included treatments for biotic (i.e. bee or by hand), non-biotic (i.e. agitation), and no pollination. From the results of these

studies, we will gain a better understanding of how much pollination can be attributed to bees as opposed to non-biotic factors.

The majority of Wisconsin cranberry growers use honey bees to meet their pollination requirements, although the optimal hive stocking density is not known. While the recommended stocking density is 2-3 hives/acre, actual management ranges from 0-9 hives/acre. In Chapter 2, I used 11 years of historical yield and honey bee records from about 40 growers to determine the economically optimal stocking density. The optimal stocking density is the point at which an additional hive results in no additional increase in yield. The results of this research will provide an updated recommended hive stocking density that can be used by the growers for their pollination management practices in the future.

Another source of biotic pollination is native bees. In chapter 3, I investigated the influence of local farm management (i.e., pesticide usage, plant upright density) and surrounding landscape on these bees, as well as cranberry yield. Over the course of three field seasons, I pan trapped bees at 49 unique sites across a landscape gradient. In 2011 and 2012, I also compared yield estimates in open plots and pollinator exclusion cages to determine whether local and landscape factors influence the contribution of bees to yield. This chapter further adds to the literature on the effects of local and landscape factors on native pollinators and provides a new angle for looking at the effect of these factors on the contribution of pollinators to crop yield.

While we can learn a lot about a system through rigorous scientific studies, communicating directly with the people who manage the system can also provide valuable

insight. A scientific study takes a snapshot of the system, but the growers have been observing patterns and activity on their farms for years and may have a multi-generational perspective on management decisions and outcomes. Therefore, the fourth and final chapter of my dissertation takes a social perspective on cranberry pollination, management decisions, and on-farm conservation. The goal of this chapter was to determine the barriers that exist which prevent Wisconsin cranberry growers from implementing on-farm conservation programs for native bees. Through a written survey of the growers, I asked about their current management practices, awareness of native pollinators and pollinator habitat, and their attitudes toward and participation in on-farm conservation programs. The results of this chapter will provide concrete recommendations for agency personnel in order to target outreach activities and adjust program requirements to increase participation in USDA-sponsored on-farm conservation programs for native bees.

From this research, we will gain an understanding of the factors that contribute to cranberry pollination, the value and optimal stocking density of honey bees for cranberry production, the influence of local and landscape factors on native bees and their contribution to cranberry yield, and a grower perspective on pollination and on-farm conservation. This dissertation provides the results of rigorous scientific studies along with guidelines for the practical application of these results. It is my hope that the results of this research will be used by the scientific, grower, and agency communities to shape further research, refine pollination management practices, and improve conservation programs to increase the adoption of on-farm conservation for native bees in Wisconsin cranberry.

Literature cited

- Colquhoun, J., and H. Johnson. 2010. Sustainable cranberry production for a vibrant future: The Wisconsin experience. University of Wisconsin-Extension.
- Delaplane, K. S., and D. F. Mayer. 2000. Crop pollination by bees. CABI Publishing, New York, NY.
- Eilers, E. J., C. Kremen, S. Smith Greenleaf, A. K. Garber, and A.-M. Klein. 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS ONE* 6:e21363.
- Ellis, J. D., J. D. Evans, and J. Pettis. 2010. Colony losses, managed colony population decline, and Colony Collapse Disorder in the United States. *Journal of Apicultural Research* 49:134–136.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, and others. 2005. Global consequences of land use. *Science* 309:570.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274:303–313.
- Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311–323.
- Luck, G. W., G. C. Daily, and P. R. Ehrlich. 2003. Population diversity and ecosystem services. *Trends in Ecology & Evolution* 18:331–336.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494.

- Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45:793–802.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation* 143:669–676.

CHAPTER 1

Biotic and non-biotic factors contribute to cranberry pollination

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Abstract: As managed and native bee populations continue to decline, farmers face possible crop failures due to insufficient pollination. Crops, however, vary in the degree to which they depend on pollinators to move pollen between flowers, suggesting that some crops may not be as sensitive to variation in pollinator availability or abundance as others. Cranberry (*Vaccinium macrocarpon*) is generally considered a pollinator-dependent crop, although estimates of yield loss in the absence of bees vary greatly from 30-100%, raising the possibility that non-biotic factors may also be important for cranberry pollination. The objective of this study was to determine the contribution of biotic and non-biotic factors to cranberry pollination. We performed complementary field and greenhouse experiments to compare the effect of biotic (i.e., bee or hand pollination) and non-biotic factors such as wind or manual agitation on yield. In the greenhouse, we found that plants in the biotic treatment produced more berries per upright, more seeds per berry, and a greater overall yield than the non-biotic treatment. Plants in the non-biotic agitation treatment, however, also had more berries per upright and overall yield than plants in the undisturbed control

treatment. In the field, plants in the biotic treatment produced heavier berries, more seeds per berry, and a greater overall yield than the non-biotic wind and agitation treatments. Plants in the non-biotic treatments also had a higher yield than the undisturbed control treatment. In both the greenhouse and the field, we found a strong correlation between berry weight and number of seeds per berry for the Stevens cultivar. These results demonstrate that both biotic and non-biotic factors contribute significantly to cranberry pollination and that cranberry is not as dependent on pollinators as previously believed.

Keywords (6): cranberry, *Vaccinium macrocarpon*, pollination, wind pollination, thrips

1.0 Introduction

Insect pollination is an important ecosystem service required by the majority of flowering plants (Ollerton et al. 2011). Bees are the most important pollinators, but are declining worldwide (Biesmeijer et al. 2006; National Research Council 2007; Potts et al. 2010). In North America, many farmers rely on the managed, non-native honey bee (*Apis mellifera*) to provide pollination services. In the past 50 years, however, managed honey bee colonies have declined over 60% due to mites, disease, pesticide exposure, poor nutrition, and stress (Ellis et al. 2010). Native bees also provide important pollination services and, in some systems, are able to provide sufficient pollination without the assistance of honey bees (e.g., cranberry, Mohr & Kevan 1987; watermelon, Winfree et al. 2008). Unfortunately, native bees are also experiencing drastic declines due to habitat destruction, intensified agriculture, agri-chemical exposure, and disease (reviewed by Potts

et al. 2010). With the decline of bees, farmers face possible crop failures due to insufficient pollination (Gallai et al. 2009; Calderone 2012).

Crops, however, vary in the degree to which they depend on pollinators, suggesting that not all crops are equally susceptible to variability in the abundance of pollinators.

While two thirds of crop plants require or benefit from insect pollination to produce economically viable fruit (Klein et al. 2007), yield response varies by crop. In the absence of pollinators, some plants produce no fruit (e.g., watermelon, Delaplane & Mayer 2000), while others produce misshapen (e.g., strawberries, Free 1968; Jaycox 1970) or small fruit (e.g., cherry tomato, Greenleaf & Kremen 2006). Understanding the pollination requirements of specific crops can provide insight on the impact of pollinator decline on crop production.

Cranberry (*Vaccinium macrocarpon*) is considered to be a pollinator dependent crop (reviewed by McGregor 1976; Eck 1986, 1990; Free 1993; Delaplane & Mayer 2000). Although the flowers are self-compatible (Reader 1977; Dana et al. 1989; Sarracino & Vorsa 1991), pollen is released before the stigma is receptive (Rigby & Dana 1972), making self-pollination unlikely. Previous research shows that bees are effective pollinators of cranberry, capable of depositing enough pollen for fruit set in one or two visits (Cane & Schiffhauer 2003). As a result, individual growers spend thousands of dollars each year on honey bee rentals to ensure sufficient pollination (USDA NASS WASS 2006).

Despite the widespread use of honey bees and over one hundred years of research, the degree to which cranberry depends on pollinators remains unclear. Although bees are efficient cranberry pollinators and cranberry does not autogamously self-pollinate (Cane &

Schiffhauer 2003), it is possible that other, non-biotic factors contribute to cranberry pollination. Few studies, however, have considered non-bee factors. Of those that do, the results are conflicting. Previous studies have estimated that as little as 30% to as much as 100% of the cranberry crop would be lost in the absence of bees (Robinson et al. 1989; Southwick & Southwick 1992; Williams 1994; reviewed by Delaplane & Mayer 2000). At one end of this range, pollinator declines would have little effect on cranberry yield, while at the other end of the range, there would be crop failure. Furthermore, despite claims that cranberry pollen is too heavy to be transferred by wind (Stricker 1947), Papke et al. (1980) demonstrated that there is enough cranberry pollen being carried in the wind and falling on cranberry marshes to potentially provide a significant contribution to pollination. And Roberts & Struckmeyer (1942) demonstrated that manually agitated cranberry plants set fruit in the absence of bees. In later studies, however, Filmer (1949) and MacKenzie (1994) concluded that wind or the manual agitation of plants do not contribute to cranberry pollination. The paucity of research investigating non-bee mechanisms of pollination, and the inconsistency in findings between the studies that do, suggest that we lack a clear understanding of the factors contributing to cranberry pollination.

The goal of this study was to understand the relative importance of biotic and non-biotic factors to cranberry pollination. We hypothesized that non-biotic factors would result in a sufficient amount of pollen transfer to produce a berry but not as much as pollination by biotic factors. To address this hypothesis, we established field and greenhouse experiments in which we manipulated biotic (i.e. bees) and non-biotic factors (i.e. wind, manual agitation) that may contribute to cranberry pollination. In this study we

use yield as a metric of pollination success since this is the universal metric used in agriculture. We acknowledge, however, that pollination is only one of many factors that may affect final yield. By comparing the effect of these treatments on cranberry yield, we quantified the individual contribution of each factor to cranberry yield.

2.0 Methods

2.1 Cranberry

Cranberry (*Vaccinium macrocarpon*, Ericaceae) is a perennial fruit crop native to North America. Commercially it is grown in artificially created marshes with sandy, acidic soil. Cranberry grows in a vining habit along the ground and sends up vegetative and flowering shoots (“uprights”). Each flowering upright produces up to 8 flowers that bloom sequentially from the bottom of the upright upwards over several weeks (Eck 1990). Although cranberry flowers contain both male and female parts, pollen is released before the stigma becomes receptive, making autogamous self-pollination unlikely (Rigby & Dana 1972). Honey bees are commonly used for pollination on commercial cranberry marshes (Delaplane & Mayer 2000).

2.2 Greenhouse

Sixty dormant cranberry plants with visible buds, thirty each of the cultivars “HyRed” and “Stevens”, were dug up from a commercial cranberry marsh in late March of 2012. Plants were rinsed thoroughly to remove all sand and possible pests from the roots and planted into 15cm pots of moist peat moss. Pots were arranged randomly in a 22°C

greenhouse with a 16 hour photoperiod. Approximately one month after potting, uprights were thinned so that only those with 3-5 flower buds remained. Pots were further thinned to 5-6 flowering uprights per pot in order to reduce the total number of flowers in a pot and to separate those that remained to make hand pollination possible. All but the first four flowers to bloom per upright were trimmed off as they opened since cranberry plants are more likely to set fruit on the lower, earlier flowers than the upper flowers (Birrenkott & Stang 1989).

Three treatments were established in the greenhouse: (1) “hand” pollination, which was meant to represent the biotic movement of pollen between flowers (mimicking bee visitation), (2) “agitation”, which was meant to represent the physical movement of plants by wind, and (3) an unmanipulated control, which provided a measure of autogamous self-pollination. To assess the potential for biotic pollination, flowers with a receptive stigma (i.e. those that were moist and protruding from the stamens) were hand pollinated daily during bloom by gently applying the stigma to a small accumulation of pollen collected from younger flowers into the cap of a micro-centrifuge tube. To assess the potential for non-biotic pollination, plants in the “agitation” treatment were gently jostled daily during bloom by moving the palm of the hand across the top of the uprights, causing the plants to bump against each other. This simulated the physical movement of plants as may be caused by wind while excluding the possibility of wind pollination *per se* in which pollen is moved through the air. Plants in the unmanipulated control treatment were left undisturbed throughout the study to assess whether fruit would be produced in the absence of either biotic or non-biotic factors (i.e., autogamous self-pollination). For each

treatment we had 10 replicates (i.e., pots) per cultivar. Pots were placed in two parallel rows ~0.2m apart and spanning 3-3.5m on both sides of a single aisle of greenhouse tables (one cultivar per side). Pots in the row closest to the aisle were assigned to the hand pollination treatment so that all flowers were easily accessible without the possibility of bumping other pots, and pots in the back row were randomly assigned either to the non-biotic or undisturbed treatment. Experimental treatments were initiated as soon as bloom began and were continued daily until all flowers were done blooming. Berries were harvested approximately two months after bloom began. Each berry was then weighed (wet weight, g) and the number of berries per upright were counted as a proxy for yield. In order to understand the level of pollination received in each treatment, the number of fully formed seeds was counted for each berry. Cane & Schiffhauer (2003) demonstrated that the number of seeds is proportional to the amount of pollen deposited on the stigma and therefore represents an indication of pollination success. Averages were taken for each pot for a total of 10 replicates per treatment.

To examine differences among experimental treatments (“hand”, “agitation”, undisturbed control) and cultivar (“Stevens”, “HyRed”), we used a fully factorial two-way analysis of variance (ANOVA) to compare berries per upright, weight per berry, yield (total berry weight per upright), and seeds per berry. Each of these variables indicate some form of pollination success. Differences among treatments by cultivar were determined using Tukey’s Honestly Significant Difference (HSD) test (Hsu 1996). Statistical analyses were performed with JMP Pro 10.0.0 (SAS Institute Inc 2007).

2.3 Field cages

To assess the influence of biotic and non-biotic factors on cranberry yield in a field setting, we established a cage study in a commercial cranberry marsh of the “Stevens” cultivar. Four treatments were established: (1) “open”, which allowed both bee visitation and agitation by wind, (2) “wind”, which blocked insect visitation with a fine nylon mesh (matte nylon tulle in ivory, Joann Fabric) but allowed wind to agitate the plants or move pollen, (3) “closed”, which prevented insect visitation and wind using floating row cover (Agribon+ AG-15 Insect Barrier, Johnny’s Selected Seeds) with a corrugated plastic wind block surrounding the cage (4mm corrugated plastic, Laird Plastics), and (4) “agitation”, which used the same cage design as the “closed” treatment but received manual agitation twice per week during bloom to mimic movement of the plants by wind but excluded the possibility of wind pollination *per se* in which pollen is moved through the air. Each treatment was replicated 10 times. Cage frames were constructed using lightweight, black irrigation tubing and $\frac{3}{4}$ ” PVC cut into 6” segments with a point at one end (i.e. 12” PVC sections were cut in half at a 45° angle). The PVC stakes were hammered into the ground at each corner of each cage and the irrigation tubing was inserted into the PVC to make a tent shape frame. Mesh was attached to the cage frames using 2” binder clips. A small sheet of 2mm plastic sheeting was placed between the binder clip and the mesh to prevent the mesh from tearing. The mesh was further secured by placing $\frac{1}{2}$ ” - $\frac{3}{4}$ ” PCV segments filled with gravel and sand at the base of each side of the cage. In order to account for possible differences in plants as a function of location within the cranberry bed, cages were arranged in a grid and treatments were assigned using a modified Latin Square design with

each treatment occurring once per column and twice per row. Cages were set up before cranberry bloom (May 25, 2012) and removed when bloom was complete (July 9, 2012). Berries were harvested from a 0.3m x 0.3m (1 ft²) plot from the center of each cage before harvest (September 20, 2012) and counted and weighed (wet) to estimate yield. Wet weight was used as this can be easily converted to yield units used by cranberry growers (barrels/acre, 1 barrel = 100 lbs = 45kg). Twenty berries from each cage were also cut in half with a razor blade and all fully formed seeds within were counted.

An additional 15 cages (5 each “open”, “wind”, and “closed”, treatments as described above) were established to measure environmental variables that may be altered by the cages including temperature, light intensity, soil moisture, and insect community. Temperature and light intensity were measured every 30 minutes for the duration of the cage study using HOBO data loggers (Onset Computer Corporation) hung inside Styrofoam sunshields. Soil moisture was measured using a TDR 300 soil moisture meter (Spectrum Technologies, Aurora, Illinois) twice during the growing season (June 14 and July 9, 2012). Four measurements were taken per cage. The insect community was measured continuously during bloom using yellow sticky strips (3” x 5”, Great Lakes IPM 025-SS-35) and blue, yellow, and white pan traps (ACE Brand Fluorescent paint) containing soapy water (Dawn blue dish soap).

To examine differences among treatments for berries per upright, weight per berry, yield, and seeds per berry, we used a one-way mixed model ANOVA with row and column locations as random effects. Differences among treatments were determined using Tukey’s

HSD test. Statistical analyses were performed using JMP Pro 10.0.0 (SAS Institute Inc. 2007).

3.0 Results

3.1 Greenhouse

In the greenhouse, significant fruit set occurred on plants in both the biotic (“hand”) and non-biotic (“agitation”) treatments but not the undisturbed control. Ninety-eight percent of “HyRed” and 92% of “Stevens” uprights in the “hand” pollination treatment produced fruit and 52% of the “HyRed” and 30% of the “Stevens” uprights in the “agitation” treatment produced fruit. Only 2% of “HyRed” and 5% of “Stevens” uprights in the unmanipulated control produced fruit, providing evidence for the lack of autogamous self-pollination in cranberry.

The number of berries per upright varied significantly among treatments in both cultivars (treatment, $F_{2,58}=248.6$, $p<0.0001$, Fig. 1a). Significantly more berries per upright were produced in the “hand” pollination treatment than in the “agitation” treatment, and more in the “agitation” treatment than in the unmanipulated control. This difference was greater in the “HyRed” cultivar than in “Stevens” (treatment x cultivar, $F_{2,58}=3.9$, $p=0.028$). Berry weight did not vary across treatments ($F_{2,41}=2.4$, $p=0.11$, Fig. 1b) or cultivar ($F_{1,41}=0.0021$, $p=0.96$). The number of seeds per berry was greater in the “hand” pollination treatment than both of the other treatments and did not vary between the “agitation” treatment and the unmanipulated control ($F_{2,58}=136.3$, $p<0.0001$, Fig. 1c). The number of seeds per berry for the undisturbed treatment in “HyRed” is based on a single

berry that formed in this treatment and is therefore not representative of the treatment as a whole. Yield was estimated by total berry weight per upright which is a function of berry weight and berries per upright. Overall, yields were higher in the “hand” pollination treatment than in the other treatments (treatment, $F_{2,58}=210.3$, $p<0.0001$, Fig. 1d). Total berry weight per upright was also significantly greater in the “agitation” treatment than the “no-pollination” treatment for “HyRed” but not for “Stevens”.

3.2 Field experiment

In the field, open plots had the highest fruit set, although even when insects were excluded, there was substantial fruit set in both of the non-biotic treatments (“agitation” and “wind”). The number of berries per upright was fairly consistent across treatments and did not vary between the “open” treatment and any other treatment but was lower in the “agitation” treatment than in the “wind” or “closed” treatments (treatment, $F_{3,24.6}=4.6$, $p=0.011$, Fig. 2a). The weight per berry was significantly different among treatments ($F_{3,24.2}=36.6$, $p<0.0001$, fig. 2b) with the heaviest berries in the “open” treatment, followed by “agitation”, and lowest in the “wind” treatment and “closed” control. The number of viable seeds per berry varied significantly by treatment ($F_{3,23.91}=64.9$, $p<0.0001$, Fig. 2c) with the most found in the “open” treatment followed by “agitation” and the least in “wind” and “closed” treatment. Yield, as estimated from small plots, was highest for the “open” treatment followed by “wind” and “agitation” and lowest for the “closed” treatment ($F_{3,23.1}=70.5$, $p<0.0001$, fig. 2d).

Because the number of seeds is proportional to the amount of pollen deposited (Cane & Schiffhauer 2003), we used seeds per berry as a measure of pollination success.

We found a strong relationship between berry weight and seed number for “Stevens” in both the greenhouse ($p=0.0011$, $R^2=0.42$, fig. 3a) and the field ($R^2=0.83$, $p<0.0001$, fig. 3a) but not for “HyRed” ($p=0.39$, $R^2=0.04$, fig. 3b). This pattern suggests that the number of pollen tetrads deposited on flowers varied significantly among treatments and that even in the “open” treatment, pollen can be limited, preventing the berry from reaching a maximum weight.

3.2.1 Environmental effects

The environmental variables we measured to test cage effects provide evidence that the cages successfully excluded pollinators while maintaining comparable conditions within each cage type. The abundance of insects varied significantly among all treatments with the lowest abundance in the “closed” (row cover) treatment, suggesting that cage treatments effectively excluded all but the smallest insects (e.g., thrips). Soil moisture did not vary among cage treatments ($F_{2,23}=0.17$, $p=0.84$). The temperature was on average 1.1°C higher in the “closed” treatment cage than the open or “wind” (nylon mesh) treatments ($F_{2,7038}=13.5$, $p<0.0001$). Light varied significantly as well with the most light in the open treatment followed equally by the “wind” and “closed” treatments ($F_{2,13163}=42.4$, $p<0.0001$). Shading can result in a higher production of vegetative material resulting in lowered yields (Roberts and Struckmeyer 1942).

4.0 Discussion

The requirement of bees for cranberry pollination is generally assumed although the evidence is lacking. In over one hundred years of research, only four studies have

considered the contribution of non-bee factors to cranberry pollination (Roberts & Struckmeyer 1942; Filmer 1949; Papke et al. 1980; MacKenzie 1994). In this study we demonstrate that in the absence of bees, cranberry is still able to produce fruit. In a field setting, we found that plants, from which insect pollinators, but not wind, were excluded, produced a greater overall yield than plants from which both insects and wind were excluded. This finding, combined with manual agitation treatments in the field and greenhouse, challenges the notion that bees are the only way for cranberry to produce fruit (reviewed by McGregor 1976; Eck 1990; Free 1993; Delaplane and Mayer 2000), and suggests that both biotic and non-biotic factors contribute significantly to cranberry pollination.

Previous research on cranberry pollination has mainly compared the effect of bee pollination versus autogamous self-pollination. The majority of these studies have concluded that bees are required to produce fruit, although what their data actually demonstrate is that cranberries are not autogamous and are unable to self-pollinate within a single flower (Hutson 1925; Farrar & Bain 1947; Filmer & Doehlert 1959; Marucci 1966; Marucci & Moulter 1977; Cane & Schiffhauer 2003). Our study supports the finding that cranberry does not autogamously self-pollinate, but also provides evidence that other, non-bee factors play a role in cranberry pollination.

The increased yield in the non-biotic treatments (i.e. agitation, wind) as compared to the closed treatment in the field may be attributable to uncontrolled variables in the field such as non-bee insect pollinators, agronomic variation (i.e. upright density), or a combination of the two. In the greenhouse, the agitation treatment produced

approximately 25% of the yield compared to the hand pollination treatment, whereas the no-pollination treatment had virtually zero yield. In the field, the non-biotic treatments produced approximately 50% of the yield compared to the open treatment, and even the no-pollination treatment had some yield. Through careful cage construction and pan trapping within cages, we are confident that bees were not contributing to the increased yield within the field cage treatments. However, thrips, tiny pollen-eating insects, were found in all treatments in the field and have been shown to be effective pollinators in other systems, including Ericaceous plants which are in the same family as cranberry (Hagerup & Hagerup 1953; Kirk 1988; Baker & Cruden 1991; Ananthakrishnan 1993), although their influence in cranberry pollination has not been investigated (but see Appendix 1.1). The absence of thrips in the greenhouse (pers. obs.) and abundance in the field suggests that they may be a contributing factor.

Another factor that may have caused increased yield in the non-biotic and closed treatments in the field is flowering upright density. In the greenhouse, flowering uprights were thinned to a very low density to make hand pollination manageable (279 flowering uprights/m²), whereas in the field, flowering uprights were six times as dense (1705 flowering uprights/m²). With a higher density of flowering uprights, pollen is more abundant and flowers are closer together, increasing the likelihood that pollen could be transferred between flowers with even slight agitation. A high density of uprights not only increases the probability of pollen transfer between flowers when agitated, but may also make movement of thrips among flowers easier.

Another difference between the field and greenhouse was the pattern among treatments in berry weight. In the field, berry weight was significantly different among treatments, whereas in the greenhouse, berry weight did not vary among treatments. Previous studies have found a strong correlation between berry weight and seed number (Hall & Aalders 1965; Rigby & Dana 1971), demonstrating that when pollen is limited, berry weight is low. In our study, we found a significant relationship between berry weight and seed number in the Stevens cultivar in the field and the greenhouse, although the relationship was weaker and shallower in the greenhouse. Despite evidence in previous studies that cranberry can produce seedless fruit through parthenogenesis (Roberts & Struckmeyer 1942), even berries in the no-pollination treatment had some viable seeds, suggesting that parthenogenesis is not occurring here. Additionally, the number of seeds per berry was similar between treatments in the field and greenhouse, suggesting that other factors, such as water and nutrient availability and not just pollen limitation, may play a role in berry weight. The lack of relationship between berry weight and seed number in the HyRed cultivar in the greenhouse further suggests that berry weight is influenced by factors other than seed number. Cane and Schiffhauer (2003) found that in the Stevens cultivar, the berry reaches a maximum weight when the flower receives 8 tetrads of pollen resulting in about 15 seeds. In our study, berries in the Stevens cultivar only reached 15 seeds per berry in the hand pollinated treatment in the greenhouse, suggesting that even in the open treatment in the field, pollen may be limited. In HyRed, however, the relationship was flat suggesting that the seed number/berry weight relationship may vary among cultivars.

Previous studies, on which current pollination management recommendations are derived (McGregor 1976), were designed to test the importance of bees to cranberry pollination but did not account for the possibility of non-bee pollination vectors. Other, more recent studies (e.g., Cane and Schiffhauer 2003) have demonstrated the efficiency of bee pollinators and the lack of autogamous self-pollination in cranberry, but still overlook alternative mechanisms for pollination. Phillips (2011) also demonstrated the lack of autogamous self-pollination in cranberry but incorrectly concluded that cranberry requires insect pollination. In these studies, individual cranberry flowers were isolated to demonstrate the inability to self-pollinate. However, in the field, flowers are not isolated, rather they are exposed to a variety of biotic and non-biotic factors. In several influential studies, Hutson (1925) and Filmer and Doehlert (1955) demonstrated the dependence of cranberry on bees in a field cage study, but when berries formed within the cages, attributed the berries to faulty cages rather than considering alternative mechanisms of pollination.

Our study was specifically designed to test the co-existence of pollination mechanisms including bees, wind, mechanical action, and autogamous self-pollination. We found that mechanical agitation by wind or hand, can effectively move pollen between cranberry flowers. In small plots at our study site, as much as 50% of yield could be attributed to non-bee pollinators, resulting in economically competitive yields. The results of this study suggest that in the absence of bee pollinators, cranberry growers may still be able to produce a significant crop yield. These results further suggest that mechanical

agitation may be more prevalent in other cropping systems than previously believed and provides further rationale for detailed pollination studies in other crop plants.

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Literature cited

- Ananthkrishnan TN (1993) The role of thrips in pollination. *Current Science* 65:262–264.
- Baker JD, Cruden RW (1991) Thrips-mediated self-pollination of two facultatively xenogamous wetland species. *American Journal of Botany* 78:959–963.
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–354.
- Birrenkott BA, Stang EJ (1989) Pollination and pollen tube growth in relation to cranberry fruit development. *Journal of the American Society for Horticultural Science* 114:733–737.
- Calderone NW (2012) Insect pollinated crops, insect pollinators and US agriculture: Trend analysis of aggregate data for the period 1992-2009. *Plos One* 7:e37235.
- Cane JH, Schiffhauer D (2003) Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). *American Journal of Botany* 90:1425–1432.

- Dana MN, Steinmann S, Goben L (1989) Pollen source and fruit set of cranberry. *Cranberries* 53:10–14.
- Delaplane KS, Mayer DF (2000) *Crop pollination by bees*. CABI Publishing, New York, NY.
- Eck P (1986) Cranberry. In: Monselise, S.P. (ed) *CRC handbook of fruit set and development*. CRC Press, Boca Raton, FL, pp 109–117.
- Eck P (1990) *The American cranberry*. Rutgers University Press New Brunswick, NJ.
- Ellis JD, Evans JD, Pettis J (2010) Colony losses, managed colony population decline, and Colony Collapse Disorder in the United States. *Journal of Apicultural Research* 49:134–136.
- Farrar CL, Bain HF (1947) Honeybees as pollinators of the cranberry. *Cranberries* 11
- Filmer RS (1949) Cranberry pollination studies. In: *American Cranberry Growers' Association Proceedings of the Annual Meeting*.pp 14–20.
- Filmer RS, Doehlert CA (1959) Use of honeybees in cranberry bogs. New Jersey Agricultural Experiment Station, New Brunswick, NJ.
- Filmer RS, Doehlert. CA (1955) Use of honeybees in cranberry bogs. *Gleanings in Bee Culture*:265–268.
- Free JB (1968) The pollination of strawberries by honey-bees. *Journal of Horticultural Science* 48:107–11.
- Free JB (1993) *Insect pollination of crops*, 2nd ed. Academic Press Inc., London.
- Gallai N, Salles J-M, Settele J, Vaissière BE (2009) Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* 68:810–821.
- Greenleaf SS, Kremen C (2006) Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133:81–87.
- Hagerup E, Hagerup O (1953) Thrips pollination of *Erica tetralix*. *New Phytologist* 52:1–7.
- Hall IV, Aalders LE (1965) The relation between seed number and berry weight in the cranberry. *Canadian Journal of Plant Science* 45:292–292.
- Hsu JC (1996) *Multiple comparisons: theory and methods*. Chapman & Hall, London.
- Hutson R (1925) The honey bee as an agent in the pollination of pears, apples and cranberries. *Journal of Economic Entomology* 18:387–391.
- Jaycox ER (1970) Pollination of strawberries. *American Bee Journal*:176–177.

- Kirk WDJ (1988) Thrips and pollination biology. In: Ananthakrishnan, T.N., Raman, A. (eds) Dynamics of Insect-Plant Interaction: Recent Advances and Future Trends. Oxford & IBH Publishing Company, New Delhi
- Klein A-M, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences* 274:303–313.
- MacKenzie KE (1994) The foraging behaviour of honey bees (*Apis mellifera* L) and bumble bees (*Bombus* spp) on cranberry (*Vaccinium macrocarpon* Ait). *Apidologie* 25:375–383.
- Marucci PE (1966) Cranberry Pollination. *Cranberries* 30:11–13.
- Marucci PE, Moulter HJ (1977) Cranberry pollination in New Jersey. *Acta Horticulturae (ISHS)* 61:217–222.
- McGregor SE (1976) Insect pollination of cultivated crop plants. Agricultural Research Service, US Department of Agriculture, Washington, D.C.
- Mohr NA, Kevan PG (1987) Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.) and lingonberry (*V. vitis-idaea* L.). In: *Proceedings of the Entomological Society of Ontario*.pp 149–154.
- National Research Council (2007) Status of Pollinators in North America. Committee on the Status of Pollinators in North America, The National Academies Press, Washington, D.C.
- Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- Papke AM, Eaton GW, Bowen PA (1980) Airborne pollen above a cranberry bog. *HortScience* 15:756.
- Phillips KN (2011) A comparison of bumble bees (*Bombus* spp.) and honey bees (*Apis mellifera*) for the pollination of Oregon cranberries (*Ericaceae: Vaccinium macrocarpon*). M.S. Thesis. Oregon State University
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.
- Reader RJ (1977) Bog ericad flowers: self-compatibility and relative attractiveness to bees. *Canadian Journal of Botany* 55:2279–2287.
- Rigby B, Dana MN (1971) Seed number and berry volume in cranberry. *HortScience* 6:495–496.
- Rigby B, Dana MN (1972) Flower opening, pollen shedding, stigma receptivity, and pollen tube growth in the cranberry. *HortScience* 7:84–85.

Roberts RH, Struckmeyer BE (1942) Growth and fruiting of the cranberry. In: Proceedings of the American Society for Horticultural Science. pp 373–379.

Robinson WS, Nowogrodzki R, Morse RA (1989) The value of honey bees as pollinators of U.S. crops. *American Bee Journal* 129:411–423, 477–487.

Sarracino JM, Vorsa N (1991) Self and cross fertility in cranberry. *Euphytica* 58:129–136.

SAS Institute Inc. (2007) JMP Pro 10. SAS Institute Inc., Cary, NC.

Southwick EE, Southwick L (1992) Estimating the Economic Value of Honey Bees (Hymenoptera: Apidae) as Agricultural Pollinators in the United States. *Journal of Economic Entomology* 85:621–633.

Stricker MH (1947) Bees and pollinating cranberries. *American Cranberry Growers' Association Proceedings of the Annual Meeting* 77

USDA NASS WASS (2006) 2005 Cranberry production and pollination survey.

Williams I (1994) The dependence of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews* 6:229–257.

Winfrey R, Williams NM, Gaines H, Ascher JS, Kremen C (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45:793–802.

Figure captions

Figure 1: Metrics of pollination success for the cranberry cultivar “HyRed” and “Stevens” as measured in the greenhouse: (a) the number of berries per upright (mean \pm SE), (b) the berry weight (mean \pm SE), (c) the number of seeds per berry (mean \pm SE), and (d) the yield estimate (mean wet weight per upright \pm SE). Treatments included “hand” pollination which represented biotic pollination, “agitation” which represented non-biotic pollination, and an undisturbed control.

Figure 2: Metrics of pollination success for the cranberry cultivar “Stevens” as measured in the field: (a) the number of berries per upright (mean \pm SE), (b) the berry weight (mean \pm SE), (c) the number of seeds per berry (mean \pm SE), and (d) the yield estimate (mean \pm SE). Treatments included “open” pollination which represented ambient pollination, “wind” which represented non-biotic pollination through wind pollination *per se* and physical movement of the plants due to wind, “agitation” which represented non-biotic pollination due to physical movement of the plants in the absence of wind pollination *per se*, and a closed control.

Figure 3: Relationship between berry weight and seeds per berry for the cranberry cultivars (a) “Stevens” and (b) “HyRed”.

Figure 1

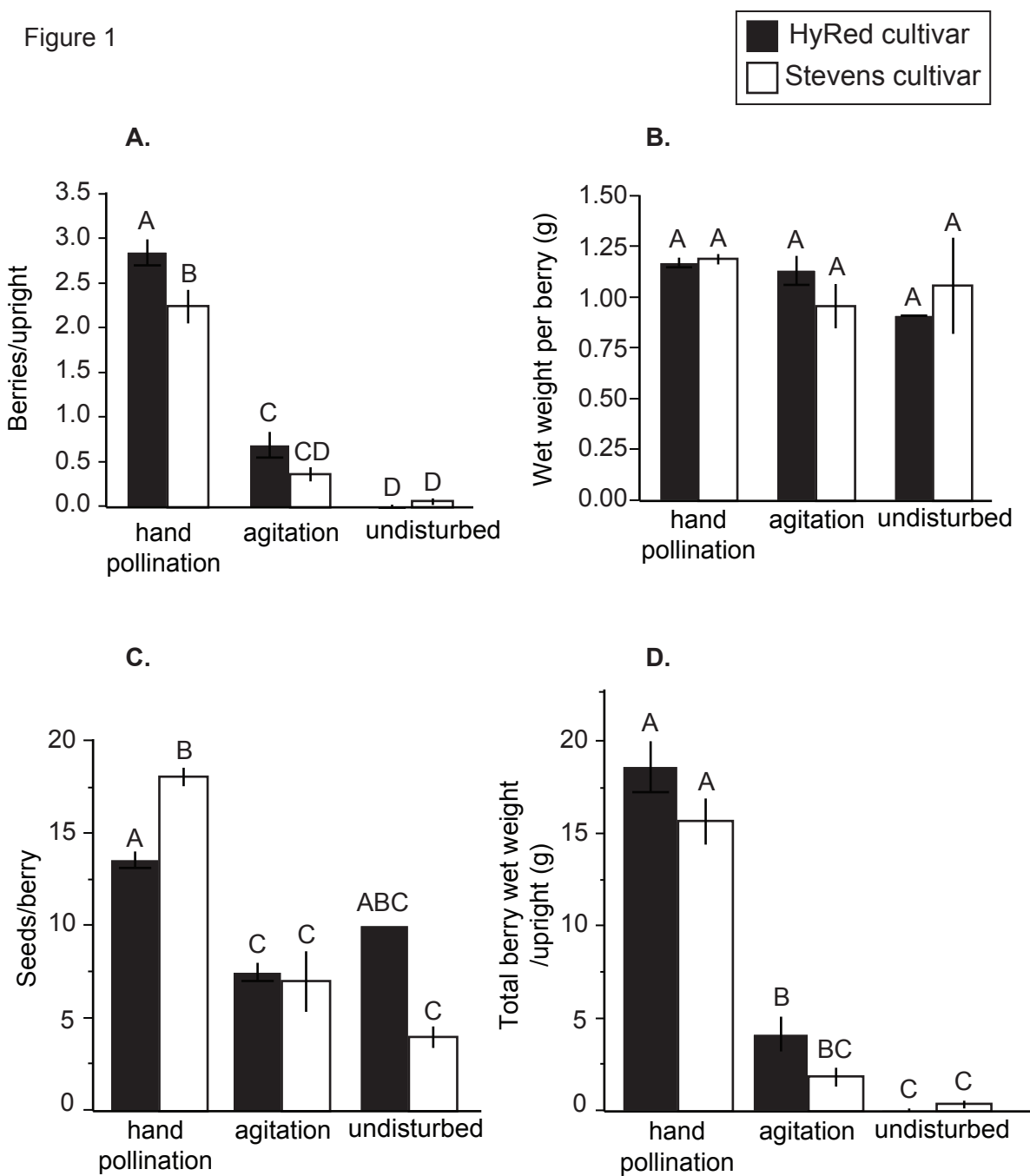


Figure 2

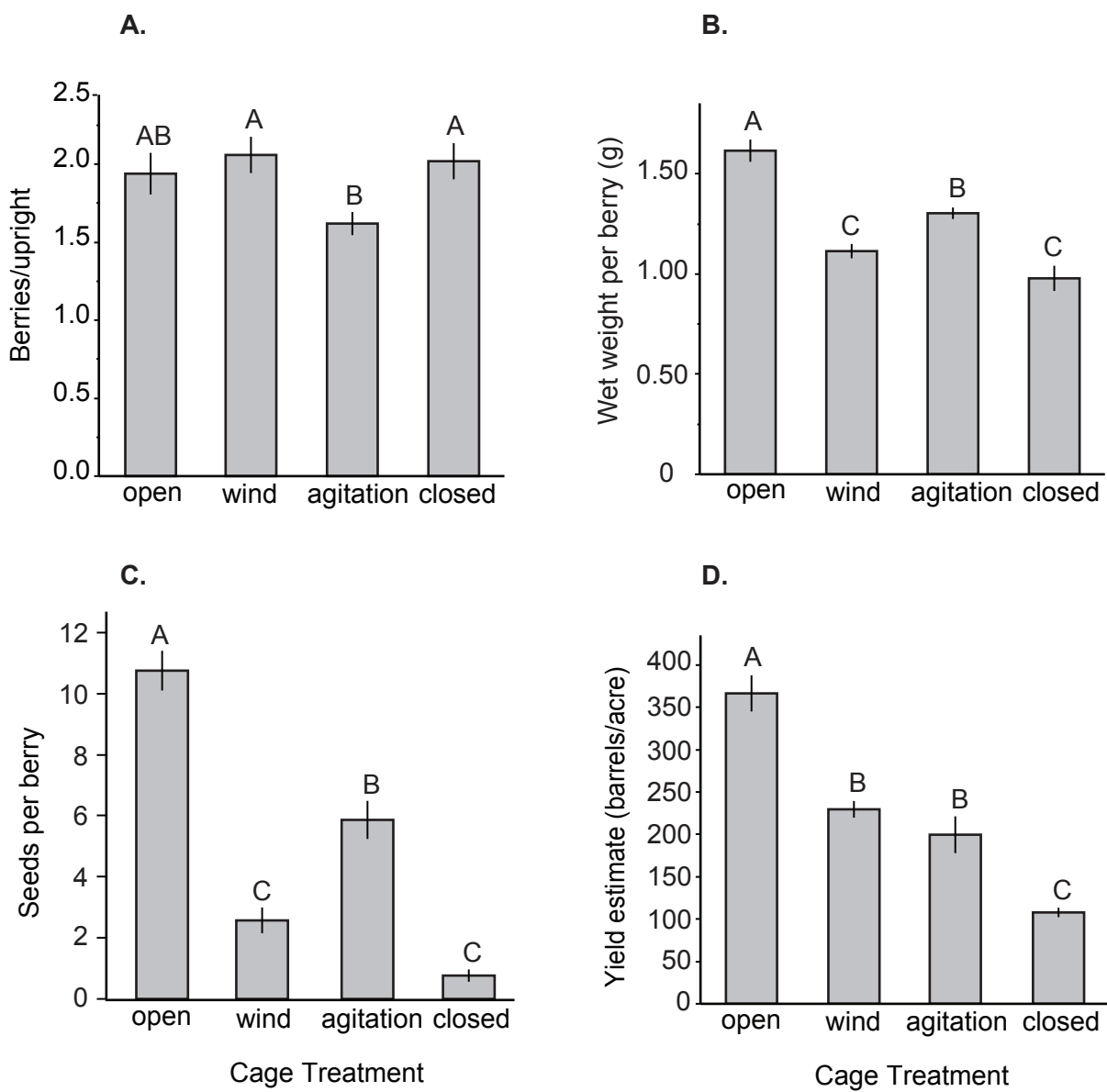
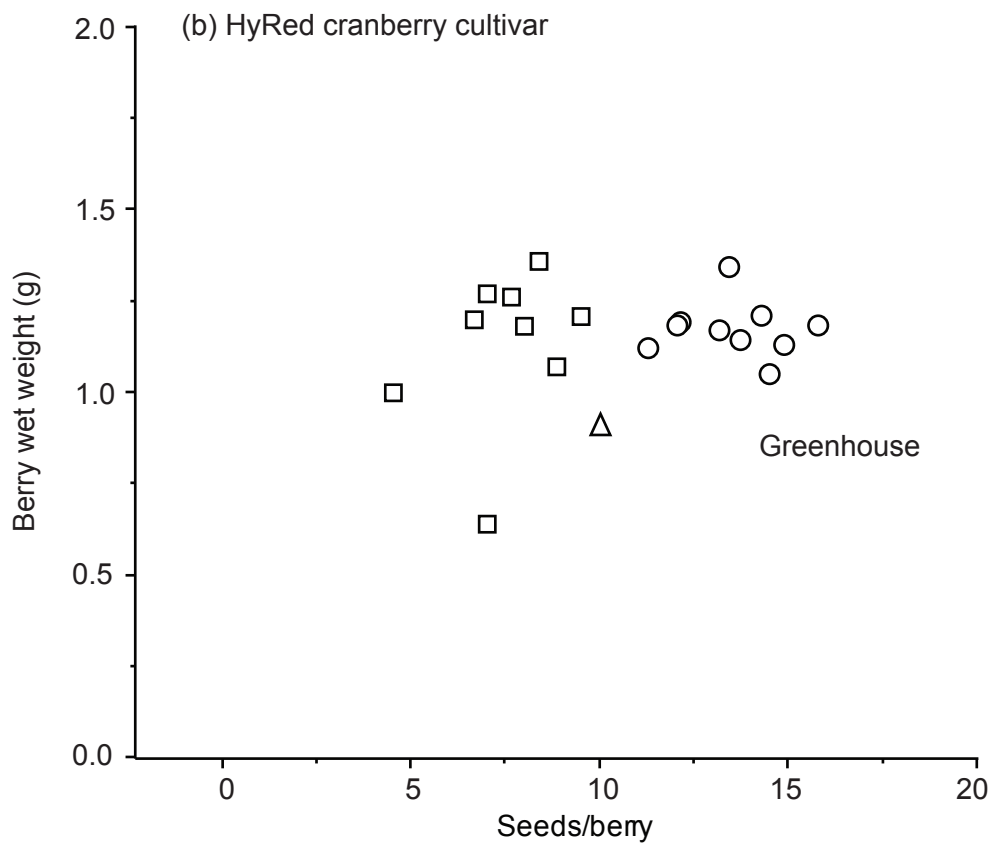
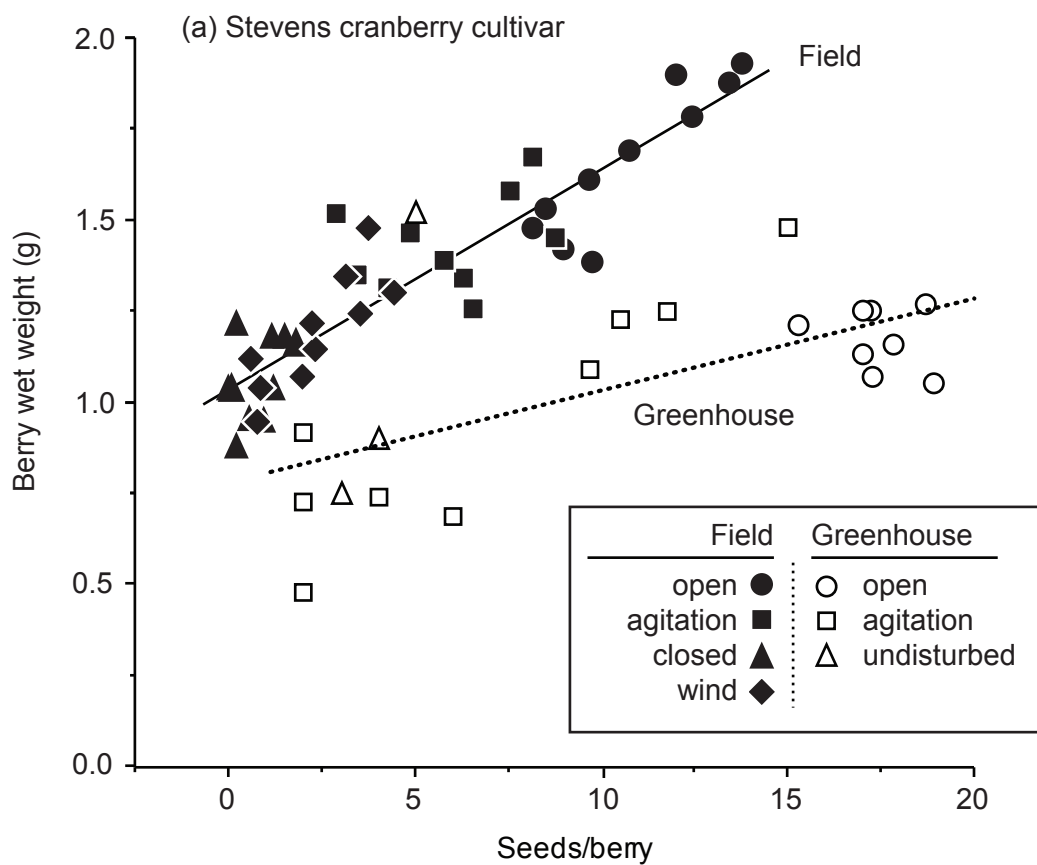


Figure 3



Appendix 1.1: Assessing the role of thrips (Thysanoptera) in cranberry pollination

Introduction

Cranberry is considered a pollinator dependent crop (Delaplane and Mayer 2000), but in field experiments in 2011 and 2012, caged (“closed”) cranberry plants produced a significant amount of fruit. In a follow-up greenhouse study, plants in the “closed” treatment produced nearly no fruit at all. These results suggest that additional, uncontrolled factors exist in the field that effect cranberry pollination. One possible factor is the presence of thrips, tiny pollen-eating insects. Thrips are known to be important pollinators in some systems (Kirk, W.D.J. 1988, Baker and Cruden 1991, Ananthakrishnan 1993) and were found on sticky cards in all field treatment types (Gaines, unpubl. data). Another factor that may influence pollination is the density of flowering uprights. Field plots had a significantly higher density of flowering uprights as compared to the greenhouse. A higher flowering upright density could make movement of thrips from one plant to another easier or simply increase the probability that flowers bump into each other when agitated. Therefore, the objective of this study was to determine the contribution of thrips and the influence of upright density on cranberry pollination.

Methods

Cranberries

Cranberry plants of the cultivar Stevens were dug from a commercial cranberry marsh in late fall 2012. Since the ground in the marsh was already frozen, plants were only

collected at the edge of the marsh where chunks of plants could be extracted with an ice pick. Plants were brought back to the greenhouse and kept in cold storage (4°C with an 8-hour photoperiod) for one month. Ice was placed over the plants once per week to keep the plants from drying out.

After one month in cold storage, the plants were rinsed off and transplanted into 6" pots filled with moist peat. Pots were set in a 22°C greenhouse with a 16 hour photoperiod and assigned a treatment (table 1). Plants were watered every 4 days and excessive vine growth trimmed. After about three weeks, plants were fertilized with ½ teaspoon fertilizer per gallon water.

The study was intended to be a 2-factor, full factorial design to compare fruit set due to hand pollination, thrips pollination, agitation, and no pollination as a function of upright density. Ten pots were assigned to each treatment (table 1).

Approximately four weeks after potting, plants were expected to begin showing signs of flower development.

Unfortunately, very few plants did so and the experimental design had to be drastically reduced (table 2). This was likely due to poor plant material dug from the marsh in the fall. Because of the frozen ground, we were unable to be selective in which plants we dug. The plants that did show signs of flowering were placed into large cages with fine mesh to keep

Table 1: Number of pots per treatment for intended study design

		Upright density	
		Low	High
Pollination treatment	Hand	10	10
	Thrips	10	10
	Agitation	10	10
	None	10	10

thrips in or out. Each cage had two pots with six cages per treatment (n=12 pots per treatment).

Thrips

Once the cranberry plants were re-potted into peat, a thrips colony was established in the lab. To start the colony, a few dozen green beans containing thrips eggs were acquired from an existing colony. The colony was maintained using previously established methods (Tom

German, pers. comm.) as follows. Two to three of the beans from the established colony were placed in plastic deli cups with mesh tops. Fresh beans were purchased and soaked for 10 minutes in a bleach solution (50mL bleach to 500mL water) to kill any microorganisms and prevent molding on the beans. Once dry, two to three fresh beans were added to each deli cup to provide food for emerging thrips. Fresh beans were added and old beans removed every ~4 days.

When cranberry bloom began, plants in the “thrips” treatment were inoculated with 3 late instar or adult thrips per flower. Thrips were transported to the greenhouse using centrifuge tubes. Tubes were stuck into the soil of the pots in the thrips treatment and the caps removed to allow the thrips to crawl onto the cranberry plants. This was done twice during the three week bloom. Plants in the no pollination treatment were left undisturbed.

Table 2: Number of pots per treatment for actual study design.

		Upright density	
		Low	High
Pollination treatment	Hand	0	0
	Thrips	0	12
	Agitation	0	0
	None	0	12

After bloom, blue sticky cards were placed in each cage to verify the presence of thrips (Chen et al. 2009). We also intended to count and measure berries once they were full size. This never happened because no berries formed on any plants in either treatment.

Results

No cranberry fruits were produced in either treatment (table 3). We were also unable to recapture any thrips on the blue sticky cards in either the cages or in the open greenhouse.

		Pots	Berries per upright	Thrips per sticky card
Pollination treatment	Thrips	12	0±0	0±0
	None	12	0±0	0±0

Conclusions

The results of this study are unable to support the hypothesis that thrips contribute to cranberry pollination. It is possible that thrips are not contributing to cranberry pollination or that experimental design failed to effectively test this. Future studies should dig cranberry plants earlier in the fall or in the spring to allow for better plant material selection (i.e., plants with large buds present). Additionally, instead of inoculating plants with thrips, placing plants in greenhouses with known thrips infestations may be more

effective. Thrips are a serious greenhouse pest and finding a greenhouse with thrips problem should not be difficult.

Literature cited

- Ananthakrishnan, T. N. 1993. The role of thrips in pollination. *Current Science* 65:262–264.
- Baker, J. D., and R. W. Cruden. 1991. Thrips-Mediated Self-Pollination of Two Facultatively Xenogamous Wetland Species. *American Journal of Botany* 78:959–963.
- Chen, T.-Y., C.-C. Chu, G. Fitzgerald, E. T. Natwick, and T. J. Henneberry. 2009. Trap Evaluations for Thrips (Thysanoptera: Thripidae) and Hoverflies (Diptera: Syrphidae). *Environmental Entomology*:1416–1420.
- Delaplane, K. S., and D. F. Mayer. 2000. *Crop pollination by bees*. CABI Publishing, New York, NY.
- Kirk, W.D.J. 1988. Thrips and pollination biology. *in* Ananthakrishnan, T.N. and Raman, A., editors. *Dynamics of Insect-Plant Interaction: Recent Advances and Future Trends*. Oxford & IBH Publishing Company, New Delhi.

CHAPTER 2

The contribution of honey bees to cranberry yield varies with the amount of woodland in the surrounding landscape

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Abstract: Two-thirds of crop plants require or benefit from insect pollination. To ensure sufficient pollination of their crops, many farmers rent hives of honey bees. Cranberry (*Vaccinium macrocarpon*), a perennial fruit crop native to North America, is generally considered pollinator dependent and most cranberry growers rent honey bees for pollination. The economically optimal hive stocking density, or the point at which the cost of adding an additional hive is greater than the economic return, however, is unknown, resulting in wide variation in management practices. The recommended stocking density is 4.9-7.4 hives/ha (2-3 hives/ac), but some Wisconsin cranberry growers rent as many as 22 hives/ha (9 hives/ac). Another explanation for this variation in management is that the economically optimal stocking density varies depending on the surrounding landscape due to differing levels of background pollination by native bees. Therefore, the objective of this

study was to determine the relationship between cranberry yield and honey bee hive stocking density and whether this relationship is consistent across the landscape. To address this objective, we collected historical production records from Wisconsin cranberry growers regarding the use of honey bees and cranberry yield for 2000-2011. We found a strong positive relationship between yield and hives/ha but only when the proportion of woodland within 1km of the cranberry marsh was low (< 41.6%). Furthermore, the variation in yield at marshes in low-woodland landscapes decreased as the number of hives increased, indicating that increasing hives leads to higher yields with less variation in that yield. Although there was no evidence that increasing hives was beneficial at marshes in high-woodland landscapes, the yield at these marshes when honey bees were absent was marginally higher than at marshes in low-woodland landscapes. Over the range of hives observed, we were unable to determine the optimal hive stocking density although Wisconsin cranberry growers with marshes in low-woodland landscapes can expect increasing returns on yield up to and above 17 hives/ha (7.6 hives/ac). The value of each additional hive was 1098 kg/hive (24.2 bbl/ac) at marshes in low-woodland landscapes and 0 kg/hive in high-woodland landscapes. These results suggest that the habitat surrounding a cranberry marsh influences the effectiveness and economically optimal stocking density of honey bees for cranberry pollination.

Keywords: honey bees, *Apis mellifera*, cranberry, hive stocking density, pollinator

1.0 Introduction

Pollination is an important ecosystem service valued at \$15 billion/year to US agriculture alone (Calderone 2012). Two-thirds of crop plants require or benefit from insect pollination (Klein et al. 2007) and provide the main source of several key vitamins and minerals in the human diet (Eilers et al. 2011). As a result, managed honey bees are widely used in many agricultural systems for crop pollination. Honey bees (*Apis mellifera*) occur in large colonies, are easy to manage, and will visit many different plant species, making them an ideal species for pollination in modern agricultural systems (Kremen and Chaplin-Kramer 2007, Calderone 2012). Native bees are also effective crop pollinators, but occur in small numbers, are more difficult to manage, and often times are specialized pollinators of one plant family or genus (Delaplane and Mayer 2000, Michener 2000). Even so, native bees alone are able to provide full pollination services in some systems (e.g., watermelon, Winfree et al. 2008, cranberry, Mohr and Kevan 1987).

Cranberry is one crop where honey bees are commonly used to fulfill pollination requirements, although hive stocking densities vary greatly. Current management recommendations for Wisconsin cranberry call for 4.9-7.4 hives/ha (2-3 hives/ac, McGregor 1976), but growers use anywhere from 0-22 hives/ha (0-9 hives/ac, H. Gaines, pers. obs.). One explanation for the variation in management practices may be that some marshes have a higher level of background pollination rates due to the presence of native bees and therefore do not require as many honey bees. Previous studies have also shown that some native bees are, in fact, more efficient cranberry pollinators than honey bees (Cane and Schiffhauer 2003). Additionally, current management recommendations are

based on research from over 50 years ago when yields were much lower, landscapes were less developed, and the pollination requirements of cranberry were not fully understood, resulting in conflicting recommendations. For example, Filmer and Doehlert. (1955) suggest using 0.5 hives/ha (1 hive/5ac) whereas Farrar and Bain (1947) suggest from 2.5-24.7 hives/ha (1-10 hives/ac). Changes in technology and management practices along with a better understanding of the pollination requirements (Gaines chp. 1) suggest that updated recommendations may be needed. Furthermore, economic theory regarding optimal input use implies that the optimal stocking density will depend on the crop price and the cost of renting hives (Beattie et al. 2009). The optimal input is reached when the cost of adding an additional hive exceeds the economic return of adding that hive.

One factor that may influence the optimal stocking density for honey bees is the amount of natural habitat in the surrounding landscape. Previous studies have shown that native bees respond positively to amount of and proximity to natural habitat and that pollination services and yield increase with bee diversity (Kremen et al. 2002, Ricketts et al. 2008). Therefore, cranberry marshes with more natural habitat in the surrounding landscape may have higher background pollination rates than marshes with little natural habitat, reducing the amount of honey bees required. The hypothesis that optimal hive stocking densities vary with local conditions is supported by the large variation in management practices observed in Wisconsin and the fact that average stocking densities for cranberry also vary by growing region (R. Serres, pers. comm.).

Cranberry growers spend a significant amount of money on pollination services, but since the optimal hive stocking density is unknown, they may not be spending their money

in an efficient way. Because of the magnitude of the cost of honey bee hive rentals, determining the optimal hive stocking density would allow growers to maximize the rate of return on their investment in hives and potentially save them thousands of dollars every year. The goal of this study was to determine the economically optimal honey bee hive stocking density for Wisconsin cranberry and whether this rate is consistent across the landscape. We used historical data from Wisconsin cranberry growers to determine (1) the relationship between cranberry yield and honey bee hive stocking density, (2) the marginal value of each additional hive of honey bees for cranberry yield, and (3) if the economically optimal rate remains constant across the landscape.

Methods

2.1 Grower data

Data were collected from 38 cranberry growers, either through previously established grower-collaborators or other growers reached through a request at the annual meeting of the Wisconsin State Cranberry Growers Association (WSCGA). Growers were asked to complete a worksheet including information on marsh location, establishment year, varieties grown, area in cranberry production, honey and bumble bee use, and yield records for the period 2000-2011. Because cranberry takes about 3 years from marsh establishment to produce a crop, only data from marshes more than 3 years old were used. Data from years in which significant damage to the crop due to pests or hail was recorded were excluded. Data from years in which growers were following a marketing order volume control to reduce yield were also excluded. A marketing order volume control is a

tool used by agricultural industries to reduce the over-production of a crop by limiting the amount of crop a grower can sell (Jesse and Rogers 2006). This resulted in a dataset with 38 unique growers with an average of 9.6 years (min. 1- max. 12 years) of yield and hive data. The data that were reported included total acres of cranberry cultivated, total number of hives rented, and total cranberry harvest in barrels (1bbl = 100lbs or 45.4 kg) for each year. I then converted these data to hives/ha and yield/ha.

2.2 Landscape data

Since other datasets suggest that woodland is a good predictor variable for native bees and their pollination services (Gaines chp. 3), I calculated the proportion wooded habitat within 1km of each marsh using the Cropland Data Layer (USDA 2011) and ArcGIS 10.0 (ESRI 2011). A centroid was located in the center of each marsh and a 1km radius drawn around that point. Native bee abundance and species richness is positively associated with natural habitat in the surrounding landscape (Gaines chp. 3), so wooded habitat was used as a proxy for background native pollinators present in the landscape.

2.3 Statistical analyses

To determine the relationship between cranberry yield (kg/ha) and honey bee hive stocking density (hives/ha) as a function of the percent woodland within a 1km radius around each marsh, we used a multiple mixed model linear regression with hives/ha, percent woodland, and their interaction as fixed effects and farm as a random effect. Since the interaction term between hives/ha and woodland category was significant ($p = 0.0003$), the analysis was also conducted separately using the data from marshes in high- and low-woodland landscapes. A Shapiro-Wilk Goodness of Fit test on yield indicated that

the data were normally distributed ($W=0.993$, $p=0.0757$), so no transformations were used. A term for year and second order term for hives (an indication of curvature) were initially included in the model but were found not significant and were therefore dropped from the final model (year, $p=0.095$ $F_{1,212.1}=2.82$, hives², $p=0.50$ $F_{1,205.1}=0.45$).

To determine whether the variation in yield varied as a function of hive stocking density, we used a linear model with the coefficient of variation (standard deviation of yield divided by the mean) as the dependent variable and the honey bee stocking density as the independent variable. Separate regressions were estimated for sites in high-woodland areas and low-woodland areas.

To determine the density at which the effect of honey bees on yield was significantly greater than yield with no hives, we used the prediction equation to predict yield at a given hive density. We varied hives/ha to identify the lowest stocking density at which the upper limit of the 95% confidence interval with zero hives/ha was less than the lower limit of the 95% confidence interval. All statistical analysis was done using JMP Pro 10 (SAS Institute Inc. 2007).

2.0 Results

Cranberry yield was, on average, positively associated with the number of honey bee hives/ha ($p<0.0001$, Adj. $R^2=0.49$, fig. 1), but this relationship varied depending on the amount of woodland in the surrounding landscape (hives \times landscape, $p=0.0091$). At farms with a low amount of wooded habitat (less than average, $<41.6\%$) within a 1km radius, the relationship was strong and positive ($p<0.0001$, Adj. $R^2=0.58$), but at sites with a high

amount of wooded habitat (above average, $\geq 41.6\%$) within 1km, the relationship was not significant ($p=0.51$, Adj. $R^2=0.25$). From the slope of these relationships, we determined that the marginal value of each additional hive was 1098 kg/hive (24.2bbl/hive) at low-woodland sites and 0 kg/hive (no significant relationship) at high-woodland sites.

Variation in cranberry yield was also effected by hive density, but again, only at sites in low-woodland landscapes. When the proportion of wooded habitat is high, increasing hive density has no effect on the coefficient of variation (CV, $p=0.3088$, Adj. $R^2=0.006$, fig. 2). When the proportion of wooded habitat is low, increasing hive density results in decreased yield CV ($p=0.0392$, Adj. $R^2=0.10$). These results suggest that growers at high-woodland sites do not gain any benefit from the use of honey bees but growers at low-woodland sites see an increase in yield and a decrease in variation by using honey bees.

The minimum number of hives needed to realize a significant yield increase was 4.2 hives/ha (1.7 hives/ac) for sites in low-woodland landscapes. Growers in high-woodland landscapes never realized a statistically significant yield increase regardless of the number of hives/ha used. However, growers in a high-woodland landscape had a marginally higher yield at zero hives/ha than growers in a low-woodland landscape and all growers had a significant yield at zero hives/ha (intercept, $p<0.0001$). At zero hives/ha, yield was 21.5 metric tons/ha (95% CI, 19.1-24.0)(192.4 bbl/ac, 95% CI, 170.9 – 213.9) at low-woodland sites and 25.3 metric tons/ha (95% CI, 22.6-28)(226.2 bbl/ac, 95% CI 202.2-250.1) at high-woodland sites, which represents an 18% increase in yield.

Based on these data, the effect of variation in hive stocking density depends on the surrounding landscape, however, an optimal stocking density, the point at which yield is

maximized, could not be estimated since yields continue to increase past the ranges reported in this study for farms in low-woodland landscapes. We found no evidence of yield increases with the use of honey bees at any observed stocking density for farms set in high-woodland landscapes. We were unable to determine the optimal honey bee hive stocking density for low-woodland sites because the relationship between yield and hives/ha did not reach a point of diminishing returns (fig. 1). The relationship between yield and hives/ha is linear from 0 hives/ha to 18.8 hives/ha, the highest stocking density of reported by the growers for the twelve years of data reported.

3.0 Discussion

Individual cranberry growers spend tens of thousands of dollars each year renting honey bees for pollination and stocking densities vary widely, suggesting that growers may not be optimizing their use of honey bees. By taking advantage of a wealth of data already held by the growers, we were able to assemble a powerful dataset consisting of more than a decade of harvest data from nearly 40 different marshes. These data revealed that yield is positively associated with hive stocking density, but that this relationship depends on the surrounding landscape. Our results suggest that growers whose marshes are set in landscapes with a high proportion of woodland may be wasting money on honey bees, where increasing honey bee stocking densities did not significantly increase cranberry yield. In contrast, at current cranberry prices and hive costs, growers whose marshes are set in landscapes with a low proportion of woodland should increase their net income by using a hive stocking density greater than the maximum of 18.8 hives/ha (7.6 hives/ac)

seen in our data. This study provides the first rigorous assessment of the value of honey bee hives for cranberry yield that we are aware of.

The most obvious pattern in our dataset was the positive relationship between cranberry yield and hives/ha in simplified landscapes. Furthermore, for marshes in these low-woodland landscapes, the relationship has not reached a point of diminishing returns, suggesting that growers could increase stocking densities to achieve higher yields. This relationship supports the use of managed honey bees for cranberry yield, but also suggests that the previous recommendation of 4.9-7.4 hives/ha (2-3 hives/ac) requires updating. Our data suggest that growers in low-woodland landscapes can increase their cranberry yield by over 1000 kg/hive for each additional honey bee hive/ac used. Beyond 18.8 hives/ha (7.6 hives/ac), we cannot predict what will happen.

From an economic perspective, cranberry growers appear to be below the maximum economic return they could achieve using managed honey bees. Growers in high-woodland landscapes using 10 hives/ha may be wasting \$700/ha (\$380/ac) which on an averaged sized marsh of 32 ha (80 ac), amounts to \$22,400/year. In low-woodland landscapes at the stocking density reported in our data, however, the economic returns are still increasing (Beattie and Taylor 2009). For the most economically profitable level of production, growers should operate at the point where diminishing returns to input use occurs. A recent study of blueberry pollination found a similar result with a strong linear relationship between yield and hive stocking density, suggesting that blueberry growers are also not maximizing their use of honey bees (Eaton and Nams 2012).

Economic theory recommends increasing use of an input until the market value of the additional yield generated by the additional input just equals the cost of the additional input. At current market price for cranberries (\$1.21/kg for cooperative and \$0.49/kg for independent growers, \$65/bbl and \$22/bbl respectively) and hive rental fees (\$70/hive), the addition of a single hive/ha provides an 18:1 return on investments for cooperative growers and a 6.6:1 return on investments for independent growers in low-woodland landscapes. With a linear response of yield to hives/ha, growers in low-woodland landscapes have not reached the economically optimal hive stocking density and could continue to increase stocking density above the maximum of 18.8 hives/ha (7.6 hives/ac) reported in these data. The interacting effect of the landscape also suggests, however, that there is not, in fact, a single optimal stocking density for cranberry industry-wide.

The interaction between hive stocking density and surrounding landscape suggests that honey bees are less effective at increasing cranberry pollination in high-woodland landscapes. One possible explanation for this is that honey bees are moving from the crop into the non-crop in order to access floral resources. Vaissière (1990) found that honey bee foraging density was greater in cotton fields surrounded by “poor” habitat which may explain the pattern seen in our study of a higher contribution of honey bees to cranberry pollination in low-woodland landscapes. Pettis et al. (2013) further demonstrated that honey bees on a New Jersey cranberry marsh collected minimal amounts of cranberry pollen, further supporting the idea that honey bees are foraging in non-crop habitats surrounding the cranberry marshes.

Another pattern evident from our dataset is that even when there are no hives of honey bees present, growers still achieve a significant yield. This could be due to a number of factors including feral honey bees, native bees, or other non-biotic vectors of pollination. Based on additional data collected by the authors, marshes where honey bees were not rented had very few if any honey bees present, native bees were present in high abundance and diversity (nearly 200 species) especially at marshes in high-woodland landscapes (Gaines chapter 3), and other, non-biotic factors can contribute 20-80% of total cranberry yield (Gaines chapter 1). Previous studies have demonstrated that native bees are efficient cranberry pollinators (Cane and Schiffhauer 2003, Cariveau unpubl. data), suggesting that native bees may be contributing to this yield in the absence of honey bees. Additionally, assuming that pollination services also increase with native bee abundance and diversity, this could explain why the high-woodland marshes where no honey bees are used have about 20% greater yields than low-woodland sites, since native bees are positively associated with natural habitat (Ricketts et al. 2008).

Despite the strong and significant patterns found in this study, other unmeasured correlates of landuse could contribute to the observed patterns. Hive stocking density may be correlated with other management practices that also affect yield. For example, the use of high honey bee stocking densities could also be associated with more intensive farming practices with higher overall inputs (e.g., fertilizer, pesticide, irrigation). More data regarding management practices, such as the application of fertilizer or pesticides, irrigation, and the intensity of crop scouting which may be correlated with hive density could be obtained from growers. These data would allow for the effect of hive density to be

disentangled from other management practices. Finally, smaller-scale field studies that experimentally vary the hive stocking density could be used to verify the patterns observed in this historical dataset.

This study represents the first attempt to determine economically optimal use of honey bees for cranberry production using data from a large time span and across many sites. Our results suggest that the optimal stocking density has not been reached on Wisconsin cranberry marshes and further research should explore at what point the yield response curve reaches a rate of diminishing marginal returns. Our results further suggest that Wisconsin cranberry growers in low-woodland landscapes should be using more than 18.8 hives/ha (7.6 hives/ac) to optimize the economic value of honey bees.

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Literature cited

- Beattie, B. R., C. R. Taylor, and M. J. Watts. 2009. The economics of production, 2nd edition. Krieger Publishing Company, Malabar, Fla.
- Calderone, N. W. 2012. Insect pollinated crops, insect pollinators and US agriculture: Trend analysis of aggregate data for the period 1992-2009. Plos One 7:e37235.
- Cane, J. H., and D. Schiffhauer. 2003. Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). American Journal of Botany 90:1425–1432.

- Delaplaine, K. S., and D. F. Mayer. 2000. Crop pollination by bees. CABI Publishing, New York, NY.
- Eaton, L. J., and V. O. Nams. 2012. Honey bee stocking numbers and wild blueberry production in Nova Scotia. *Canadian Journal of Plant Science* 92:1305–1310.
- Eilers, E. J., C. Kremen, S. Smith Greenleaf, A. K. Garber, and A.-M. Klein. 2011. Contribution of pollinator-mediated crops to nutrients in the human food supply. *PLoS ONE* 6:e21363.
- ESRI. 2011. ArcGIS. Environmental Systems Research Institute, Redlands, CA.
- Farrar, C. L., and H. F. Bain. 1947. Honeybees as pollinators of the cranberry. *Cranberries* 11.
- Filmer, R. S., and C. A. Doehlert. 1955. Use of honeybees in cranberry bogs. *Gleanings in Bee Culture*:265–268.
- Jesse, E. V., and R. T. Rogers. 2006. The cranberry industry and Ocean Spray Cooperative: Lessons in cooperative governance. *Food System Research Group Monographs* 19.
- Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274:303–313.
- Kremen, C., and R. Chaplin-Kramer. 2007. Insects as providers of ecosystem services: Crop pollination and pest control. Pages 349–382 in A. J. A. Stewart, T. R. New, and O. T. Lewis, editors. *Insect Conservation Biology*. CABI Publishing, Wallingford, Oxfordshire.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* 99:16812–16816.
- McGregor, S. E. 1976. Insect pollination of cultivated crop plants. Agricultural Research Service, US Department of Agriculture, Washington, D.C.
- Michener, P. C. D. 2000. *The bees of the world*, 2nd edition. The Johns Hopkins University Press, Baltimore, Maryland.
- Mohr, N. A., and P. G. Kevan. 1987. Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.)

- and lingonberry (*V. vitis-idaea* L.). Pages 149–154 Proceedings of the Entomological Society of Ontario.
- Pettis, J. S., E. M. Lichtenberg, M. Andree, J. Stitzinger, R. Rose, and D. vanEngelsdorp. 2013. Crop pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen *Nosema ceranae*. PLoS ONE 8:e70182.
- Ricketts, T., J. Regetz, I. Steffan-Dewenter, S. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. Greenleaf, A. Klein, M. Mayfield, L. Morandin, A. Ochieng, and B. Viana. 2008. Landscape effects on crop pollination services: Are there general patterns? Ecology Letters 11:499–515.
- SAS Institute Inc. 2007. JMP Pro 10. SAS Institute Inc., Cary, NC.
- USDA. 2011. National Agricultural Statistics Service Cropland Data Layer. USDA-NASS, Washington, D.C.
- Vaissière, B. E. 1990. Honey bee stocking rate, pollinator visitation, and pollination effectiveness in upland cotton grown for hybrid seed production. Acta Horticulturae (ISHS) 288:359–363.
- Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. Journal of Applied Ecology 45:793–802.

Figure captions

Figure 1: Cranberry yield versus honey bee hive stocking density. Each point represents a single marsh in a single year. There was a strong positive relationship between yield and hive stocking density but only when the percent woodland in the surrounding landscape was low.

Figure 2: Coefficient of variation in yield versus honey bee hive stocking density. Variation in yield decreased with increasing hive stocking density at cranberry marshes where the surrounding landscape was low in woodland. At marshes set in high-woodland landscapes, there was no relationship between variation in yield and hive stocking density.

Figure 1

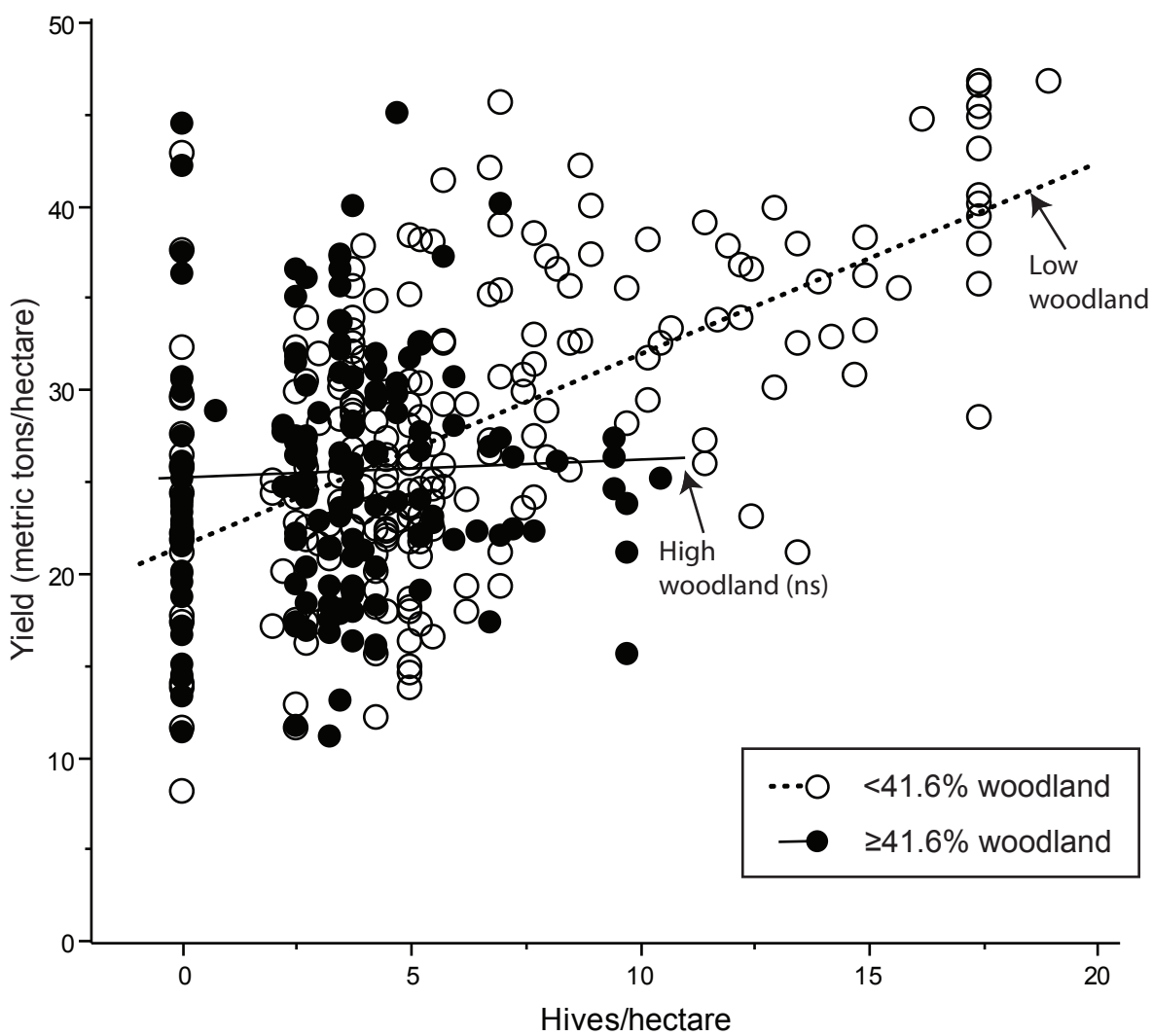
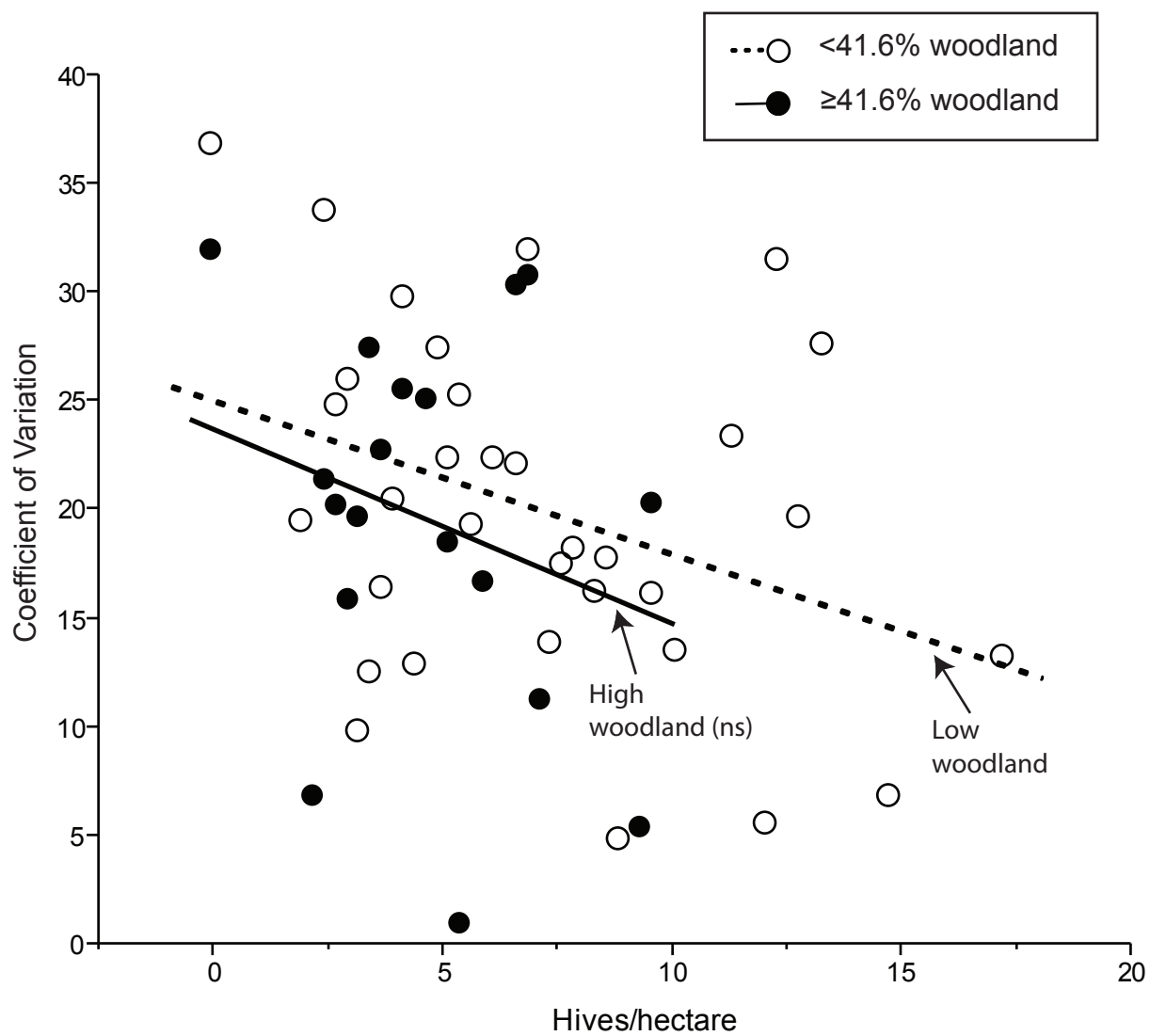


Figure 2



CHAPTER 3

Local and landscape factors influence native bees, yield, and the contribution of bees to yield

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Abstract: Habitat loss and fragmentation, changes in land use, and intensive farming practices are leading causes of biodiversity loss around the world. Of particular importance in agroecosystems is the loss of beneficial insects that provide services to farmers including pollination. Native bees provide the majority of pollination services in some farming systems and have the potential to act as a buffer against the current decline in managed honey bees. In order to ensure the persistence of native bees and the pollination services they provide in agroecosystems, it is important to understand how they respond to features of the surrounding landscape and local farm practices. Therefore, the objective of this study was to determine to what extent native bees, yield (a measure of pollination success), and the contribution of bees to yield respond to surrounding habitat and local factors in a perennial cropping system. To address our objective, we pan-trapped bees at 49 commercially managed cranberry marshes in central Wisconsin across a

landscape gradient from highly agricultural to highly wooded. Yield was estimated at a local field level and collected from growers as a marsh-wide average. Native bee abundance and species richness were positively associated with open, herbaceous and wooded habitat. Species richness was also positively correlated to wooded edge density and an index of local pesticide use. Yield was positively correlated with honey bee hive stocking density and cranberry floral density but was not associated with native bees or landscape factors. Cage manipulation studies were done at sites along a landscape gradient and at sites varying in local honey bee use. The contribution of bees to cranberry pollination did not vary as a function of surrounding landscape but increased with cranberry flowering upright density. These results suggest that both local and landscape factors are important predictors of both native bee abundance and richness while local factors are more important predictors of yield and the contribution of bees to yield. Our results do not provide strong evidence that native bees are a strong predictor of yield in this system.

Keywords: native bees, landscape ecology, Environmental Impact Quotient, cranberry, *Vaccinium macrocarpon*, structural equation modeling, lavaan

1. Introduction

The expansion of modern agriculture and human activity have led to the alteration and fragmentation of the landscape and destruction of natural habitat. Agriculture is currently the dominant land-use, covering 38% of the terrestrial area of the globe (Foley et al. 2005, 2011). This large scale alteration of the landscape has profound effects on the ability of

organisms to survive. Insects are one group of organisms that provide valuable ecosystem services in agroecosystems such as pollination. In order to fulfill their feeding and nesting resource requirements, many of these beneficial insects move between crop and non-crop habitats throughout their life cycle (Kremen et al. 2007, Blitzer et al. 2012). Because of their limited ability to travel long distances (from tens of meters to a few kilometers, Zurbuchen et al. 2010), the availability of non-crop habitat within the agricultural landscape is of vital importance (Banaszak 1992).

Although changes to the landscape can affect the movement and survival of organisms, local farm management practices can also have a strong influence on the persistence of organisms in the area, especially those with limited flight distances that may exist primarily within the farm landscape. For example, previous research has shown that farms that use organic practices or have abundant flowering non-crop plants support a more diverse beneficial insect community (Bengtsson et al. 2005, Morandin and Kremen 2013). Additionally, the timing and use of pesticides can have a significant lethal or sub-lethal impact on beneficial insects (e.g., bees, Desneux et al. 2007, Brittain et al. 2010). Local management practices, such as tillage and herbicide use, affect the floral and nesting resource availability on the farm which may directly affect local scale persistence.

Bees, one such example of mobile organisms that deliver key services to agriculture (Kremen et al. 2007), are the most important pollinators for crop production and are sensitive to the composition and configuration of the landscape, exposure to agricultural chemicals, and local resource availability (Potts et al. 2010). Historically, farmers have relied upon one species, the non-native honey bee (*Apis mellifera*), for their pollination

requirements. In recent years, however, honey bees have experienced drastic declines as a result of mites, disease, and the recent emergence of Colony Collapse Disorder (CCD)(Ellis et al. 2010). As honey bees decline, farmers pay a higher price for hives and, for some crops, may need to seek alternative ways of pollinating their crops.

Native bees also provide valuable pollination services (Losey and Vaughan 2006, Winfree et al. 2008) and in some systems are able to fully meet the pollination requirements in the absence of honey bees (watermelon, Winfree et al. 2008, cranberry, Mohr and Kevan 1987). Additionally, researchers have demonstrated that as native bee visitation increases, crop yield also increases regardless of honey bees (Garibaldi et al. 2013). By using management practices that protect or increase forage and nesting resources for native bees, farmers may also be able to increase their yields. Although farmers are not likely to abandon the use of honey bees for pollination, native bees may provide insurance against the decline in honey bees (Winfree et al. 2007). Unfortunately, declines in native bee populations (Potts et al. 2010, Cameron et al. 2011) threaten the continued provisioning of these pollination services, making understanding how local and landscape factors influence native bee populations of great importance.

Multiple studies have documented that the abundance and diversity of native bees increase with proximity to natural habitat (Kremen et al. 2004, Morandin and Winston 2006) and areas with diverse floral resources (Potts et al. 2003, Morandin and Kremen 2013). Current research provides increasing evidence that the type and availability of habitat in the landscape (i.e., landscape composition) is important in determining native bee abundance and diversity. A recent study provides evidence that the arrangement of

habitat (i.e. landscape configuration) is also important (Kennedy et al. 2013). Few studies, however, have considered how these landscape factors relate to yield (but see Ricketts et al. 2004) or the contribution of bees to yield. Since yield is a universal metric indicating pollination success, understanding how it relates directly or indirectly to local and landscape factors could provide insight into future management decisions in agro-ecosystems.

In this study we examined how native bees, crop yield, and the contribution of native and managed bees to crop yield vary as a function of local and landscape features in the Wisconsin cranberry agro-ecosystem. Previous studies have shown that native, wild bees are efficient cranberry pollinators (Cane and Schiffhauer 2003) suggesting that their conservation could provide economic benefits to cranberry growers. The objectives of this study were to determine the influence of local management and landscape factors on (1) native bee abundance and species richness, (2) cranberry yield, and (3) the contribution of bees to cranberry yield. An understanding of the relationships between these variables could have implications for future management and conservation decisions.

2. Methods

2.1 Study System and Site Selection

This study was conducted on commercial cranberry marshes in central Wisconsin (USA), the main cranberry growing region in the country. This region is known as the Central Sand Plains and is characterized by sandy soil and flat open terrain (Dott and Attig

2004). The area is heavily agricultural and produces most of the states' cranberry and potato crops.

Commercial cranberry marshes (sites) were selected to span the existing landscape gradient from highly wooded to highly agricultural (fig. 1). We used digital orthophotos to identify all possible sites and then characterized the landscape surrounding each site using remotely sensed land-cover data (USDA 2011). Potential sites were plotted on a graph of percent woodland versus percent agriculture and a subset of these sites were chosen to represent the entire gradient. Sites were at least 2km apart from each other to ensure a minimum degree of spatial independence among bee communities (Greenleaf et al. 2007, Zurbuchen et al. 2010). We sampled at 15 sites in 2008, 30 sites in 2010, and 20 sites in 2011 for a combined 49 unique sites (i.e. some sites were sampled multiple years). Sampling took place in a corner of the marsh closest to non-crop habitat. Each marsh is composed of a group of individual beds (~40m x 200m) and sampling was done within the corner bed and the bed immediately adjacent to it.

2.2 Local variables

To determine cranberry floral density, flowers within ten randomly placed 1ft² quadrats per site were counted during peak bloom in 2010 and 2011.

Local pesticide toxicity scores were calculated for each site based on pesticide spray records collected from the growers for each sampling year. We used a modified version of the Environmental Impact Quotient of Pesticides Field Score (Kovach et al. 1992) which simplifies spray records to a single index based on a variety of factors including toxicity to a target organism, active ingredients, and the number of applications made.

$$mEIQ = \sum (Z*P*3)(\% \text{ active ingredient}/100)(\text{application rate})(\# \text{ of applications})$$

where Z = bee toxicity

and P = plant surface half-life

When an application rate was not indicated on spray records, the rate recommended on the material label was used. The percent active ingredient was extracted from the Material Safety Data Sheet (MSDS) for each chemical. When rate was in pounds/acre, one pound was considered 16 oz.

2.3 Landscape variables

To describe the landscape around each site, we calculated both composition and configuration metrics using Patch Analyst 4 (Rempel et al. 2008) in ArcGIS 10 (ESRI 2011). The composition provides an index of habitat and resource availability while configuration describes the accessibility of that habitat to organisms in the landscape. For composition (i.e. percent cover), we narrowed the original 56 CDL land-cover categories down to 14 categories which represented at least 1% of the total land area within 1km of all sites. These 14 categories combined represent 96.4% of the land-cover within 1km of all sites. To further simplify the landscape composition to just two axes, we performed a Principle Components Analysis (PCA) using the 14 categories (fig. 2). The PCA values for axis 1 and axis 2 were then used in our statistical analysis to represent landscape composition. Landscape configuration was represented by wooded edge density (i.e. length of wooded edges within 1km). Wooded edges are expected to provide good bee habitat with access to

multiple habitat types (woodland and open/agriculture) and create a unique habitat type with an abundance of nesting and foraging resources (Diaz-Forero et al. 2013).

2.4 Native bee abundance and species richness

To measure native bee abundance and species richness, we pan trapped specimens from May to August of 2008, 2010, and 2011. Each year, samples were taken before, during and after cranberry bloom. Pan traps were filled with soapy water and set down in the cranberry vines in two parallel transects located either immediately adjacent to a non-crop marsh edge or 50 meters away from the edge. The decision to locate the transects near a non-farm edge was based on research indicating that bees respond positively to proximity to natural habitat (reviewed by Ricketts et al. 2008), so if there were any response by bees to landscape, it would be captured in our study design. Each transect included 5 sets of three pan traps (blue, yellow, and white, ACE Fluorescent spray paint) set at 10m intervals.

Specific trapping methods varied slightly from year to year. In 2008, traps were made from 5oz plastic bowls (Chinette brand). Traps were left in each marsh for 6-hour intervals between 8am and 4pm and all sites were visited within three days (5 sites per day). Data were only collected on days deemed to be good bee days (wind below 2.5 m/s, temperature above 15°C, sky conditions sunny to bright overcast). In 2010 and 2011, traps were made from 12oz plastic cups. Traps were left in each marsh for 3-day intervals and all sites were visited within two days (~15 sites per day).

Specimens were stored into 70% alcohol then dried, pinned, labeled, and sorted to morphospecies in the lab before being sent to a taxonomist for species level identification.

2.5 Yield

Yield data was collected both empirically on a small plot scale in the field and at a marsh-wide scale from growers. To estimate the plot level yield, four 1ft² berry samples were taken from each site during the 2011 field season. This method is used by crop scouts and farmers to estimate yield before harvest (J. Sojka, pers. comm.). All berries within randomly selected 1ft² quadrats were harvested in late September before cranberry harvest and weighed in the lab. Wet weight was used as this is easily converted to the industry standard yield metric of barrels/acre (1 bbl = 100 lbs).

To determine the direct effects of local and landscape effects on native bee abundance and species richness and the direct and indirect effects on yield, we used path analysis which is a form of Structural Equation Modeling (SEM). SEM is a useful way to analyze complex, multivariate linear relationships, intercorrelation of predictors, and provides a method to allow separation of direct and indirect effects (Grace 2006). For data collected at the plot level (n=17), the small number of variables and paths was limited by our sample size. In contrast, our marsh-wide data had far more observations (n=42) allowing us to include more variables and paths in our model. Our hypothesized model for our estimated plot level yield included direct effects of honey bee hive stocking density, native bee abundance, and native bee richness on yield; direct effects of PC1, PC2, and wooded edge density on native bee abundance and species richness; and indirect effects of PC1, PC2, and wooded edge density on yield (fig. 3). Our hypothesized model for the marsh-wide average yield included direct effects of honey bee hive stocking density, cranberry floral density, mEIQ, native bee abundance and native bee species richness on yield; direct effects of mEIQ, cranberry floral density, wooded edge density, PC1, and PC2

on native bee abundance and species richness; and indirect effects of mEIQ, PC1, PC2, and wooded edge density on yield (fig. 4). All local and landscape variables used in both models were from the same data. In order to determine indirect effects, we multiplied the standardized coefficients of direct effects (Matteson et al. 2013). A χ^2 goodness of fit test was used to determine whether the model was a good fit of the data. All SEM analysis was done using the Lavaan package (Rosseel 2012) in RStudio 0.97.551 (RStudio 2012).

2.6 Contribution of bees to yield

To determine how the contribution of bees to cranberry pollination varies as a function of local or landscape factors, we did cage manipulation studies in 2011 and 2012. Cages were 50cm x 50cm and were covered with nylon tulle to exclude pollinators. Cages were set up before cranberry bloom and removed once bloom was complete. All berries within a 1ft² area in the center of the cages and in separate open plots were harvested in late September and counted and weighed (wet) to estimate yield. In 2011, 3 cages/site were established at 30 sites (n=90 cages) along a landscape gradient of high wooded to high agriculture. In 2012, 10 cages/site were established at 11 sites (n=110 cages), 5 of which had honey bees present and 6 absent. All sites in 2012 were located in high wooded landscapes to control for landscape effects on native bees or yield.

To determine whether the contribution of bees to yield varies as a function of local and landscape factors, we did a multiple regression on yield with cage treatment, local, and landscape factors as predictor variables. For our 2011 cage manipulation across a landscape gradient, our predictor variables included cage treatment, PC1, PC2, cage*PC1, and cage*PC2 as predictor variables and site as a random term. To understand the

influence of local effects, we did a multiple regression on our yield data collected in our 2012 cage manipulation study that was on farms set in high woodland landscapes only. Our predictor variables included cage treatment, honey bee hive stocking density, native bee abundance, density of cranberry flowering uprights, cage*honey bees, cage*native bee abundance, cage*upright density, and farm site as a random term. This analysis was done using JMP 10.0.0 (SAS Institute Inc. 2007).

3. Results

We collected a total of 6673 specimens representing 182 species of bees over three field seasons (Appendix 3.1). These include several new records for the state of Wisconsin including *Coelioxys immaculata*, *Lasioglossum lusorium*, *Megachile addenda*, and *Xenoglossa kansensis* as well as 19 specimens of *Bombus terricola*, a species believed to be in decline throughout the Midwestern United States (Cameron et al. 2011). Overall the most abundant species collected were *Lasioglossum admirandum* (n=523 representing 8% of the total sample), *Agapostemon texanus* (n=425, 6%), and *Lasioglossum pilosum* (n=367, 5%). These data represent an expanded species list and species ranges for Wisconsin (Wolf and Ascher 2008) and provide a comprehensive list of bee species found in the Wisconsin cranberry system.

3.1 Principle Components Analysis on landscape

Our PCA indicated a strong gradient of landcover from wooded habitat to row crop agriculture (e.g., corn, soybeans)(PC1, 26.1%) and from wetland and cranberry to open, herbaceous and wooded habitat (PC2, 15.8%)(fig. 2). Because of the water requirements

for cranberry production and the historic practice of managing natural wetlands for cranberry production, cranberry marshes, herbaceous wetland, and open water were clustered together.

3.2 Bee abundance, species richness, and yield

3.2.1 Model based on marsh level estimates

Our model based on cranberry yield as reported by growers at the marsh level found a strong positive correlation between native bee abundance and open, herbaceous and wooded habitat in the landscape (PC2, $R^2=0.30$, standardized path coefficient = 0.52, $p<0.001$, fig. 3). There was also a marginally significant positive association between bee abundance and local pesticide intensity (mEIQ, standardized path coefficient = 0.25, $p=0.06$). Bee species richness was also associated with both landscape characteristics and local factors. Open, herbaceous and wooded habitat in the landscape had a strong positive association with native bee species richness (PC2, $R^2=0.45$, standardized path coefficient = 0.61, $p<0.001$). Local pesticide intensity also had a positive association with bee species richness, possibly as a result of a correlation between spray intensity and bee-friendly management practices such as the use of less toxic chemicals (mEIQ, standardized path coefficient = 0.32, $p=0.005$). Cranberry floral density had a marginally significant, weak negative association with native bee species richness (standardized path coefficient = -0.11, $p=0.11$).

Cranberry yield as measured at the marsh scale was directly, positively correlated with honey bee hive stocking density ($R^2=0.56$, standardized path coefficient = 0.65, $p<0.001$) and marginally with cranberry floral density (standardized path coefficient =

0.18, $p=0.13$). There were no indirect effects of landscape on yield. The ΔAIC between the hypothesized model and our final model was 12.64. A non-significant χ^2 goodness of fit test indicated that our model was a good fit ($p = 0.62$).

3.2.2 Model based on plot level estimates

Native bee abundance was strongly correlated with increasing wooded and open, herbaceous habitat in the surrounding landscape (PC2, $R^2=0.43$, standardized path coefficient = 0.66, $p<0.001$, fig. 4) but not with any local variables. Native bee species richness was also strongly correlated with increasing wooded and open, herbaceous habitat (PC2, $R^2=0.46$, standardized path coefficient = 0.52, $p=0.002$), as well as the length of wooded edges in the landscape (wooded edge density, standardized path coefficient = 0.25, $p=0.014$). Richness was not associated with local factors.

Cranberry yield as measured at the plot scale was strongly associated with local factors but only marginally with landscape factors. There was a direct, positive association between yield and honey bee hive stocking density ($R^2=0.32$, standardized path coefficient = 0.43, $p=0.02$). Yield was marginally, negatively associated with native bee abundance (standardized path coefficient = -0.36, $p=0.054$) and indirectly, negatively with increasing wooded and open, herbaceous habitat in the landscape (PC2, standardized path coefficient = -0.24). The ΔAIC between the hypothesized model and our final model was 7.84. A non-significant χ^2 goodness of fit test indicated that our model was a good fit ($p = 0.81$).

3.3 Contribution of bees to yield

Excluding bees had a significant effect on yield, as did the surrounding landscape. From our 2011 cage manipulation along a landscape gradient, we found that excluding

pollinators (cage, $p=0.0012$, $F_{1,25}=14.0$) and increasing woodland in the surrounding landscape (PC2, $p=0.0165$, $F_{1,25}=6.6$, fig. 5) had significant negative effects on yield. The effect of excluding bees had the same effect whether woodland in the surrounding landscape was high or low (cage*PC2, $p=0.12$, $F_{1,25}=2.6$).

When we had fine scale cranberry floral density data, we found that floral density and the pollinator exclusion had an interacting effect on the contribution of bees to yield. The results of our 2012 cage manipulation indicate that the most important factors affecting yield were pollinator exclusion (cage, $p<0.0001$, $F_{1,9}=58.3$), flowering upright density ($p<0.0001$, $F_{1,9}=96.6$), and their interaction ($p=0.0051$, $F_{1,9}=13.5$), indicating that the contribution by bees is different when floral density is high compared to low (fig. 6).

4. Discussion

Previous research has investigated the influence of local and landscape factors on native bee abundance and species richness, but few have considered how these factors influence yield or the contribution of bees to yield. In this study, we found that native bees respond strongly to landscape factors (i.e., open, herbaceous and wooded habitat) but weakly to local management (i.e., spray intensity, cranberry floral density). Cranberry yield, in contrast, responds strongly to local management (i.e., honey bee hive density, cranberry floral density) but weakly to landscape factors and native bees. The contribution of native and managed bees to cranberry yield was influenced by local factors (i.e., cranberry floral density) but not landscape factors. As the density of crop flowers increased, the contribution of bees also increased. These results suggest that, at least in

this system, the effect of local management on yield is much stronger than that of the landscape. We found no evidence that native bees contribute to cranberry yield.

The clearest pattern from our study was the positive influence of woodland on native bees. Both native bee abundance and species richness were strongly associated with increasing woodland in the surrounding landscape. This supports previous studies showing that bees respond positively to natural habitat in the surrounding landscape (reviewed by Ricketts et al. 2008, Kennedy et al. 2013). This pattern is likely due to the fact that natural habitats provide forage and nesting resources throughout the season, whereas agricultural land with flowering crops, like cranberry, only provide forage resources for a very short time span. We also found a positive influence of wooded edge density on species richness. Wooded edges likely provide good nesting sites for stem, ground, and cavity nesting bees in close proximity to open habitats where forage resources could be abundant.

The positive relationship between local pesticide intensity (i.e., mEIQ) and native bee species richness was unexpected. We hypothesized that local pesticide spray intensity would be negatively associated with native bees since more exposure to pesticides should have a detrimental effect on bees (Desneux et al. 2007, Brittain et al. 2010). One possibility is that summarizing spray into a single index is an inadequate method for representing actual spray exposure. Previous studies that used spray indices as an index of pesticide use have also found unexpected (Crampton et al. 2010), inconsistent (Singleton 2010), or no effects (Jenkins and Isaacs 2007) of spray index on beneficial insects suggesting that this may be the case. Another possibility is that a high spray index rating is correlated with other bee-conscious practices such as spraying at night or using less harmful sprays during

bloom. Even if growers spray more often or use harsher chemicals, when and how they apply the chemicals will have a big influence on how it affects beneficial insects. Wisconsin cranberry growers have a documented record of following environmentally conscious management decisions (Colquhoun and Johnson 2010) so it might be expected that they would follow pollinator-conscious practices as well.

Another clear pattern in our study was the strong relationship between cranberry yield and honey bee stocking density, but the lack of association between yield and native bee abundance. While there is a strong relationship between cranberry yield and hive stocking density (Gaines, chp. 2), the pattern here may partly be an artifact of scale. The association between yield and honey bee hive stocking density was stronger in our model based on the marsh-wide yield estimates than in our model based on plot scale yield estimates. Not surprisingly, honey bee hive stocking density were also based on marsh-wide averages provided by the growers, whereas native bee abundance was based on a plot level sample taken in the same area of the marsh as the plot scale yield estimates. Additionally, honey bee hives are often dispersed across the entire marsh whereas native bee abundance decreases towards the center of the marsh and away from a non-crop farm edge (Gaines, unpubl. data). This may allow honey bees to have a more even influence on marsh-wide yield, whereas the native bees would have a stronger influence at the edge of the marsh (Evans and Spivak 2006).

The lack of influence of landscape on the contribution of bees to cranberry yield was surprising. We expected that the contribution by bees would increase with increasing woodland in the surrounding landscape because there would be a greater abundance and

richness of bees present. Furthermore, previous studies have found a positive influence of natural habitat on crop yield (Ricketts 2004, Morandin and Winston 2006). Instead, we found that yield decreased as wooded and open, herbaceous habitat in the landscape increased and that the contribution of bees to yield did not change. This pattern suggests either that the native bees are not contributing to cranberry yield or that the contribution of local honey bees masks any contribution by native bees.

Despite a lack of influence of the landscape on bee contributions to yield, the local factor cranberry floral density was an important predictor of the contribution by bees to yield. As floral density increased, the contribution by bees also increased. Bees are attracted to large floral displays, so increasing the density of flowers may make the cranberry marsh more attractive to bees. Alternatively, floral density may be correlated with other management practices such as higher honey bee hive stocking densities and more intensive practices that are associated with increased yield.

The results of this study suggest that local farm management, including the use of managed bees, has a strong effect on crop yield. Although we found no evidence that native bees are contributing to the pollination of commercial cranberry, some Wisconsin cranberry growers do not use managed honey bees for pollination, suggesting that the native bees do contribute. Future research should consider alternative methods for determining the contribution of native bees to yield.

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Literature cited

- Banaszak, J. 1992. Strategy for conservation of wild bees in an agricultural landscape. *Agriculture, Ecosystems & Environment* 40:179–192.
- Bengtsson, J., J. Ahnström, and A.-C. Weibull. 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42:261–269.
- Blitzer, E. J., C. F. Dormann, A. Holzschuh, A.-M. Klein, T. A. Rand, and T. Tscharntke. 2012. Spillover of functionally important organisms between managed and natural habitats. *Agriculture Ecosystems & Environment* 146:34–43.
- Brittain, C. A., M. Vighi, R. Bommarco, J. Settele, and S. G. Potts. 2010. Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology* 11:106–115.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* 108:662–667.

- Cane, J. H., and D. Schiffhauer. 2003. Dose-response relationships between pollination and fruiting refine pollinator comparisons for cranberry (*Vaccinium macrocarpon* [Ericaceae]). *American Journal of Botany* 90:1425–1432.
- Colquhoun, J., and H. Johnson. 2010. Sustainable cranberry production for a vibrant future: The Wisconsin experience. University of Wisconsin-Extension.
- Crampton, L. A., G. M. Loeb, K. A. Hoelmer, and M. P. Hoffmann. 2010. Effect of Insecticide Regimens on Biological Control of the Tarnished Plant Bug, *Lygus lineolaris*, by *Peristenus* spp. in New York State Apple Orchards. *Journal of Insect Science* 10.
- Desneux, N., A. Decourtye, and J.-M. Delpuech. 2007. The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology* 52:81–106.
- Diaz-Forero, I., V. Kuusemets, M. Mänd, A. Liivamägi, T. Kaart, and J. Luig. 2013. Influence of local and landscape factors on bumblebees in semi-natural meadows: a multiple-scale study in a forested landscape. *Journal of Insect Conservation* 17:113–125.
- Ellis, J. D., J. D. Evans, and J. Pettis. 2010. Colony losses, managed colony population decline, and Colony Collapse Disorder in the United States. *Journal of Apicultural Research* 49:134–136.
- ESRI. 2011. ArcGIS. Environmental Systems Research Institute, Redlands, CA.
- Evans, E. C., and M. Spivak. 2006. Effects of honey bee (Hymenoptera: Apidae) and bumble bee (Hymenoptera: Apidae) presence on cranberry (Ericales: Ericaceae) pollination. *Journal of economic entomology* 99:614–620.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, and others. 2005. Global consequences of land use. *Science* 309:570.
- Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockström, J. Sheehan, S. Siebert, D. Tilman, and D. P. M. Zaks. 2011. Solutions for a cultivated planet. *Nature* 478:337–342.
- Garibaldi, L. A., I. Steffan-Dewenter, R. Winfree, M. A. Aizen, R. Bommarco, S. A. Cunningham, C. Kremen, L. G. Carvalheiro, L. D. Harder, O. Afik, I. Bartomeus, F. Benjamin, V. Boreux, D. Cariveau, N. P. Chacoff, J. H. Dudenhöffer, B. M. Freitas, J. Ghazoul, S. Greenleaf, J. Hipólito, A. Holzschuh, B. Howlett, R. Isaacs, S. K. Javorek, C. M. Kennedy, K. M. Krewenka, S. Krishnan, Y. Mandelik, M. M. Mayfield, I. Motzke, T. Munyuli, B. A. Nault, M. Otieno, J. Petersen, G. Pisanty, S. G. Potts, R. Rader, T. H. Ricketts, M. Rundlöf, C. L. Seymour, C. Schüepp, H. Szentgyörgyi, H. Taki, T.

- Tscharntke, C. H. Vergara, B. F. Viana, T. C. Wanger, C. Westphal, N. Williams, and A. M. Klein. 2013. Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. *Science* 339:1608–1611.
- Grace, J. B. 2006. *Structural equation modeling and natural systems*. Cambridge University Press, New York.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- Jenkins, P. E., and R. Isaacs. 2007. Reduced-risk Insecticides for Control of Grape Berry Moth (Lepidoptera: Tortricidae) and Conservation of Natural Enemies. *Journal of Economic Entomology* 100:855–865.
- Kennedy, C. M., E. Lonsdorf, M. C. Neel, N. M. Williams, T. H. Ricketts, R. Winfree, R. Bommarco, C. Brittain, A. L. Burley, D. Cariveau, L. G. Carvalheiro, N. P. Chacoff, S. A. Cunningham, B. N. Danforth, J.-H. Dudenhöffer, E. Elle, H. R. Gaines, L. A. Garibaldi, C. Gratton, A. Holzschuh, R. Isaacs, S. K. Javorek, S. Jha, A. M. Klein, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. Morandin, L. A. Neame, M. Otieno, M. Park, S. G. Potts, M. Rundlöf, A. Saez, I. Steffan-Dewenter, H. Taki, B. F. Viana, C. Westphal, J. K. Wilson, S. S. Greenleaf, and C. Kremen. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16:584–599.
- Kovach, J., C. Petzoldt, J. Degni, and J. Tette. 1992. A method to measure the environmental impact of pesticides. *New York's Food and Life Sciences Bulletin* 139.
- Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, and others. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10:299–314.
- Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters* 7:1109–1119.
- Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311–323.
- Matteson, K. C., J. B. Grace, and E. S. Minor. 2013. Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. *Oikos* 122:682–694.

- Mohr, N. A., and P. G. Kevan. 1987. Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.) and lingonberry (*V. vitis-ideae* L.). Pages 149–154 Proceedings of the Entomological Society of Ontario.
- Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* 23:829–839.
- Morandin, L. A., and M. L. Winston. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agriculture, Ecosystems & Environment* 116:289–292.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84:2628–2642.
- Rempel, R. S., A. P. Carr, and D. Kaukinen. 2008. Patch Analyst extension for ArcMap: Version 4.2. Ontario. Ministry of Natural Resources.
- Ricketts, T. H. 2004. Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee Crops. *Conservation Biology* 18:1262–1271.
- Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and C. D. Michener. 2004. Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences of the United States of America* 101:12579–12582.
- Ricketts, T., J. Regetz, I. Steffan-Dewenter, S. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. Greenleaf, A. Klein, M. Mayfield, L. Morandin, A. Ochieng, and B. Viana. 2008. Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters* 11:499–515.
- Rosseel, Y. 2012. An R package for structural equation modeling. *Journal of Statistical Software* 48:URL <http://www.jstatsoft.org/v48/i02/>.
- RStudio. 2012. Integrated development environment for R. RStudio, Boston, MA.
- SAS Institute Inc. 2007. JMP Pro 10. SAS Institute Inc., Cary, NC.

- Singleton, M. 2010. Biological Impacts of Insecticide Use in the Wisconsin Cranberry Industry. University of Wisconsin, Madison, Madison, WI.
- USDA. 2011. National Agricultural Statistics Service Cropland Data Layer. USDA-NASS, Washington, D.C.
- Winfree, R., N. M. Williams, J. Dushoff, and C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecology Letters* 10:1105–1113.
- Winfree, R., N. M. Williams, H. Gaines, J. S. Ascher, and C. Kremen. 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology* 45:793–802.
- Wolf, A. T., and J. S. Ascher. 2008. Bees of Wisconsin (Hymenoptera: Apoidea: Anthophila). *Great Lakes Entomologist* 41:129–168.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation* 143:669–676.

Figure captions

Figure 1: The distribution of cranberry marshes (sites) along a landscape gradient of wooded habitat and agriculture. Sites were chosen to span as much of the gradient as possible.

Figure 2: A Principle Components Analysis showing the relationship between landcover types surrounding our sites. Each landcover type represents at least 1% of the total area within a 1km radius of all sites.

Figure 3: Hypothesized (gray) and final (black) structural equation model explaining native bee abundance, species richness, and the marsh-wide average cranberry yield. Gray arrows indicate connections that were removed from the model. Solid black arrows indicate positive relationships while dashed arrows indicate negative relationships. Numbers adjacent to arrows are standardized regression coefficients along with their significance (*). The coefficient indicates the strength of the relationship.

Figure 4: Hypothesized (gray) and final (black) structural equation model explaining native bee abundance, species richness, and field estimated cranberry yield. Gray arrows indicate paths that were removed from the model. Solid black arrows indicate positive relationships while dashed arrows indicate negative relationships. Numbers adjacent to arrows are standardized regression coefficients along with their significance (*). The coefficient indicates the strength of the relationship.

Figure 5: Yield from the 2011 cage manipulation experiment across a landscape gradient was best estimated by a model that included cage treatment and principle component 2.

The contribution of bees to yield does not vary as a function of the landscape as indicated by a non-significant interaction term (cage*PC2, $p=0.12$).

Figure 6: Yield from the 2012 cage manipulation experiment was best estimated by a model that included cage treatment, the density of fruiting uprights and their interaction (cage*uprights, $p=0.0054$), indicating that the influence of insect pollinators on yield is greater when the density of flowering uprights is higher.

Figure 1

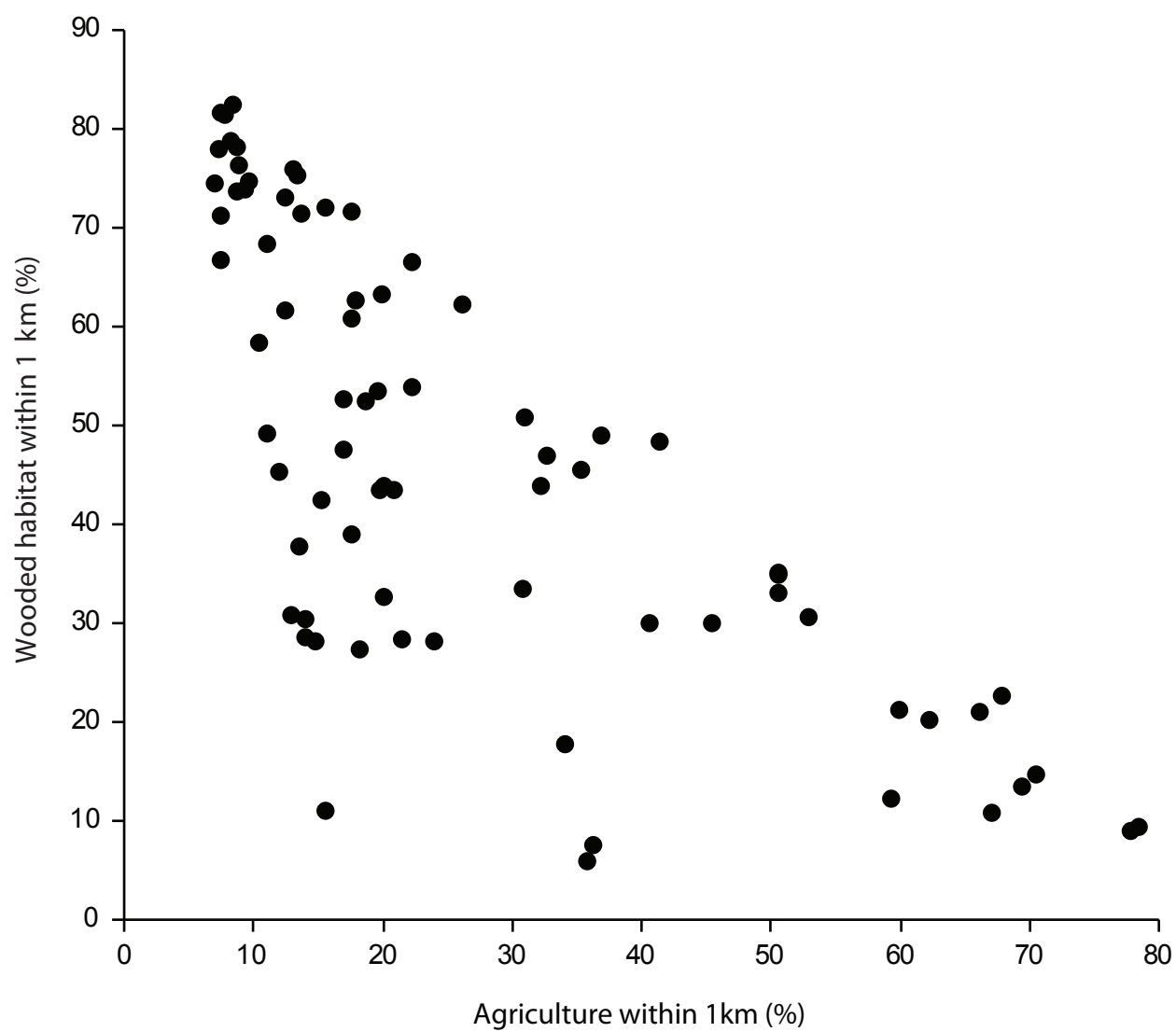


Figure 2

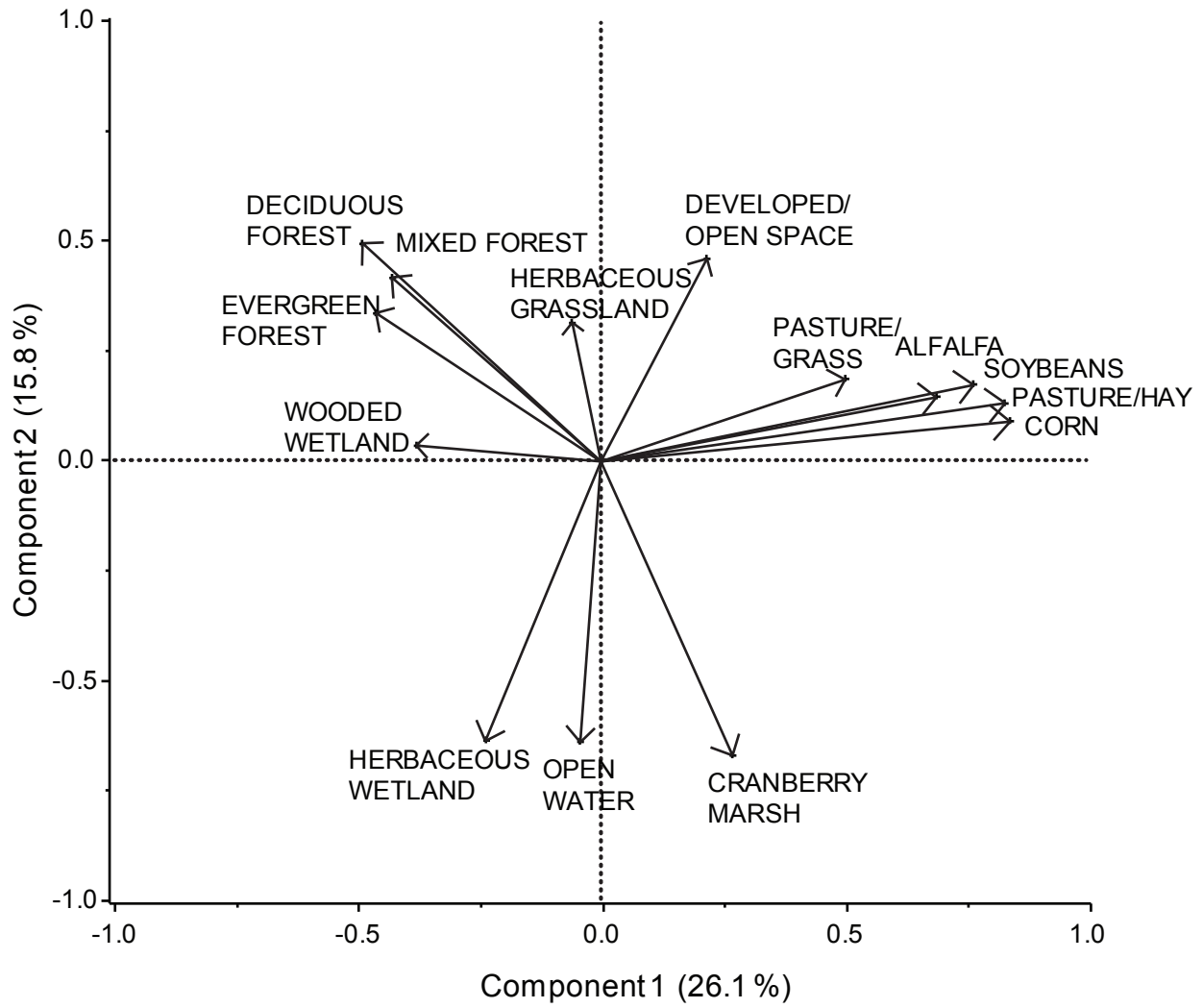
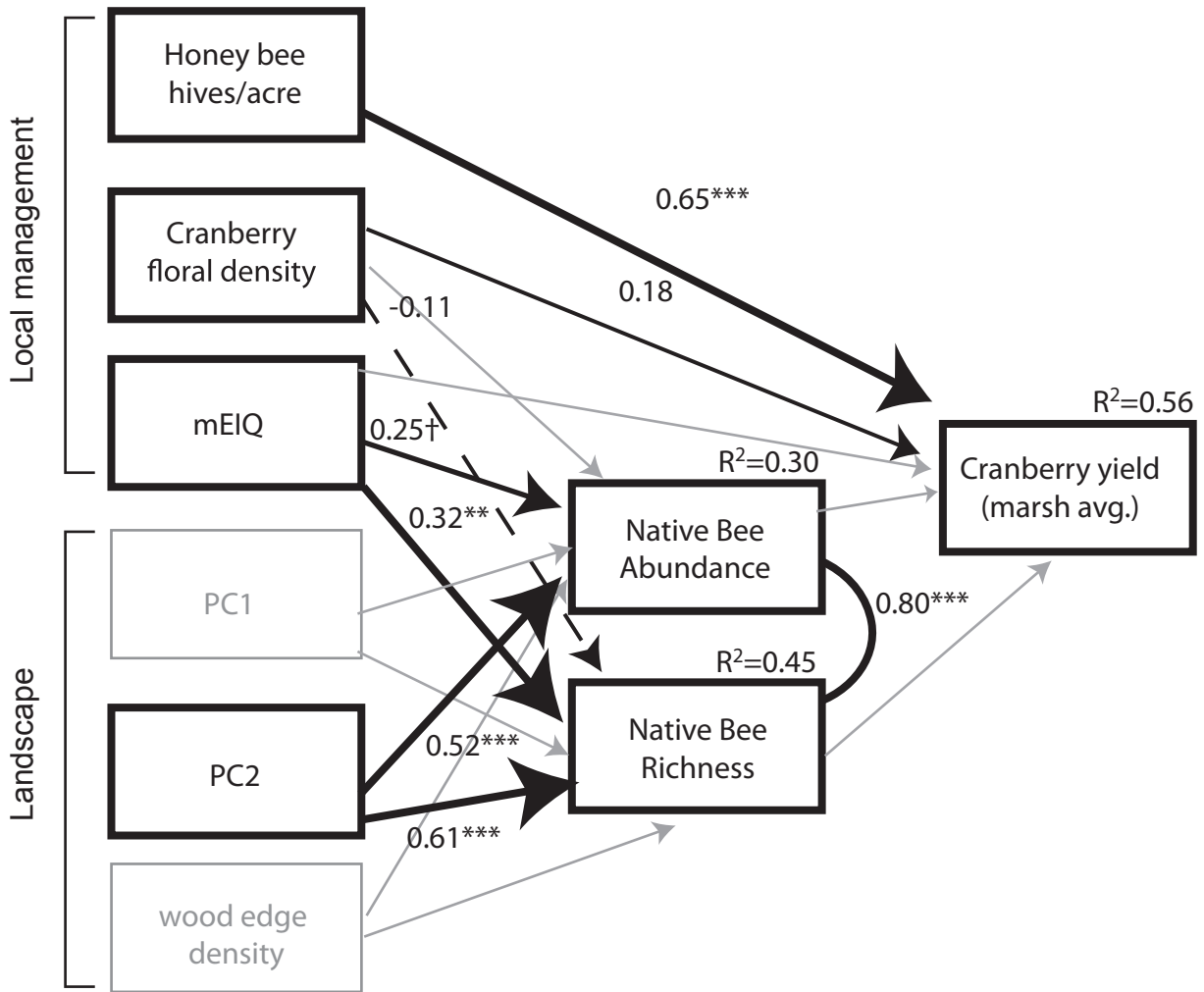


Figure 3

Marsh Scale Model



- Significant interaction, negative
- Significant interaction, positive
- Removed path
- † $p < 0.10$
- ** $p < 0.01$
- *** $p < 0.001$

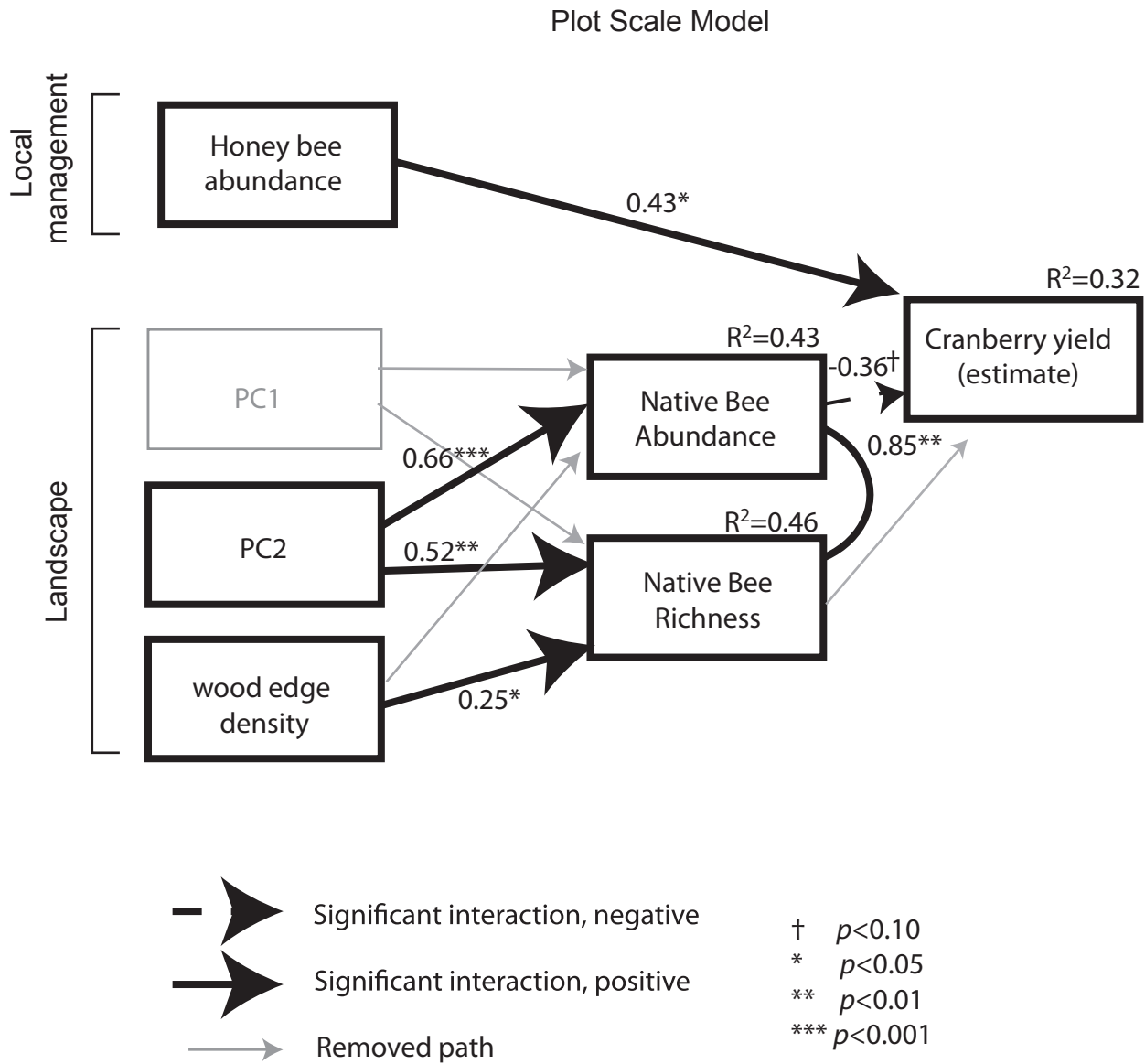


Figure 5

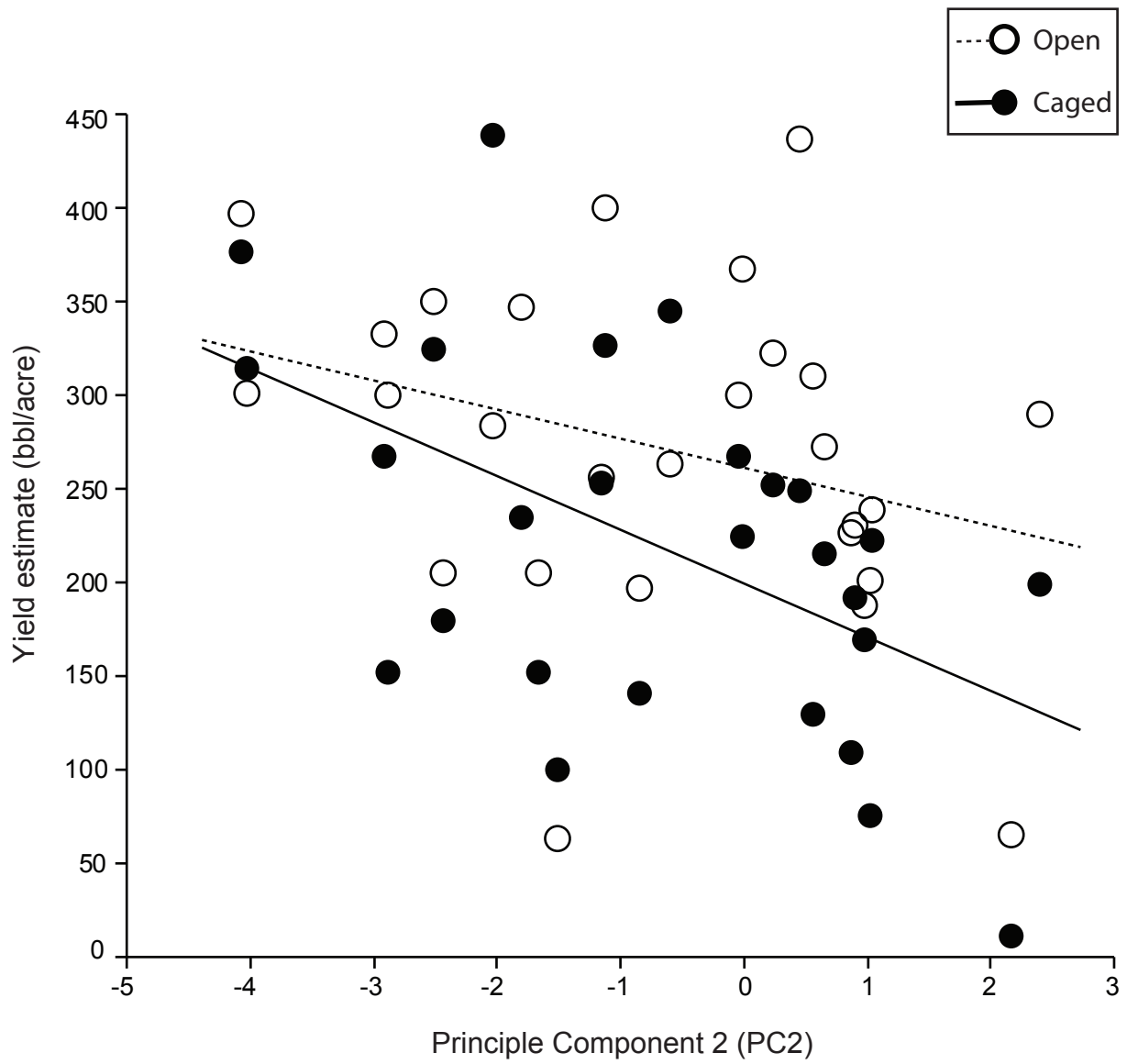
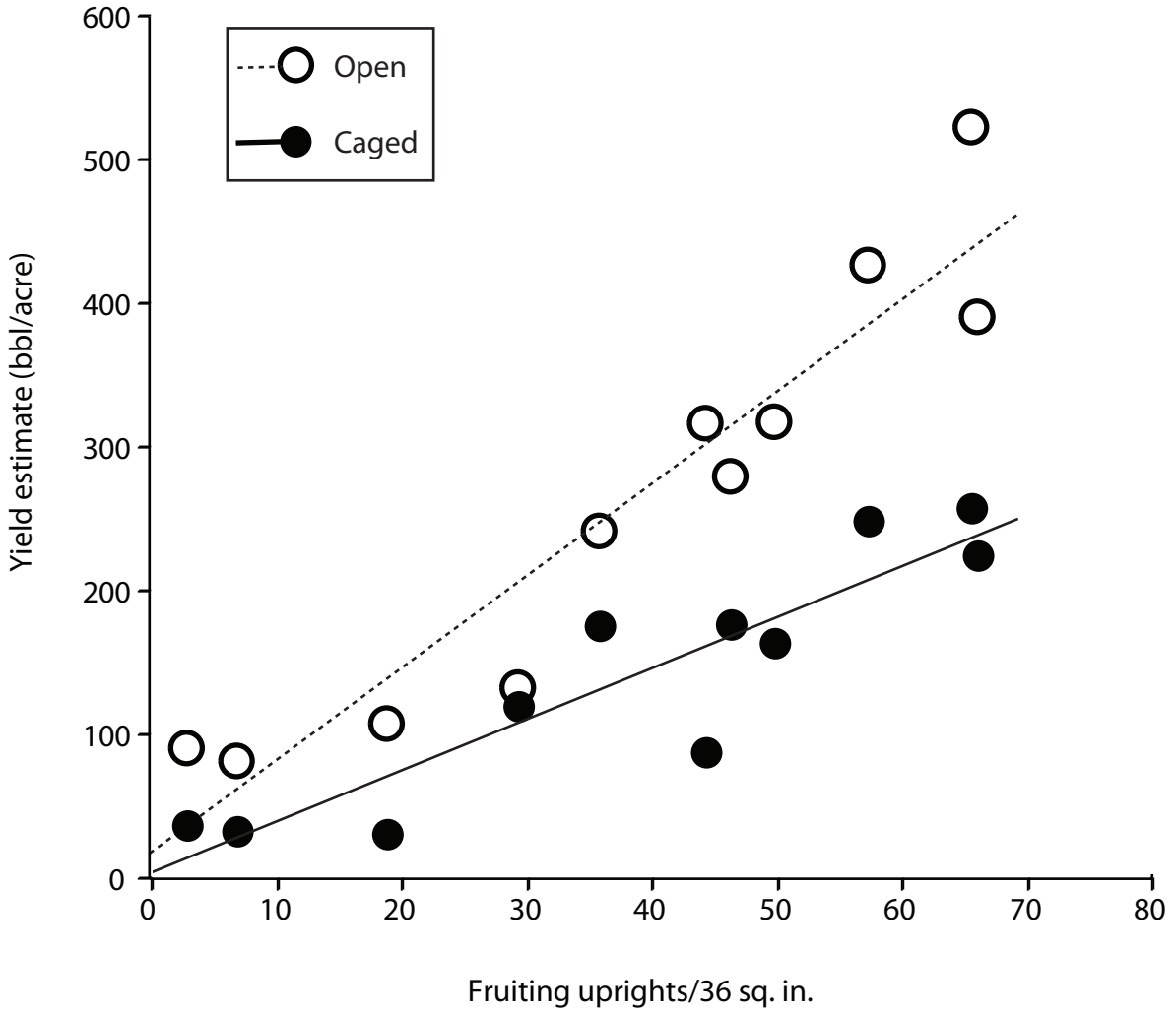


Figure 6



Appendix 3.1: List of bee species and their abundances collected in Wisconsin cranberry between 2008 and 2011. Specimen identification was verified by Mike Arduser, John Ascher, and Jason Gibbs.

Species	2008	2010	2011	TOTAL
<i>Agapostemon sericeus</i>	33	80	38	151
<i>Agapostemon splendens</i>	6	38	54	98
<i>Agapostemon texanus</i>	173	131	121	425
<i>Agapostemon texanus or splendens</i>		1		1
<i>Agapostemon virescens</i>	19	117	125	261
<i>Andrena (Ptilandrena) erigeniae</i>	9			9
<i>Andrena (Trachandrena) sp. 1</i>	2			2
<i>Andrena alleghaniensis</i>	3	1	1	5
<i>Andrena arabis</i>		1	1	2
<i>Andrena barbilabris</i>	5	1		6
<i>Andrena carlini</i>	20	13	1	34
<i>Andrena carolina</i>			2	2
<i>Andrena ceanothi</i>		7	1	8
<i>Andrena chromotricha</i>			1	1
<i>Andrena commoda</i>	1	2	3	6
<i>Andrena crataegi</i>	1	5	2	8
<i>Andrena cressonii</i>	17	16	4	37
<i>Andrena distans</i>	1	2		3
<i>Andrena erythrogaster</i>			1	1
<i>Andrena forbesii</i>	2			2
<i>Andrena fragilis (cf)</i>		1		1
<i>Andrena hippotes</i>	1			1
<i>Andrena imitatrix</i>		1		1
<i>Andrena krigiana</i>		1		1
<i>Andrena milwaukeeensis</i>	1			1
<i>Andrena miranda</i>	2	4	4	10
<i>Andrena miserabilis</i>	4	1	1	6
<i>Andrena nasonii</i>	1	4		5
<i>Andrena nivalis</i>	11	164	28	203
<i>Andrena nr dunningi</i>	1			1
<i>Andrena perplexa</i>	1	1	4	6
<i>Andrena platyparia</i>			2	2
<i>Andrena rufosignata</i>	3			3
<i>Andrena rugosa</i>	1			1
<i>Andrena sigmundi</i>	2			2
<i>Andrena vicina</i>	11	9	3	23
<i>Andrena violae</i>	1			1

<i>Andrena wilkella</i>	5	8	2	15
<i>Andrena wilmattae</i>		1		1
<i>Andrena w-scripta</i>		2		2
<i>Anthophora terminalis</i>		5	10	15
<i>Augochlora pura</i>	2	1	1	4
<i>Augochlorella aurata</i>	14	65	79	158
<i>Augochloropsis fulgida</i>		13		13
<i>Augochloropsis metallica</i>		5	9	14
<i>Augochloropsis sumptuosa</i>		1	1	2
<i>Bombus auricomus</i>		1		1
<i>Bombus bimaculatus</i>	1	24	13	38
<i>Bombus borealis</i>	4	12	8	24
<i>Bombus fernalde</i>	2			2
<i>Bombus fervidus</i>	1	6	11	18
<i>Bombus griseocollis</i>	5	25	18	48
<i>Bombus impatiens</i>	5	90	35	130
<i>Bombus pennsylvanicus</i>			1	1
<i>Bombus rufocinctus</i>		5	1	6
<i>Bombus sandersoni</i>		6	4	10
<i>Bombus sp.</i>		1		1
<i>Bombus ternarius</i>	5	56	79	140
<i>Bombus terricola</i>		17	2	19
<i>Bombus vagans</i>	2	13	18	33
<i>Calliopsis andreniformis</i>	3			3
<i>Ceratina calcarata</i>	1			1
<i>Ceratina calcarata or dupla or micmaqi</i>			1	1
<i>Ceratina dupla</i>		1		1
<i>Ceratina dupla or calcarata</i>	8			8
<i>Ceratina sp.</i>		3		3
<i>Coelioxys immaculata*</i>	2	1		3
<i>Colletes inaequalis</i>	20			20
<i>Dufourea monardae</i>		3		3
<i>Eucera atriventris</i>		1		1
<i>Eucera hamata</i>		26	60	86
<i>Halictus confusus</i>	73	66	49	188
<i>Halictus ligatus</i>	6	71	40	117
<i>Halictus parallelus</i>		19	8	27
<i>Halictus rubicundus</i>	8	11	8	27
<i>Hoplitis pilosifrons</i>	2	2	1	5
<i>Hoplitis producta</i>	4		1	5
<i>Hoplitis spoliata</i>	3	1		4

<i>Hoplitis truncata</i>	1			1
<i>Hylaeus (Prosopis) nr modestus</i>	2			2
<i>Hylaeus affinis/modestus</i>		2		2
<i>Hylaeus basalis</i>		1		1
<i>Hylaeus mesillae</i>	2	1	3	6
<i>Hylaeus modestus</i>		1		1
<i>Lasioglossum (Dialictus) lineatulum</i>	17	85	30	132
<i>Lasioglossum (Dialictus) MA WI sp. A</i>	128			128
<i>Lasioglossum (Dialictus) MA WI sp. B</i>	99			99
<i>Lasioglossum (Dialictus) MA WI sp. D</i>	12			12
<i>Lasioglossum (Dialictus) MA WI sp. E</i>	1			1
<i>Lasioglossum (Dialictus) MA WI sp. F</i>	1			1
<i>Lasioglossum (Dialictus) MA WI sp. G</i>	1			1
<i>Lasioglossum (Dialictus) MA WI sp. H</i>	1			1
<i>Lasioglossum (Dialictus) nr MA WI sp. B</i>	3			3
<i>Lasioglossum (Dialictus) perpunctatum</i>	5	9	3	17
<i>Lasioglossum (Dialictus) pilosum</i>	66	215	86	367
<i>Lasioglossum (Dialictus) rohweri</i>	53			53
<i>Lasioglossum (Dialictus) sp.</i>	3			3
<i>Lasioglossum (Dialictus) viereckii</i>	5	2		7
<i>Lasioglossum (Dialictus) zephyrum</i>	40	46	4	90
<i>Lasioglossum ?unknown</i>		1		1
<i>Lasioglossum acuminatum</i>	70	131	33	234
<i>Lasioglossum admirandum</i>		392	131	523
<i>Lasioglossum albipenne</i>	3	10	5	18
<i>Lasioglossum anomalum</i>		1		1
<i>Lasioglossum athabascense</i>	1	13	1	15
<i>Lasioglossum bruneri</i>	12	22	13	47
<i>Lasioglossum cf. floridanum</i>			1	1
<i>Lasioglossum cinctipes</i>	7	13	6	26
<i>Lasioglossum coreopsis</i>			1	1
<i>Lasioglossum coriaceum</i>	32	149	119	300
<i>Lasioglossum cressonii</i>	4	11	12	27
<i>Lasioglossum ellisiae</i>		1	2	3
<i>Lasioglossum ephialtum</i>		18		18
<i>Lasioglossum fedorense</i>		32	4	36
<i>Lasioglossum floridanum</i>		1		1
<i>Lasioglossum forbesii</i>	1	1		2
<i>Lasioglossum forbesii or paraforbesii</i>	1			1
<i>Lasioglossum foxii</i>	1			1
<i>Lasioglossum heterognathum</i>		1		1

<i>Lasioglossum laevisimum</i>		2		2
<i>Lasioglossum leucocomum</i>		127	73	200
<i>Lasioglossum leucozonium</i>	30	265	66	361
<i>Lasioglossum lusorium*</i>		1		1
<i>Lasioglossum lustrans</i>	1	29	3	33
<i>Lasioglossum lustrans (3 cells)</i>		2		2
<i>Lasioglossum michiganense</i>			1	1
<i>Lasioglossum mitchelli</i>		3	1	4
<i>Lasioglossum nelumbonis</i>	6	40	46	92
<i>Lasioglossum nigroviride</i>	1	2		3
<i>Lasioglossum novascotiae</i>			1	1
<i>Lasioglossum nymphaeorum</i>	31		85	116
<i>Lasioglossum oblongum</i>		7	1	8
<i>Lasioglossum oceanicum</i>		121		121
<i>Lasioglossum paraforbesii</i>	5	47	9	61
<i>Lasioglossum pectorale</i>	16	52	54	122
<i>Lasioglossum pictum</i>	1			1
<i>Lasioglossum pruinatum</i>		1		1
<i>Lasioglossum smilacina</i>		4		4
<i>Lasioglossum sp.</i>			1	1
<i>Lasioglossum subviridatum</i>		16	1	17
<i>Lasioglossum swenki</i>	1	17	34	52
<i>Lasioglossum taylorae</i>		2		2
<i>Lasioglossum timothyi</i>		2	1	3
<i>Lasioglossum versatum</i>		95	25	120
<i>Lasioglossum viridatum</i>		8	11	19
<i>Lasioglossum weemsi</i>			2	2
<i>Lasioglossum zonulum</i>	30	105	102	237
<i>Macropis nuda</i>	1	1	1	3
<i>Megachile addenda*</i>	11	21	7	39
<i>Megachile brevis</i>	2	2		4
<i>Megachile gemula</i>	7	6	1	14
<i>Megachile latimanus</i>	5	17		22
<i>Megachile latimus</i>			21	21
<i>Megachile relativa</i>	1		1	2
<i>Melissodes (Eumelissodes) sp.</i>			9	9
<i>Melissodes agilis</i>		10		10
<i>Melissodes bimaculata</i>		15	8	23
<i>Melissodes desponsa</i>	1	11	19	31
<i>Melissodes druriella</i>			20	20
<i>Melissodes subillata</i>		3		3

<i>Melissodes trinodis</i>		6		6
<i>Melissodes agilis or trinodis</i>			14	14
<i>Nomada sp.</i>		3		3
<i>Nomada sp. 1</i>	1			1
<i>Osmia albiventris</i>	1			1
<i>Osmia atriventris</i>	1	2		3
<i>Osmia distincta</i>	9	7	2	18
<i>Osmia georgica</i>	2			2
<i>Osmia inspurgens</i>	6			6
<i>Osmia lignaria</i>		1	1	2
<i>Osmia pumila</i>	21	5	1	27
<i>Osmia simillima</i>	1	3		4
<i>Osmia tersula</i>	2		1	3
<i>Osmia virga</i>			1	1
<i>Peponapis pruinosa</i>		6	8	14
<i>Perdita maculigera</i>		1		1
<i>Pseudopanurgus helianth</i>		1		1
<i>Psithyrus sp.</i>		4		4
<i>Sphecodes atlantis</i>		1	1	2
<i>Sphecodes confertus</i>		2		2
<i>Sphecodes coromus</i>	1			1
<i>Sphecodes davisii</i>		2	1	3
<i>Sphecodes dichrous</i>	6			6
<i>Sphecodes levis</i>		1		1
<i>Sphecodes mandibularis</i>		1	1	2
<i>Sphecodes rannacali</i>		2		2
<i>Sphecodes solonis</i>		1		1
<i>Stelis (Stelis) labiata</i>	1			1
<i>Stelis foederalis?</i>		1		1
<i>Tripeolis sp.</i>		1		1
<i>Xenoglossa kansensis*</i>		11	5	16

*indicates new record for the state of Wisconsin

CHAPTER 4

Understanding the barriers to implementation of on-farm habitat conservation of native bees in Wisconsin cranberry

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Abstract: The expansion of modern agriculture has led to the loss and fragmentation of natural habitat, resulting in a global decline in biodiversity. One way to mitigate the negative effects of agriculture on biodiversity is through the conservation of natural habitat within agricultural landscapes. In many countries, farmers can receive cost-share funding to create these habitats. These cost-share programs could be especially beneficial for farmers with pollinator-dependent crops, since local habitat can protect and enhance native bees and the pollination services they provide. Wisconsin cranberry growers should be an especially likely group to participate in such programs due to their demonstrated commitment to environmental stewardship, dependence on pollinators, and availability of non-crop land on their farms. Unfortunately, their adoption has been very low. In order to increase participation, we have to understand why growers are not participating. Therefore, the objective of this study was to understand the barriers that prevent the implementation of federally funded on-farm conservation programs for native bees on

Wisconsin cranberry marshes. We sent a paper survey regarding farming practices, pollinators, conservation, and demographics to the mailing list of the Wisconsin State Cranberry Growers Association (n=250). We found that while only 10% of growers were aware of the federal pollinator cost-share programs, one third of them were managing habitat for pollinators without federal aid and 50% were interested in participating in the program. We also found that 57% of growers manage habitat for wildlife, although none receive cost-share funding to do so either. Based on responses to additional questions, participation in cost-share programs could benefit from outreach activities that promote the cost-share programs, a reduction of bureaucratic hurdles to participate, and technical support to growers on how to manage habitat for wild bees.

Keywords (4-6): conservation, pollinator, agriculture, EQIP, classification tree analysis

1.0 Introduction

The expansion of modern agriculture has led to the destruction and fragmentation of habitat, resulting in a massive loss of biodiversity (Benton et al. 2003, Foley et al. 2005). Some of this biodiversity also provides valuable ecosystem services to humans and as this biodiversity is lost, so too are the services it provides. Insects are one group of organisms that are negatively affected by the expansion of agriculture and also provide valuable services to humans including pest suppression and pollination (Losey and Vaughan 2006, Isaacs et al. 2009). By providing habitat within the agricultural landscape, some of the negative effects of agriculture on biodiversity may be alleviated, allowing beneficial organisms and the services they provide to persist.

On-farm conservation practices to establish non-crop habitat within the farming landscape represents one approach to lessen the negative effects of agricultural expansion. Previous studies have documented the value of such non-crop habitat to beneficial insects and the services they provide (Merckx et al. 2009, Scheper et al. 2013, Morandin and Kremen 2013). Because of the large amount of the Earth's land area that is used for agriculture (Foley et al. 2011), incorporating on-farm conservation practices has the potential to make a substantial contribution to protecting biodiversity. Because of the potential value of on-farm conservation to biodiversity, many governments around the world have developed conservation incentives programs to encourage farmers to manage non-crop habitat in an effort to protect biodiversity (Wade et al. 2008). Through these programs farmers receive financial support to take cropland out of production and instead, manage it for biodiversity by planting non-crop habitat.

In the United States, conservation incentives programs exist to encourage farmers to stop farming highly erodible land (e.g., steep hills), protect waterways by installing riparian buffers, and more recently, providing habitat for pollinators (Vaughan and Skinner 2008). Farmers can receive cost-share funding for pollinator habitat through a number of different USDA conservation programs such as the Conservation Reserve Program (CRP) and the Environmental Quality Incentives Program (EQIP) and practices within those programs (e.g., field borders, conservation cover, hedgerows). In addition, as of the 2008 USDA Farm Bill, USDA conservationists must now prioritize pollinators and pollinator habitat when determining payments or reviewing and developing conservation practices (Xerces Society 2009).

With the recent decline in both managed honey bees and wild, native bees (Biesmeijer et al. 2006, Ellis et al. 2010, Potts et al. 2010, Cameron et al. 2011), these programs could be especially beneficial to farmers growing pollinator-dependent crops, such as Wisconsin cranberry growers. Cranberry is a pollinator-dependent crop (Delaplane and Mayer 2000) for which growers spend thousands of dollars each year on honey bee hive rentals. Additionally, Wisconsin cranberry growers often own significant amounts of non-crop support land that could be used for pollinator habitat (Colquhoun and Johnson 2010). Furthermore, they have a demonstrated appreciation for environmental stewardship with their high adoption rate of integrated pest management (IPM) practices (Dan Mahr, pers. comm.). For example, almost all of these growers hire crop scouts in order to determine when to spray for pests, apply reduced risk pesticides on their marshes, and use alternative cultural practices to control pests (e.g., flooding). By creating pollinator habitat on their farms, cranberry growers could receive an economically significant return on their efforts in the form of crop pollination services provided by native bees.

Despite the possible benefits to growers, participation by Wisconsin cranberry growers in USDA programs to create pollinator habitat is nearly non-existent (Julie Ammel, pers. comm.). In order to convince growers to participate in these programs, we have to understand why they aren't currently participating. Some possible factors may include a perceived pest problem from conservation habitat, lack of awareness of the programs, lack of technical knowledge or support to implement the project, or a perception that the programs require too much time, space, or money. By understanding why growers are not

participating and which factors are most important in their decision making process, we can more effectively address the root of the problem.

In order to determine the obstacles preventing growers from participating in on-farm conservation programs for native bees and provide practical solutions based on grower input, we conducted a state-wide grower survey. Our specific objectives were to determine which factors are most important in predicting whether Wisconsin cranberry growers are (1) actively managing their farms to encourage native bee pollinators, (2) actively managing habitat to protect other wildlife, and (3) participating in on-farm conservation incentive programs. The results of this study will inform the outreach and education efforts of university and agency personnel and identify ways to improve farmer participation to support conservation practices.

2.0 Methods

2.1 Grower survey

We created a 50-question written survey regarding current farming practices, pollination, on-farm conservation, and demographics (Appendix 4.1). The survey was reviewed by several cranberry growers, conservation professionals, and extension professors to ensure clarity and completeness. Questions were added, removed, or edited based on feedback from these groups. The survey was then sent to the University of Wisconsin Survey Center for review of question structure to ensure interpretability. The final survey was mailed to every cranberry grower on the Wisconsin State Cranberry Growers Association (WSCGA) mailing list (n=250) in June of 2011. Due to confidentiality

policies, the list was not shared with the authors, rather the surveys were delivered to the WSCGA office and the office staff addressed the envelopes. A cover letter explaining the purpose of the survey and a stamped addressed return envelope were included in the mailing. A reminder post-card was sent to the same recipients one week following the initial mailing.

2.2 Statistical analysis

The results of this survey were summarized using both descriptive statistics and classification and regression tree (CART) analysis (R 2.15.1, library rpart). Descriptive statistics were used to determine the frequency of responses to survey questions. CART analysis was used to determine which factors were most important in predicting the response of growers to specific questions regarding active management of habitat for wild, native bees (Q22); alteration of management to protect wild, native bees (Q25); interest in managing for native bees (Q27); management of habitat for wildlife (Q29); and interest in participating in a conservation incentives program to create habitat for wild, native bees (Q39). A CART model is a non-parametric method used in order to determine which factors are most important in predicting values of another factor (De'ath and Fabricius 2000, Chang and Wang 2006). For factors with discrete variable (e.g., yes/no responses) the classification tree is used rather than a regression tree. All other survey questions except the one designated as the predicted variable were included as possible predictors in the CART model. The results of this analysis help us identify factors which classify growers into groups with similar responses to a given question. For example, if interest levels in conservation of wild, native bees is grouped by county but participation is low in a county

where interest is high, extension activities can focus on providing information and technical support to growers in that county. By understanding which factors best predict current management or interest by growers, future extension and outreach efforts can be better targeted to address both the desired conservation outcomes and the factors contributing to why the growers decide to participate in on-farm conservation.

3. Results

3.1 Response rate and demographics

The response rate to our survey was high (49% of surveys returned, n=122). Survey responses came from growers representing a broad range of geographic locations and demographics. Growers responded from 13 counties which represented both the central and northern growing regions in the state. Forty-four percent of responses were from Wood County which has the highest density of cranberry growers in the state. The average age of respondents was 45-54 years old and the average length of time they had been growing cranberries was 24.5 years (± 1.15 SD, median 23, range 4-77). The average property size was 1,115 acres (± 159 SD, median 450, range 11-11,000) including on average 50-149 acres in cranberry production. In addition, 84% of respondents indicated that growing cranberries is their primary source of income.

3.2 Active management for bees

Despite a lack of participation in pollinator habitat cost-share programs among cranberry growers (0%), 33% of growers actively manage habitat (e.g., plant flowering shrubs and trees, provide artificial nest boxes, provide brush piles and mattresses for

nesting) for wild bees without outside assistance from a USDA program. Additionally, 30% reported that they have altered their management in some other way (e.g., reduced-risk pesticides, timing of spray, delayed mowing of dikes) to encourage wild bees on their property. The three factors that were most often selected as very or extremely important in growers' decision to manage for bees were (1) the importance of pollination for cranberries, (2) environmental stewardship, and (3) knowledge about pollinator habitat (fig. 1). Of the growers who do not manage for bees, the most important factors influencing their decision were (1) the importance of pollination for cranberries, (2) the availability of technical support, and (3) time commitment. The results of our CART analysis showed that the most important predictor of whether growers manage habitat for bees was whether they had also altered their management in other ways to encourage wild bees (fig. 2). Of the respondents who manage habitat for bees, 56% of them have also altered their management in some other way. The next best predictor variable was whether or not the grower manages habitat for other wildlife. Of those who manage habitat for bees, 51% also manage habitat for wildlife. Regardless of whether or not the growers manage for wild bees, 87% responded that bees are very or extremely important to cranberry pollination and 89% reported that they currently rent honey bees for pollination.

The best predictor of whether growers alter their management in any way other than habitat management to protect bees (e.g., timing of spray, use of reduced toxicity pesticides) was whether they manage habitat for bees (fig. 3). The next best predictor was how important they rated "environmental stewardship". Forty-one percent of growers who alter their management for wild bees rated environmental stewardship as

very/extremely important in their decision to manage for bees. These results show that growers who manage habitat for wildlife and value environmental stewardship are more likely to manage habitat for bees or alter their management in other ways to protect bees.

3.3 Active management of wildlife habitat

To understand further how growers perceive on-farm conservation in general, we asked a series of questions regarding management of habitat to protect wildlife. We found that 57% of growers actively manage habitat for the specific goal of protecting wildlife, although none are receiving cost-share funding to do so. The factors that were most often selected as very or extremely important in influencing a grower's decision to manage wildlife habitat were (1) knowledge about wildlife habitat, (2) knowledge of wildlife, environmental stewardship, and recreation such as hunting or hiking equally tied for second, and (3) time commitment (figure 4). Of the growers who do not manage for wildlife habitat, the most important factors in their decision making was (1) time commitment, (2) financial commitment, and (3) perceived pest problems from wildlife habitat. The CART analysis further indicated that the most important predictor variable for whether or not growers manage habitat to protect wildlife was how important they rated recreation (fig. 5). Of those who manage habitat, 55% also rated recreation as very/extremely important. Of those who did not rate recreation as important, the next most important predictor variable was the number of years the grower had been growing cranberries. Thirty-two percent of growers who manage habitat for wildlife have been growing cranberries for more than 28.5 years whereas only 13% have been growing cranberries for less than 28.5 years.

These results suggest that growers who manage for wildlife have knowledge of wildlife and their habitat requirements, a strong environmental stewardship ethic and interest in outdoor recreation such as hunting or hiking. While they acknowledge the time commitment as an important factor, the other factors outweigh the time commitment. These results further suggest that the perceived time and financial commitment, in addition to possible pest problems, cause some growers to not manage wildlife habitat on their farm. Growers who value recreation such as hunting or hiking are most likely to also manage wildlife habitat but of those who don't value recreation as highly, the growers who have been farming for a longer period of time are more likely to manage wildlife habitat.

3.4 Participation in conservation incentives programs

Thirty-one percent of respondents indicated that they currently or have previously participated in USDA-sponsored conservation incentives programs including EQIP (22%), CRP (8%), the Conservation Reserve Enhancement Program (CREP, 2%), and the Wildlife Habitat Incentives Program (WHIP, 2%). Growers were, however, split on whether they would participate in conservation incentives programs in the future, and more were unlikely to participate in a USDA-sponsored program (36%) than a non-USDA-sponsored program (26%). We also found that the most important factors determining whether a grower participated in a conservation incentives program were (1) the amount of paperwork, (2) time commitment, and (3) financial commitment (figure 6). Of the growers who did not participate in conservation incentive programs, the most important factors influencing their decision were (1) amount of paperwork, (2) time commitment and environmental stewardship equally, and (3) awareness of the programs.

While none of the respondents participate in an incentives program for pollinator habitat, and only 10% are aware that such programs exist, 50% of growers would be interested in participating. A CART analysis indicated that the most important predictor variable for whether or not growers are interested in participating in a cost-share program to install pollinator habitat on their property was their interest in managing habitat for bees in the future (fig. 7). The next best predictor variable was whether the grower responded positively to the usefulness of an informational pamphlet about USDA conservation incentives programs for wild bees. The final predictor variable was how important the respondent rated beauty or landscaping in their decision process. Of the 2% of respondents who rated beauty and landscaping as “extremely important”, none were interested in managing habitat for bees in the future, possibly because of a perception that this habitat would be unattractive.

These results suggest that the amount of paperwork and time commitment were enough to discourage many growers from participating in the programs despite the importance of environmental stewardship to these growers.

3.5 Sources of management information for growers

In order to address the findings above, extension and outreach efforts must reach the growers. By understanding which sources of information growers’ use or want to use, extension efforts can be more effective by communicating to growers through these channels. Currently, the most common sources of information are paper newsletters (90%), crop scouts (82%), and the annual meeting of the WSCGA (Cranberry School, 81%). In the future, growers are interested in using email listservs (38%) in addition to paper

newsletters (36%), and crop scouts (35%). We also collected information on sources the growers do not want to use in the future with the top three being social networking sites (85%), automatic text message alerts (61%), and email listservs (44%). This information is also useful so that extension and outreach is not misdirected to these sources to disseminate information.

4.0 Discussion

Despite their demonstrated commitment to environmental stewardship, participation in pollinator habitat cost-share programs by Wisconsin cranberry growers is very low. Through a written survey of Wisconsin cranberry growers, we found that awareness of pollinator habitat incentives programs is also very low. Despite the lack of participation in formal conservation programs, a third of growers are currently managing habitat for pollinators anyway. These same growers were also more likely to manage habitat for wildlife. Growers who were not managing habitat for bees or wildlife were deterred by a lack of technical support, and the perceived time and financial commitments. This suggests that outreach and extension efforts should focus both on promoting pollinator habitat incentives programs as well as providing information and technical support to growers interested in creating pollinator habitat.

The most striking finding in our survey was that, despite a lack of participation in the cost-share programs for pollinator habitat, a third of Wisconsin cranberry growers are managing habitat for wild bees anyway. These management activities included delaying mowing of non-crop areas until cranberry was in bloom, planting flowers and trees that

bloom throughout the season, and providing nesting habitat such as brush piles and bare soil. More than half of the growers surveyed also manage habitat for wildlife, yet none received cost-share funding to do so. The growers who managed habitat for wildlife were more likely to value outdoor recreation such as hunting or had been growing cranberries for many years. Wisconsin cranberry growers appear to be motivated more by their commitment to environmental stewardship or an appreciation of the outdoors than by financial incentives despite the cost of habitat management. Similar to our results, Banack and Hvenegaard (2010) found that farmers who participated in biodiversity-friendly farming practices were most commonly motivated by a moral obligation to care for the environment over economic factors. The goal of on-farm conservation is to provide habitat in agricultural landscapes to protect and enhance biodiversity. While financial incentives programs are one way to motivate growers to provide this habitat, appealing to their sense of environmental stewardship may be an equally strong and effective way to increase the conservation of non-crop habitat on farms.

The minimal participation in conservation incentives programs by Wisconsin cranberry growers seems to be due mainly to an aversion to bureaucratic hurdles and a lack of awareness of the programs rather than lack of interest. Lemke et al. (2010) also found that farmers were discouraged from participating in conservation practices on their farms because of the complexity of paperwork involved. In Michigan, where adoption of the pollinator habitat programs has been high, the key to success has been active promotion of the programs (Eric Mader, pers. comm.) as well as good financial incentives of up to a 90% cost-share (FSA 2010). In other regions of the country and the world, successful

implementation of conservation programs has been a result of engaged conservation professionals developing personal relationships with the farmers and promoting the benefits of conservation through workshops and one-on-one assistance (Mendham et al. 2007, Lemke et al. 2010, Whitten et al. 2012). Currently in Wisconsin, minimal technical support is available for growers interested in participating in on-farm pollinator conservation practices, although interest in promoting these programs is growing at the state level (J. Ammel, pers. comm.).

This study highlights four key areas that can be addressed to increase participation in cost-share programs aimed at creating habitat. First, the specific programs and practices intended for pollinator conservation need to be promoted in Wisconsin. Only a small percentage of cranberry growers were aware of the programs, although half of the growers were interested in participating in a cost-share program for pollinator habitat. Since 80-90% of the cranberry growers get their management information from industry newsletters, crop scouts, and Cranberry School, these would be appropriate outlets through which to promote conservation programs.

Second, the paperwork required by the growers to participate in these programs needs to be reduced. Lowering the bureaucratic hurdles to participation would greatly reduce the time commitment and make participation easier. In order to participate in USDA-sponsored conservation incentives programs, growers have to go through a long, bureaucratic process of determining eligibility through the Farm Service Agency (FSA), developing conservation plans, selecting appropriate programs and practices, and submitting proposals to the FSA through the NRCS (USDA 2013). On top of all of the

paperwork already required by the growers regarding application of pesticides, water use, and permits for marsh renovation and expansion, additional paperwork can discourage growers from participating in cost-share programs (Lemke et al. 2010). Streamlining the process by reducing the amount of paperwork could have a big impact on participation.

Third, creating pollinator habitat may seem overwhelming because of the knowledge required for establishing and maintaining native plants. There is a need for technical support to design and implement conservation plans that include pollinator habitat (Traoré et al. 1998, White and Selfa 2013), but without a person available to direct the growers, answer their questions, and provide practical on-the-ground solutions, few growers will attempt to install pollinator habitat. Several informational pamphlets and job sheets exist to help growers plan their pollinator planting (Vaughan and Mader 2008, Vaughan and Skinner 2008, Vaughan et al. 2012), but with many farmers without high speed internet (Volenberg and Jensen 2010) accessing these resources is difficult.

And finally, NRCS program administrators should establish a peer-mentoring program to connect growers who are currently managing pollinator habitat with growers who are interested in managing pollinator habitat. Sixty-four percent of growers indicated that they get information regarding management practices from their neighbors and friends, suggesting that peer mentoring could be an effective way to increase participation. Providing growers with an example of an established pollinator habitat planting and connecting them with a grower who has gone through the process has the potential to increase the success of interested growers while reducing the demand put on agency personnel to address every concern from new participants. Although it is beyond the scope

of this research project, further thought and development will need to be given to create incentives for growers acting as mentors to be part of the program.

In order to make it easier for growers to manage habitat for pollinators and participate in cost-share programs to do so, we need to promote the available programs, simplify the process, provide direction, and encourage peer mentorship. These steps have the potential to greatly increase participation among Wisconsin cranberry growers as well as other pollinator-dependent fruit crops. Without these steps, the incentive programs for pollinator habitat will likely continue struggling to gain participants. By following the steps outlined above, we can make it easier for farmers to participate and show that on-farm conservation is a priority to the USDA.

Acknowledgements

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Literature cited

Banack, S. A., and G. T. Hvenegaard. 2010. Motivations of landowners to engage in biodiversity-friendly farming practices in Alberta's central parkland region. *Human Dimensions of Wildlife* 15:67–69.

- Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution* 18:182–188.
- Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–354.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* 108:662–667.
- Chang, L.-Y., and H.-W. Wang. 2006. Analysis of traffic injury severity: An application of non-parametric classification tree techniques. *Accident Analysis & Prevention* 38:1019–1027.
- Colquhoun, J., and H. Johnson. 2010. Sustainable cranberry production for a vibrant future: The Wisconsin experience. University of Wisconsin-Extension.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.
- Delaplane, K. S., and D. F. Mayer. 2000. *Crop pollination by bees*. CABI Publishing, New York, NY.
- Ellis, J. D., J. D. Evans, and J. Pettis. 2010. Colony losses, managed colony population decline, and Colony Collapse Disorder in the United States. *Journal of Apicultural Research* 49:134–136.
- Foley, J. A., R. DeFries, G. P. Asner, C. Barford, G. Bonan, S. R. Carpenter, F. S. Chapin, M. T. Coe, G. C. Daily, H. K. Gibbs, and others. 2005. Global consequences of land use. *Science* 309:570.
- Foley, J. A., N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockström, J. Sheehan, S. Siebert, D. Tilman, and D. P. M. Zaks. 2011. Solutions for a cultivated planet. *Nature* 478:337–342.
- FSA. 2010. CRP-SAFE Native Pollinator Planting. Farm Service Agency, Michigan Department of Agriculture.
- Isaacs, R., J. Tuell, A. Fiedler, M. Gardiner, and D. Landis. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment* 7:196–203.

- Lemke, A. M., T. T. Lindenbaum, W. L. Perry, M. E. Herbert, T. H. Tear, and J. R. Herkert. 2010. Effects of outreach on the awareness and adoption of conservation practices by farmers in two agricultural watersheds of the Mackinaw River, Illinois. *Journal of Soil and Water Conservation* 65:304–315.
- Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* 56:311–323.
- Mendham, E., J. Millar, and A. Curtis. 2007. Landholder participation in native vegetation management in irrigation areas. *Ecological Management & Restoration* 8:42–48.
- Merckx, T., R. E. Feber, P. Riordan, M. C. Townsend, N. A. D. Bourn, M. S. Parsons, and D. W. Macdonald. 2009. Optimizing the biodiversity gain from agri-environment schemes. *Agriculture, Ecosystems & Environment* 130:177–182.
- Morandin, L. A., and C. Kremen. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications* 23:829–839.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.
- Scheper, J., A. Holzschuh, M. Kuussaari, S. G. Potts, M. Rundlöf, H. G. Smith, and D. Kleijn. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters* 16:912–920.
- Traoré, N., R. Landry, and N. Amara. 1998. On-farm adoption of conservation practices: The role of farm and farmer characteristics, perceptions, and health hazards. *Land Economics* 74:114–127.
- USDA. 2013. Natural Resources Conservation Service. www.nrcs.usda.gov.
- Vaughan, M., and E. Mader. 2008. Wisconsin biology technical note 8: Pollinator biology and habitat. USDA NRCS Washington, DC.
- Vaughan, M., E. Mader, J. Guisse, J. Goldenetz-Dollar, J. Hopwood, B. Borders, and R. Hirsch. 2012. Conservation cover (327) for pollinators: Upper Midwest installation guide and job sheet. The Xerces Society for Invertebrate Conservation, Portland, OR.
- Vaughan, M., and M. Skinner. 2008. Technical note no. 78. Using Farm Bill programs for pollinator conservation. USDA NRCS.

- Volenberg, D., and B. Jensen. 2010. Cranberry grower education.
www.uwex.edu/ces/ag/teams/fruit/.
- Wade, M. R., G. M. Gurr, and S. D. Wratten. 2008. Ecological restoration of farmland: progress and prospects. *Philosophical Transactions of the Royal Society B-Biological Sciences* 363:831–847.
- White, S. S., and T. Selfa. 2013. Shifting lands: exploring Kansas farmer decision-making in an era of climate change and biofuels production. *Environmental Management* 51:379–391.
- Whitten, S. M., A. Reeson, J. Windle, and J. Rolfe. 2012. Designing conservation tenders to support landholder participation: A framework and case study assessment. *Ecosystem Services*.
- Xerces Society. 2009. Invertebrate conservation fact sheet: 2008 Farm Bill: Benefits to crop pollinators.

Figure captions

Figure 1. Percent of growers responding “very” or “extremely” to how important each factor is in their decision whether or not to manage for wild, native bees (Q26).

Figure 2. A classification tree that predicts whether growers responded positively to managing habitat for wild bees on their farm. Cranberry growers who manage habitat for bees are also likely to have altered their management in some other way to protect bees and manage habitat for wildlife. 56% of growers who manage habitat for wild bees have also altered their management in some other way to protect bees as opposed to 21% who have not altered their management practices. 51% of growers who manage habitat for wild bees also manage habitat for wildlife as opposed to 5% who do not.

Figure 3. A classification tree that predicts whether growers responded positively to altering their management in some way to protect wild bees on their farm. 59% of growers who have altered their management in some way to protect bees also manage habitat for wild bees as opposed to 41% who do not. 41% of growers who have altered their management to protect bees also manage habitat for wildlife as opposed to 19% who do not.

Figure 4. Percent of growers responding “very” or “extremely” to how important each factor is in their decision whether or not to manage habitat for wildlife (Q32).

Figure 5. A classification tree that predicts whether growers responded positively to managing habitat for wildlife. 55% of growers who manage habitat for wildlife rated recreation such as hunting or hiking as very or extremely important in their decision to manage habitat for wildlife. 45% of growers who manage habitat for wildlife rated

recreation as only slightly or not at all important in their decision to manage habitat for wildlife. 32% of growers who manage habitat for wildlife and did not consider recreation as very important had been growing cranberries for more than 28.5 years. Only 13% of growers who manage habitat for wildlife and did not rate recreation as important have been growing cranberries for less than 28.5 years.

Figure 6. Percent of growers responding “very” or “extremely” to how important each factor is in their decision whether or not to participate in a conservation incentives program (Q38).

Figure 7. A classification tree that predicts whether growers are interested in participating in a cost-share program for wild bees in the future. 98% of growers who are interested in the cost-share program were also interested in managing habitat for bees in the future. 95% of growers who were interested in a bee habitat cost-share program expressed utility in an informational pamphlet about USDA cost-share programs for wild bees. And 95% of growers who were interested in cost-share programs for pollinators rated beauty and landscaping as less than extremely important in their decision to manage habitat for bees.

Figure 1

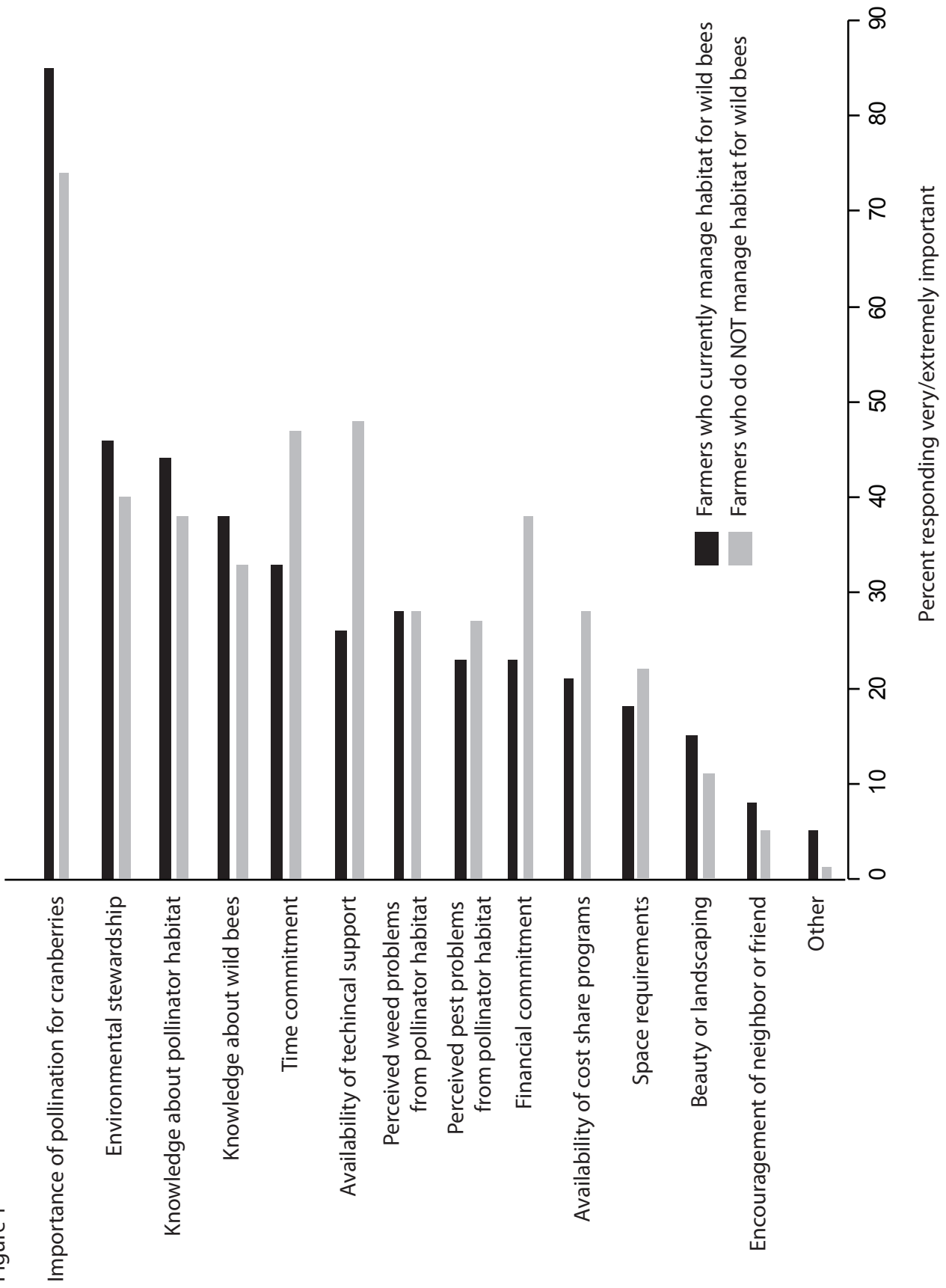


Figure 2

Growers who actively manage habitat to encourage wild bees on their property (Q22)

Altered management for wild bees (e.g., spray at night)

YES
(56%)

NO
(21%)

Manages habitat for wildlife

YES
(51%)

NO
(5%)

Figure 3

Growers who have altered their management in some way to protect wild bees (Q25)

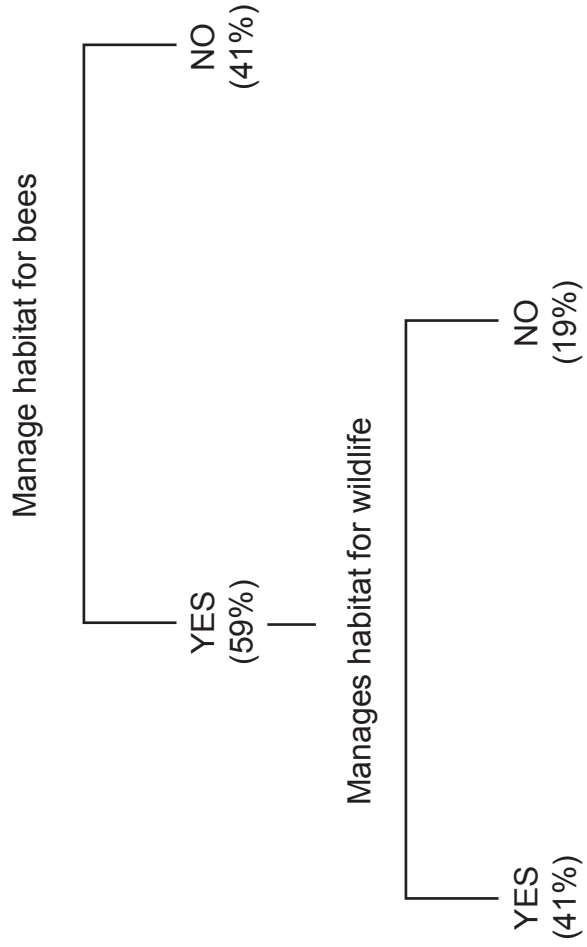


Figure 4

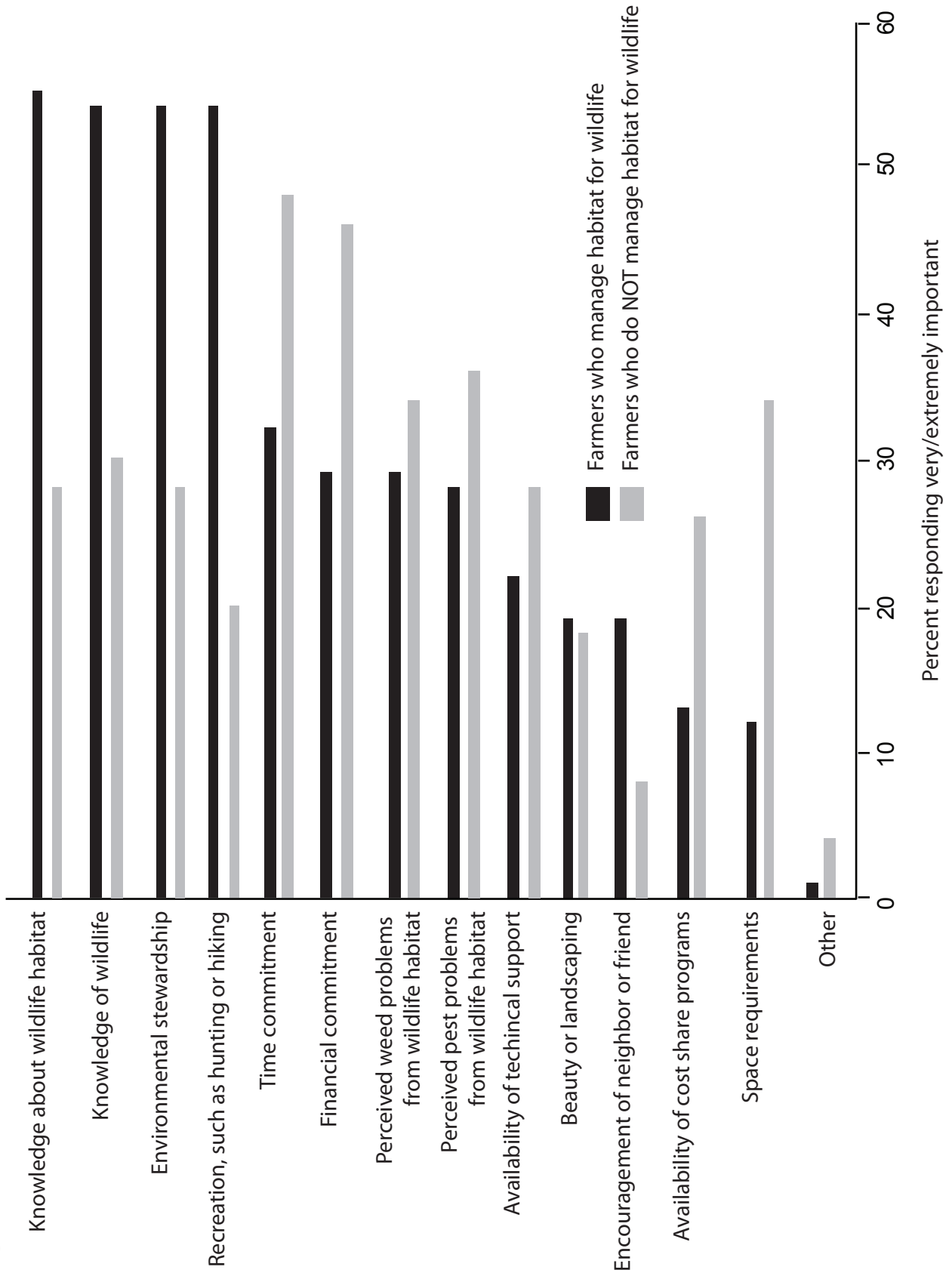


Figure 5

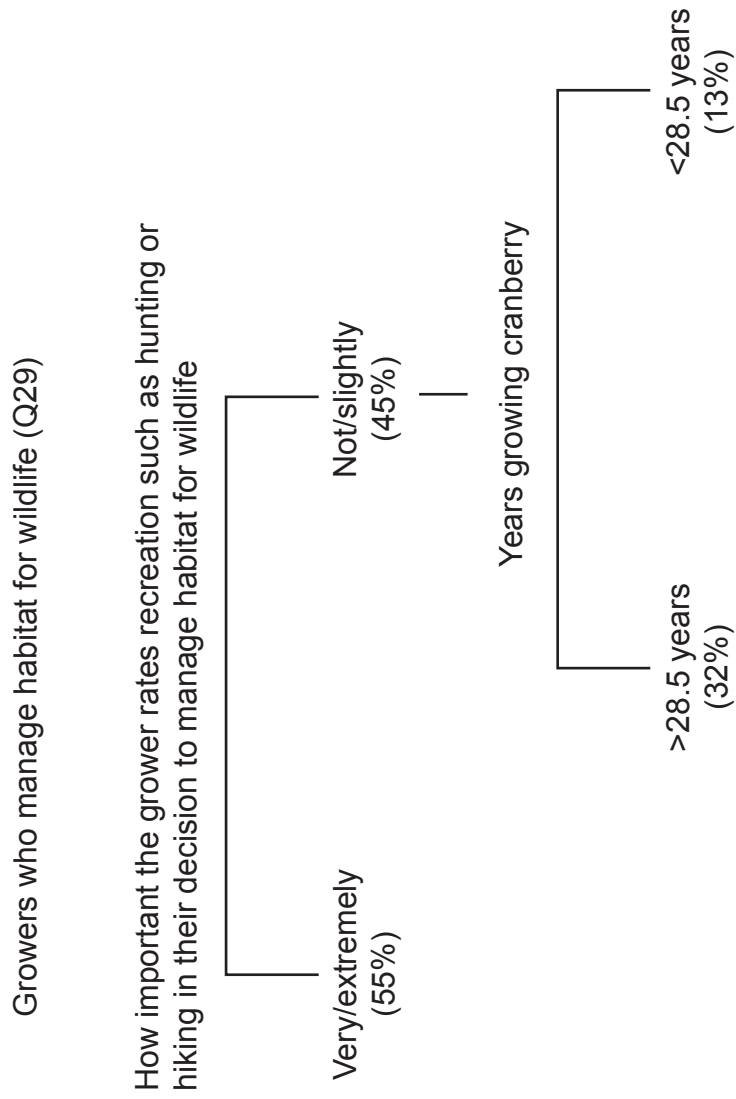


Figure 6

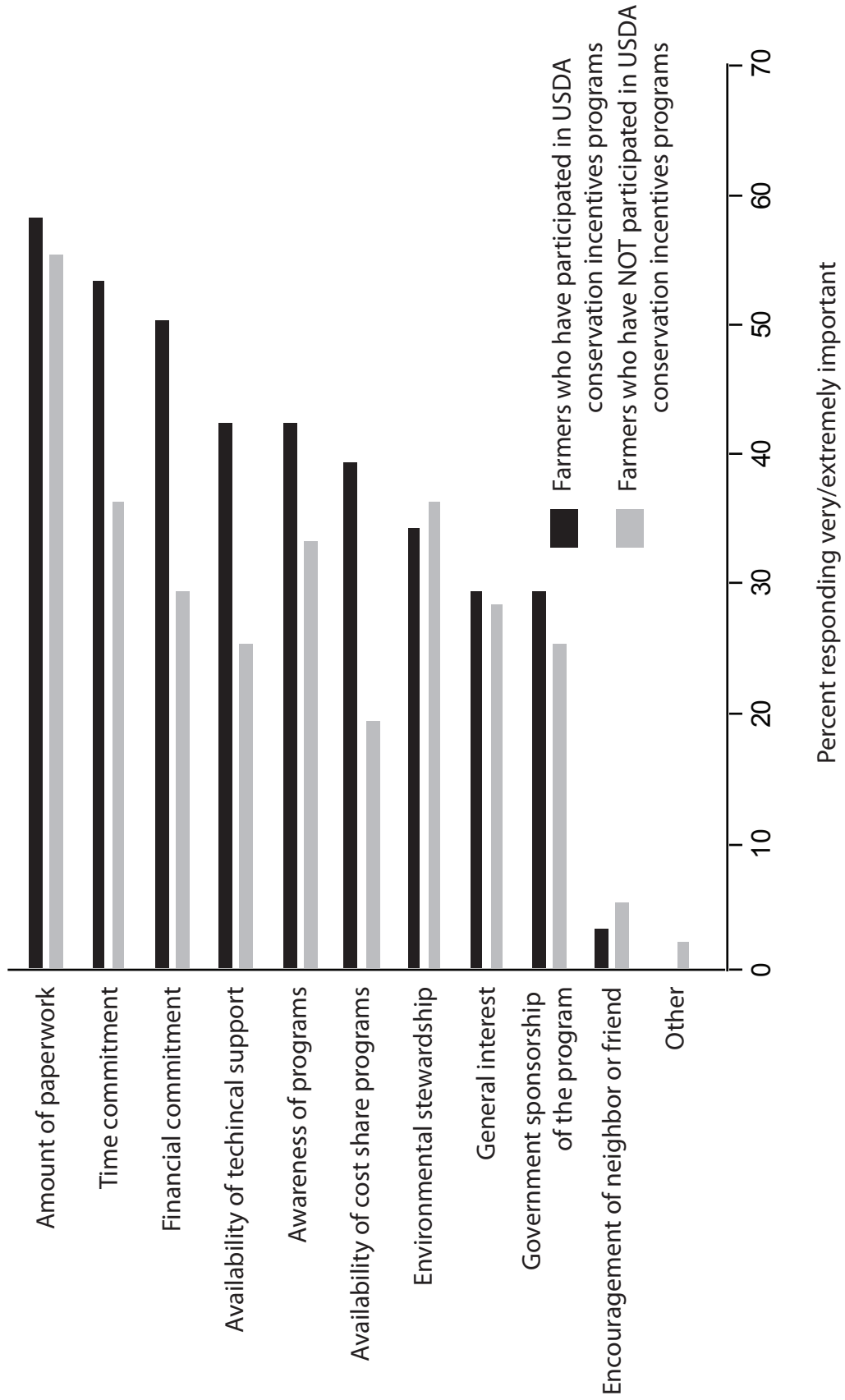
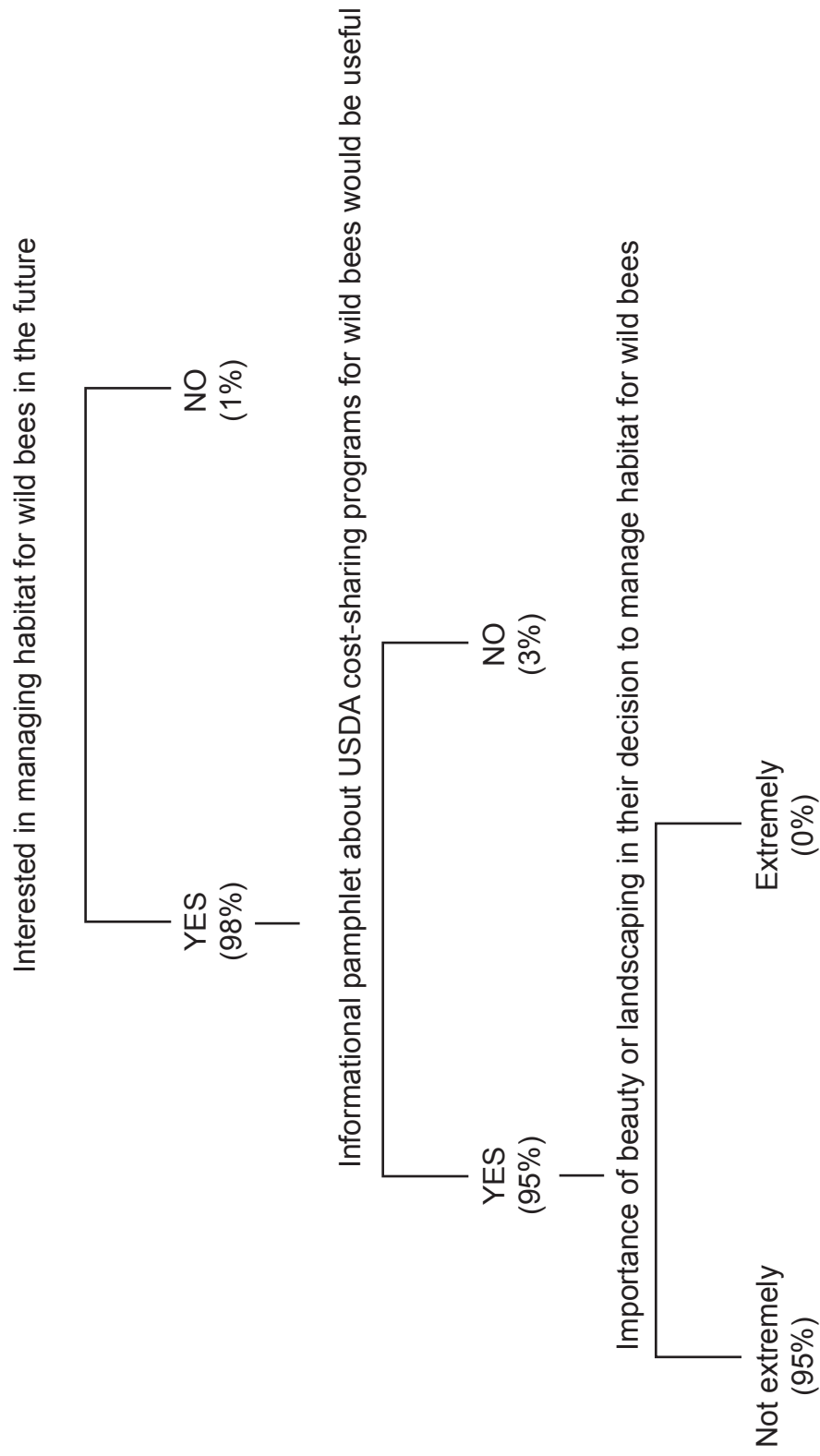


Figure 7

Growers who expressed interest in participating in a cost-share program for pollinators





Cranberry Grower Survey

This study is being conducted in order to understand how cranberry growers regard on-farm conservation programs in general and pollinator conservation programs in particular.

Your answers will be kept confidential, and not released in a way that would allow you to be identified.

1. Are you currently acting as the primary farm operator for your cranberry farm? Acting as the primary farm operator would include handling day to day operations and making decisions regarding farming practices for cranberry production done on your farm.

Yes → Go to question 2

No
↓

We would appreciate your assistance in passing this survey on to the person who is the primary farm operator for your Cranberry farm.

If you are unable to pass the survey on to that person, please make note of that here and return the blank survey in the enclosed postage paid envelope.

Thank you!

This section is about current management practices and where you obtain information on management practices.

2. Within the past 5 years, if you ever irrigated, in general, what time of day did you irrigate your cranberry beds? (Check all that apply)

- Before 8:00 a.m.
- Between 8:00 a.m. and 3:00 p.m.
- Between 3:00 p.m. and 7:00 p.m.
- After 7:00 p.m.
- I never irrigated over the past 5 years

3. Within the past 5 years, if you applied any of the following substances, what time of day did you usually apply them to your cranberry beds? (Check all that apply)

	Before 8:00 a.m.	Between 8:00 a.m. and 3:00 p.m.	Between 3:00 p.m. and 7:00 p.m.	After 7:00 p.m.	I did <u>not</u> apply in past 5 years
a. Insecticide	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
b. Herbicide	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
c. Fungicide	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

4. Within the past 5 years, if you applied any of the following substances, how many applications, on average, did you spray per year of each of the following? If you did not spray at all, please write '0' for that substance.

	Number of applications per year
a. Insecticide	<input type="text"/>
b. Herbicide	<input type="text"/>
c. Fungicide	<input type="text"/>
d. Other, please describe <input type="text"/>	<input type="text"/>

5. Within the past 5 years, did you ever use the following types of insecticide products on your cranberry beds?

Yes No

a. Insect growth regulators such as Confirm or Intrepid

b. Neonicotinoids such as Assail

c. Organophosphates such as Diazinon or Lorsban

d. Some other products, please describe

6. Is your farm certified organic?

Yes

No

7. Do you hire a scout to monitor for insect pests?

Yes

No

8. Within the past 5 years, which of the following methods did you use to determine when to spray for insect pests? Did you use...

Yes No

a. ...a calendar schedule?

b. ...scout reports?

c. ...some other method? please describe

9. Within the past 5 years, what insect pest management strategies did you use in addition to or instead of insecticides? Did you use...

Yes No

a. ...flooding?

b. ...biological control?

c. ...sanding?

d. ...some other strategy? please describe

10. Below is a list of sources of information about pest, nutrient, water, frost and other management practices. For each source of information, please indicate if you have used that source in the past, if you are using it now, if you want to use it in the future, or if you have NEVER used that source of information, and would not want to in the future. (Check all that apply)

	Used it in the past	Use it now	Want to use it in the future	Never used it and will not in the future
a. Crop Scout	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
b. University Extension Agent	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
c. Natural Resources Conservation Service (NRCS) Staff	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
d. Neighbor or friend	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
e. Cranberry School	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
f. Information hotline (phone)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
g. Newsletter (paper)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
h. Email listserv	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
i. Text message (automatic alerts)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
j. Social networking site (Facebook, Twitter)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
k. Website (please list below) ↴ <input type="text"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
l. Other (please list below) ↴ <input type="text"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

POLLINATORS - WILD AND MANAGED

This section is about your current pollination practices and your awareness about wild bees and pollinator habitat.

11. Do you currently rent honey bees for pollination?

- Yes
 No → Go to question 13

12. How many hives per acre?

hives

13. Have you ever rented honey bees for pollination in the past?

- Yes
 No

14. Do you use commercial bumble bees for pollination?

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- Yes
 No → Go to question 16

15. How many hives per acre?

hives

16. Have you noticed a change in the availability of honey bee hives in the past 5 years?

- Yes → Please explain
 No

17. Have you observed a change in the quality of rented honey bee hives in the past 5 years?

- Yes → Please explain
 No

18. How familiar are you with Colony Collapse Disorder (CCD)?

- Not at all familiar
 Slightly familiar
 Somewhat familiar
 Very familiar
 Extremely familiar

19. Can you distinguish between wild bees and honey bees?

- Yes
 No

20. How important do you think honey bees are for cranberry pollination?

- Not at all important
 Slightly important
 Somewhat important
 Very important
 Extremely important

21. Are you aware of any wild bees on your property?

- Yes
 No

22. Do you actively manage habitat to encourage wild bees on your property?

Yes → Please explain

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No → Go to question 24

23. If you do manage habitat for wild bees, did you receive cost-share funding to do this?

Yes → Through whom?

No

24. Are you aware of cost-share programs for establishing pollinator habitat?

Yes

No

25. Have you altered your management in any way to encourage wild bees on your property?

Yes → Please explain

No

26. How important are each of the following in your decision about whether or not to manage for wild bees?

	Not at all	Slightly	Somewhat	Very	Extremely	Not applicable
a. Financial commitment	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
b. Time commitment	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
c. Space requirements	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
d. Availability of cost share programs	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
e. Availability of technical support	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
f. Environmental stewardship	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
g. Encouragement of neighbor or friend	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
h. Knowledge about wild bees	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
i. Knowledge about pollinator habitat	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
j. Perceived weed problems from pollinator habitat	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
k. Perceived pest problems from pollinator habitat	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
l. Beauty or landscaping	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
m. Importance of pollination for cranberries	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
n. Other (please explain) ↓	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

27. If you do not currently manage for wild bees on your property would you be interested in managing for wild bees in the future?

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Yes

No

28. Which of the following would be useful to you?

	Useful	Not useful
a. Field day demonstration of a pollinator habitat project	<input type="radio"/>	<input type="radio"/>
b. Informational pamphlet about wild bees	<input type="radio"/>	<input type="radio"/>
c. Field guide to wild bees	<input type="radio"/>	<input type="radio"/>
d. Informational pamphlet about USDA cost-sharing programs for wild bees	<input type="radio"/>	<input type="radio"/>
e. Website about wild bees	<input type="radio"/>	<input type="radio"/>
f. Website about pollinator habitat	<input type="radio"/>	<input type="radio"/>
g. Website about USDA cost-sharing programs for wild bees	<input type="radio"/>	<input type="radio"/>
h. Other (please explain) <input type="text"/>	<input type="radio"/>	<input type="radio"/>

ON-FARM CONSERVATION PROGRAMS

The next questions are about on-farm conservation programs in general.

29. Do you currently manage habitat (prairie plantings, woodlots, wetland, etc.) for the specific goal of protecting wildlife (birds, beneficial insects, mammals, etc.)?

Yes

No → Go to question 32

30. If yes, do you receive cost-share funding to support these conservation management activities?

Yes

No → Go to question 32

31. Through whom do you receive cost-share funding to support these conservation management activities?

32. How important are the following in your decision whether or not to manage habitat for wildlife such as **birds, beneficial insects, and mammals**?

124
Not applicable

	Not at all	Slightly	Somewhat	Very	Extremely	Not applicable
a. Financial commitment	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
b. Time commitment	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
c. Space requirements	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
d. Availability of cost share programs	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
e. Availability of technical support	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
f. Environmental stewardship	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
g. Encouragement of neighbor or friend	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
h. Knowledge of wildlife	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
i. Knowledge of wildlife habitat	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
j. Perceived weed problems from wildlife habitat	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
k. Perceived pest problems from wildlife habitat	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
l. Beauty or landscaping	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
m. Recreation, such as hunting or hiking	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
n. Other (please explain) ↴	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

33. Do you or have you ever participated in any of the following United States Department of Agriculture (USDA)-sponsored conservation incentive programs? (Check all that apply.)

- Conservation Reserve Program (CRP)
- Conservation Reserve Enhancement Program (CREP)
- Environmental Quality Incentives Program (EQIP)
- Wildlife Habitat Incentives Program (WHIP)
- Other, please explain

34. Do you currently participate in the Whole Farm Planning Incentives Program (WFPIP)?

- Yes
- No

35. Do you currently participate in any programs that address the following environmental/conservation issues? (Check all that apply.)

- Nutrient management
- Pest management
- Water quality and conservation
- Soil conservation


36. In the future, how likely are you to participate in a USDA-sponsored conservation incentive program?

- Extremely unlikely
- Very unlikely
- Somewhat unlikely
- Not sure
- Somewhat likely
- Very likely
- Extremely likely

37. In the future, how likely are you to participate in a non-USDA-sponsored conservation incentive program?

- Extremely unlikely
- Very unlikely
- Somewhat unlikely
- Not sure
- Somewhat likely
- Very likely
- Extremely likely

38. How important are the following in your decision whether or not to participate in a conservation incentive program?

	Not at all	Slightly	Somewhat	Very	Extremely	Not applicable
a. Financial commitment	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
b. Time commitment	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
c. Availability of cost share programs	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
d. Availability of technical support	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
e. Environmental stewardship	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
f. Encouragement of neighbor or friend	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
g. Awareness of programs	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
h. General interest	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
i. Amount of paperwork	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
j. Government sponsorship of program	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
k. Other (please explain) 	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
<input type="text"/>						

39. Would you be interested in participating in a cost-share conservation program to enhance wild bees through the planting of pollinator habitat on your property?

- Yes
- No

40. Do you know who your NRCS officer or representative is?

- Yes
- No

41. Are you comfortable working with or getting information from your NRCS officer or representative?

- Yes
- No

YOUR BACKGROUND

These last questions are about you.

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42. What is your age?

- Less than 25 years old
- 25-34
- 35-44
- 45-54
- 55-64
- 65 or older

43. What is your gender?

- Male
- Female

44. In which county (or counties) do you grow cranberries?

45. How many acres of cranberries do you manage?

- Less than 50 acres
- 50 – 149 acres
- 150 – 300 acres
- Over 300 acres

46. How many total acres do you own or manage, including all cranberry and non-cranberry?

 acres

47. How long have YOU been growing cranberries?

 years

48. How long has YOUR FAMILY been growing cranberries?

128

years

49. Do you regularly attend Cranberry School?

- Yes
 No

50. Is growing cranberries your primary source of income?

- Yes
 No

THANK YOU for your participation!

If you have any questions or concerns, please contact Hannah Gaines by phone (774-392-0498) or email (hgaines@gmail.com).

If there is anything else you would like us to know, please use the space below to do so.

THESIS CONCLUSION

The research presented in my dissertation contributes to our understanding of how local and landscape factors influence bees and cranberry pollination. From the scale of a single cranberry flower to the landscape of central Wisconsin, the results of my dissertation provide new evidence regarding the pollination requirements of cranberry, the contribution of native and managed bees to cranberry yield, and the interacting effect of landscape on hive stocking densities. This research also provides practical information that can be applied to future management and conservation practices.

1. **Native bees in the Wisconsin cranberry agroecosystem respond positively to a gradient of increasing woodland in the surrounding landscape.** Similar to the findings of previous research in other agroecosystems, I found that native bee abundance and species richness increase as the amount of wooded habitat in the surrounding landscape increases. Since agricultural landscapes are highly managed and provide foraging resources for only a short time during the growing season, close proximity to non-crop habitats would allow bees to use resources in both the crop and non-crop habitats.
2. **The contribution of native bees to cranberry yield is highly variable from year to year and only becomes evident with years of data from many sites.** While I was unable to find evidence of an effect of native bees to cranberry yield in my field studies (chp. 3), when I analyzed over a decade worth of historical data from the growers, I found evidence that, in the absence of honey bees, cranberry marshes in high wooded

landscapes achieved a marginally higher yield than marshes in low woodland landscapes (chp. 2). Since native bee abundance and species richness increased with the amount of woodland in the surrounding landscape, it seems logical that this marginal increase may be due to pollination by native bees. Additionally, studies from other systems have found that crop yield increases with bee diversity, further supporting the hypothesis that the yield increase is due to native bees. In a short term field study, any effect of native bees on yield is likely masked by the strong influence of local management practices including the use of managed honey bees. My results suggest that the use of large historical datasets could be a valuable source of information regarding the contribution of native bees to crop yield for a diversity of cropping systems around the world. Furthermore, this data should be available for many crops as growers often keep careful records of their yield and management practices.

- 3. Non-biotic factors contribute significantly to cranberry pollination.** The results of my field and greenhouse experiments clearly demonstrate that, contrary to previous research, in the absence of bees, cranberry is still able to produce viable fruit (chp. 1). At the same time, my data also support previous research confirming that cranberry is unlikely to self-pollinate. Previous studies were designed to compare self-pollination and biotic pollination only, ignoring the possibility of alternative mechanisms. I suggest that pollination without bees is due to the physical agitation of the plants (e.g., by wind) causing flowers to bump into each other, resulting in the transfer of pollen between flowers. This mechanism is facilitated by horticultural practices in commercial

cranberry production where plants grow densely and produce a superfluous number of flowers. Much of the cranberry pollination literature was done decades ago when yields were much lower. Advances in technology and management practices have led to higher yields and more densely planted cranberry uprights, suggesting that horticultural differences may be partially responsible for differences between my results and older studies. In natural bog communities, where cranberry grows sparsely, these findings may not be applicable.

4. The effectiveness of honey bees as cranberry pollinators is landscape dependent.

In low woodland landscapes, yield is strongly correlated with hive density, but in high woodland landscapes, there is no evidence that increasing hive density has any effect on yield (chp. 2). This suggests that on some marshes, bringing in honey bees for pollination has a big effect, while on others, honey bees provide little or no added benefit. One explanation for this pattern is that honey bees may be drawn away from the marshes to forage on non-crop floral resources. A previous study in cranberry found that honey bees returning to the hive carried very little cranberry pollen, supporting the idea that the bees are foraging elsewhere. This has implications for management decisions including whether to use honey bees for pollination and whether providing supplemental foraging resources within agricultural areas may enhance the crop pollination activity of honey bees.

5. Cranberry yield responds most strongly to local factors including honey bee hive stocking density and flowering upright density. This suggests that growers have quite a bit of control over yield through their management decisions. There was also an

interacting effect of floral density and hive stocking density (chp. 3) indicating that if growers can increase their floral density, they will also be increasing the amount of pollination services contributed by bees. Alternatively, if floral density is low, increasing the number of bees will not lead to a higher yield.

6. **Interest among cranberry growers regarding on-farm pollinator habitat conservation is high, but a lack of technical support and bureaucratic hurdles create barriers to their participation in federal cost-share programs.** The results of my research suggest that participation could be increased through outreach activities that promote the cost-share programs, a reduction of bureaucratic hurdles to participate, and increasing the availability of technical support to growers on how to manage habitat for native bees (chp. 4). I also suggest that a peer-mentor program may be useful as many of the growers reported getting management information from their friends and neighbors.