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The Enhancement of Wild Bees (Hymenoptera: Apoidea) For Pollination Security

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THE ENHANCEMENT OF WILD BEES (HYMENOPTERA: APOIDEA) FOR POLLINATION SECURITY

By

Eric Matthew Venturini

B.S. University of Maine, 2006

A THESIS

Submitted in Partial Fulfillment of the

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THESIS ACCEPTANCE STATEMENT

On behalf of the Graduate Committee for Eric Venturini I affirm that this manuscript is the final and accepted thesis. Signatures of all committee members are on file with the Graduate School at the University of Maine 42 Stodder Hall, Orono, Maine.

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THE ENHANCEMENT OF WILD BEES (HYMENOPTERA: APOIDEA) FOR POLLINATION SECURITY

By Eric Matthew Venturini

Thesis Advisor: Dr. Francis A. Drummond

An Abstract of the Thesis Presented
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The acreage of pollinator-dependent crops continues to expand across the globe. Simultaneously, honey bee hives – an annually rented commodity that growers rely on – are more expensive every year and in some cases, scarce. In response, pollinator-dependent growers seek alternative pollinators. One approach is installing bee pasture on farms, a strategy that enables systems-based farmers to become in-situ farm-scale habitat managers. This thesis first presents a review of the literature on bee pasture plantings and provides a brief overview of some methods for assessing their impacts on the pollinator community. There are three major gaps in current bee pasture research. First, can bee pasture actually enhance bee populations? Second, what ratio of bee pasture to crop is required to significantly increase pollination services in a crop field? Last, research that assesses that attractiveness of easily established, phenologically diverse region- and crop-specific flowers that are unlikely to become weedy in crop fields is still rare.

The second chapter of this thesis presents the results of a comprehensive two-year study of bee pasture plantings within the context of New England’s wild lowbush blueberry agroecosystem. Using a randomized complete block design I investigate the effects of nurse crops and mowing regimes on bee pasture establishment success in terms of floral density and species diversity. Three types of bee pasture (clovers, wildflowers, and naturally regenerating margins) were installed at four replicated sites in Maine. Bee pastures were compared in terms of both floral density and insect visitation. Bumble bees were collected at the four treatment sites, and the species' group composition of their pollen loads were compared with those of bumble bees collected in three control sites.

Similar patterns of visitation to bee pasture are apparent among years. Analysis of visitation in the second year alone suggests that naturally regenerating agricultural margins supported 3-4 times fewer wild bee pollinators than other treatments ($\chi^2 = 5.808$, $P = 0.055$). These differences are significant when wild bees are parsed into social and solitary groups. Social bees utilize clover plantings at a significantly greater rate than solitary bees ($\chi^2 = 7.269$, $P = 0.026$) and solitary bees utilize wildflower plantings over clover and naturally regenerating plots ($\chi^2 = 7.423$, $P = 0.024$). On average, across all blueberry fields adjacent to sown bee pasture, bumble bee pollen loads contained 37% bee pasture pollen. Our findings suggest that in lowbush blueberry fields, even relatively small sown flowering strips can provide over 1/3 of the dietary pollen for bumble bees, clover plantings are highly utilized by bumble bees, and wildflower plantings show great potential to provision resources for solitary bees.

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1.1. Background

1.1.1. Agricultural Intensification

In the 1940s United States' agriculture experienced a drastic increase in the intensity and scale of agricultural production. Only a decade later, American farmers were told to "get big or get out" by the U.S. Secretary of Agriculture, Ezra Taft Benson (Berry 1999). In the 30 years following 1939 the number of farms in the U.S. decreased by 56%, almost concurrently (between 1900 and 2000), their energy usage increased by 8000% (Cochrane 1993). Despite this growth in energy consumption, food production increased by a relatively scant 400% (Morris 2010). Increases energy inputs do not necessarily correspond proportionally to increases in in production. It also highlights a tendency to externalize the true costs of production. During the industrialization of agriculture, small farmers unable or unwilling to incorporate new technologies and externalize costs set aside their plows. Their land was abandoned or bought by the farmers who could adapt to these changes. The fundamental causes of agricultural intensification are still in operation today in the 21st century.

The tendency to expand production and decrease per unit costs is prevalent in the agricultural sector that depends upon pollination. This is exemplified by the exponential expansion of the California almond industry from 430,000 acres to 810,000 in 17 years (Sumner & Boriss 2006, USDA 2013a) and the great yield increases in lowbush blueberry production in Northeastern North America. The latter, a crop grown primarily in Maine and Eastern Canada, has increased production by an average of 2.3 million kg/year. In Maine, lowbush blueberry production increased by almost 50% over two decades (1992-2012) without a significant concurrent increase in acreage (Strik & Yarborough 2005, USDA 2013b). Rather than attributed to differences in acreage, this production increase is attributed to more intensive use of herbicides, fertilizers, and honey bees (Yarborough 2004). Such large scale mechanized production systems produce vast quantities of food, but in their wake contaminate ground and surface waters with agro-chemicals and deplete local ecosystem services (Jones et al. 2014, Kremen & Miles 2012). They devalue the grower's labor (Cochrane 1958, Levins & Cochrane 1996) and decrease landscape heterogeneity (Benton et al. 2003).

1.1.2. Externalities: Who Pays?

A large body of research links agricultural intensification to decreases in ecosystem services, specifically crop pollination (Heard et al. 2007, Klein et al. 2007, Kremen et al. 2002) but also, natural enemy activity (Bianchi et al. 2006), biodiversity, carbon sequestration, soil water-holding capacity, resilience to extreme weather events (Kremen & Miles 2012) and increases in pest populations (Bianchi et al. 2006). These external costs are rarely paid by industry or accounted for in summary statistics reported by the United States Department of Agriculture (USDA) or other groups. Instead they are paid for by the public. In Europe, tax dollars support an array of agro-environmental schemes aimed at stemming declining populations of bumble bees by increasing pollinator habitats on farmland (Critchley et al. 2004, Haaland et al. 2011). In the U.S., the USDA grants millions of dollars per year to research groups to identify and address concerns of pollination security that are often linked to agricultural intensification (Buri et al. 2014, Holzschuh at al. 2007, Kremen et al. 2002). Is there a better model? Is agriculture that produces great abundance of food by disproportionally increasing energy inputs and externalizing costs economically viable?

1.2. The Pollination Problem

1.2.1. Increases in Pollinator-Dependent Crops

Pollinators are an essential component of a healthy national agricultural system. One-third of all the food that we eat depends on animal-mediated pollination (Buchmann & Nabham 1997). Further, 90% of vitamin C, the majority of the folic acid, and many other essential nutrients are found only in crops that require pollination (Eilers et al. 2011). Orchard crops, berries, nuts, squash, coffee, chocolate, and watermelon are a few of the products that would become scarce or non-existent without insect-mediated pollination (Delaplane & Mayer 2000). This is only a small sample of the pollinator-dependent crops that represent many of the world's most valued agricultural products. One of them, lowbush blueberry, directly and indirectly contributes $250 million dollars to Maine's relatively depressed economy every year (Smith 2004). Another, the California almond industry, representing 100% of national almond production, brought 3.87 billion dollars to growers in 2012 and is the state's number one agricultural commodity (Tolomeo & Krug 2012).

The disproportionately high value of pollinator-dependent crops creates a great incentive for farmers. Across the globe, the percentage of cropped land devoted to pollinator-dependent crops has increased at a significantly higher rate than that devoted to pollinator independent crops (Aizen et al. 2008, Spivak et al. 2011). Pollinator-dependent crop land has increased in developed countries from 18.2% in 1961 to 34.9% in 2006 and in the same time period increased in the developing world from 23.4% to 32.8% (Aizen et al. 2008). Thus, pollinators are becoming increasingly important in maintaining the stability of our food supply (Aizen et al. 2008, Aizen & Harder 2009, Torchio 1990).

1.2.2. Honey Bee Declines

Although the demand for pollinators is increasing, the number of honey bees available for crop pollination in the United States is decreasing (Biesmeijer et al. 2006, Colla & Packer 2008, Potts et al. 2010, Steffan-Dewenter et al. 2005). Honey bee colonies in the United States have decreased by 59% from 1947-2005 (NRC 2007). Central Europe experienced a 25% loss in *Apis mellifera* from 1985 to 2005 (Potts et al. 2010). A recent meta-analysis of pollination in Europe found that insufficient numbers of honey bee hives exist to pollinate crops in 90% of the 22 countries studied (Breeze et al. 2014).

Colony Collapse Disorder (CCD)—generally believed to be the synergistic effect of a multitude of stressors (Core et al. 2012, Drummond et al. 2012, Neumann & Carreck 2010)—is a leading cause of declining honey bee supply (Rucker et al. 2011). *Varroa destructor* (mite), the use of insecticides and fungicides (Klein et al. 2007, Kevan et al. 1990, Neumann & Carreck 2010), and even the interactions of multiple pesticides (Gill et al. 2012) are major players in the honey bee crisis.

Together, increasing reliance on pollinators (Torchio 1990) and difficulty maintaining honey bee hives in the face of multiple stressors have caused hive rental prices to increase. In California, almond growers paid $60 in 2002 and $160 in 2010 (Rucker et al. 2011). Based on a grower survey in 2013, Maine blueberry growers paid an average of $98.44 per hive (Hoshide et al. unpublished data) compared to just $45 in 2000 (Stubbs & Drummond 2001). Considering the increasing costs of honey bee pollination and the unreliability of the supply, scientists are increasingly calling into question the wisdom of relying on a single species to pollinate our crops (Goulson 2003, Klein et al. 2007, Potts et al. 2010). The future economic and environmental sustainability of pollinator-dependent agriculture requires a fundamental shift in our pollination strategy.

1.3. Alternatives

Farmers and researchers concerned about the future of honey bee-mediated pollination are beginning to explore alternative models. First introduced into the United States in the 1940s, the alfalfa leaf-cutter bee (*Megachile rotundata*) is now the most intensively managed solitary bee in the world. Its use in the alfalfa industry heralded a tripling in seed production (Pitts-Singer & Cane 2011). Stubbs et al. (1994) found this leaf-cutter promising as an alternative managed pollinator in lowbush blueberries but later research suggests that it is not suited to the cold spring nighttime temperatures common in the Northeast (Sheffield 2008). Other pollinators, like the orchard bee (*Osmia lignaria*), are commonly purchased by hobbyists and commercial growers for fruit tree pollination (Bosch & Kemp 2002). Greenhouse tomatoes were among the first agricultural industries to use managed colonies of bumble bee hives for pollination. They are now the major pollinator of greenhouse tomatoes (Calderone 2012). These commercial “quads,” each containing 4 colonies, are also used in blueberry fields and are an effective replacement for honey bee-mediated pollination at a 1:4 bumble bee quad to honey bee hive ratio (Stubbs & Drummond 2001, Drummond 2012). On average, 30% of surveyed lowbush blueberry growers purchase commercially produced *Bombus* quads for pollination (Hanes et al. 2013), often stocking them in addition to rented honey bee hives.

Despite the increasing use of alternative managed pollinators, honey bees remain the primary pollinator of U.S. crops (Calderone 2012), and although modern honey bee culture is plagued with problems, alternative managed pollinators have many of their own. In England a recent study found that 77% of commercial *Bombus terrestris* colonies from three different producers were contaminated with microbial parasites that were capable of infecting wild bumble bees and honey bees (Graystock et al. 2013). Additionally, not all managed pollinators are native to the regions in which they are used and could become invasive (Lye et al. 2011).

Where they are native, managed pollinators may alter the genetic stock of the wild population, decreasing genetic diversity (Averill et al. unpublished data). Relative to apiculture, alternative managed pollinators are new and in many cases best management practices are a process of trial and error.

1.3.1. Wild Bee Habitat Enhancements

Conservationists and managers across the world are investing time and resources into sowing wildflowers in and around crop fields to increase bee populations, often with the goal of improved crop pollination. According to a survey of lowbush blueberry growers in Maine, 15% planted flowers to provide wild bees with more food and increase their population (Hanes et al. 2013). In Massachusetts, several commercial cranberry producers have invested in wildflower plantings for the same reason (Hoshide et al. submitted). Anecdotally, one cranberry grower reports higher wild bee abundances as a result. On Prince Edward Island in Canada, a large-scale conventional lowbush blueberry company is collaborating with researchers, changing production practices, and maintaining large areas of wild bee habitat. The same company is now beginning a similar enhancement strategy in Maine. The Xerces Society for Invertebrate Conservation regularly provides workshops focused on bee pasture plantings for pollinator conservation and reports of successful bee pasture installations abound. Similarly, the USDA's Natural Resources Conservation Service offers cost-share programs for pollinator habitat improvement projects.

Logically, addressing site-specific flower phenology gaps and increasing the abundance of floral resources should increase local bee populations. However, experimental evidence to support this is still lacking (Morandin & Kremen 2013). True population level effects of wild bee habitat enhancement are difficult to untangle from the changes in landscape level bee aggregations that result from new resource patches (Blaauw & Isaacs 2014). Social bees may respond to enhanced food resources by increasing worker numbers, while any measureable increase in univoltine solitary bee populations is necessarily delayed by at least one year (Crone 2013). These are only a few of the factors complicating an accurate understanding of how bee populations respond to increased floral resources.

The question of whether or not pollinator plantings can increase pollination services in the crop itself is of utmost importance. To answer this question, researchers must experimentally test the strength of the link between the presence/absence of pollinator plantings and indicators of crop pollination such as fruit set, fruit size, seed count, and ultimately marketable yield.

Following the USDA's prioritization of wild bee habitat enhancement (Vaughan & Skinner 2008), a number of researchers initiated studies to assess the effectiveness of pollinator habitat enhancement strategies in the United States, specifically, the planting of bee forage resources in crop margins. Despite this interest, published results have not been forthcoming. If enhancement schemes are effective, wild bee populations may be able to replace a proportion of commercial honey bee pollination (Winfree et al. 2007). In at least some cases, crop fields nested in heterogeneous landscapes (Winfree et al. 2008) and on organic farms with nearby natural habitat (Kremen et al. 2002) are completely reliant on wild pollinators, achieving sufficient pollination services in the absence of managed pollinators.

This chapter reviews the literature on pollinator plantings, specifically identifying the few studies that attempt to quantify their effectiveness.

1.4. Introduction

Research supports the hypotheses that adding floral resources to the landscape (1) attracts wild bees (Carreck & Williams 1997, Carvell et al. 2001, Carvell et al. 2006b, Fussel & Corbet 1992, Miñarro & Prida 2013, Tuell et al. 2008, Wilson 2011, Xerces 2011) and (2) increases bee abundance, diversity, and/or richness (Carvalheiro et al. 2011, Haaland & Gyllin 2010, Haaland et al. 2011, Korpela et al. 2013, Morandin & Kremen 2013, Morandin et al. 2011, Pywell 2005, Pywell et al. 2006, Pywell et al. 2011, García & Miñarro 2014), and that (3) bee communities increase pollination services in adjacent crop fields (Albrecht et al. 2007, Greenleaf 2005, Hoehn et al. 2008, Klein et al. 2003, Morandin 2005). Only two published studies assess the ability of bee pasture to increase crop yields (Blaauw & Isaacs 2014, Carvalheiro et al. 2012). Considering that more farmers install bee pastures to increase yields and decrease reliance on honey bees each year, the linkage between habitat enhancement and yield is in need of further testing. There is no scientific consensus on the effectiveness of pollinator habitat enhancement schemes, especially the wildflower plantings commonly referred to as "bee pasture." A growing body of evidence suggests that landscape level heterogeneity—specifically the proportion of natural habitat to cropland—has a positive effect on the bee community and increases crop yields (Greenleaf & Kremen 2006a, Holzschuh et al. 2012).

The installation of bee pasture in a farm landscape can hypothetically impact the wild bee community and farm profits through a number of pathways. Although Figure 1.1 (below) is simplified, it illustrates many of these pathways.

Considering the lack of data that directly link event A to event E or F, I will review the literature for evidence of each of these linkages. Do pollinator habitat enhancements increase farm-scale abundance or diversity of pollinators? Is greater abundance or diversity of wild bees associated with higher visitation rates to crop flowers, fruit set, or yield? Is there evidence that increases in pollination services increase farmers' profits? If pollinator plantings can contribute to crop yields how do we select plants for this role?

Figure 1.1. Flowchart illustrating a series of cause and effect interactions that can cause a pollinator habitat enhancement to increase farmer profitability.

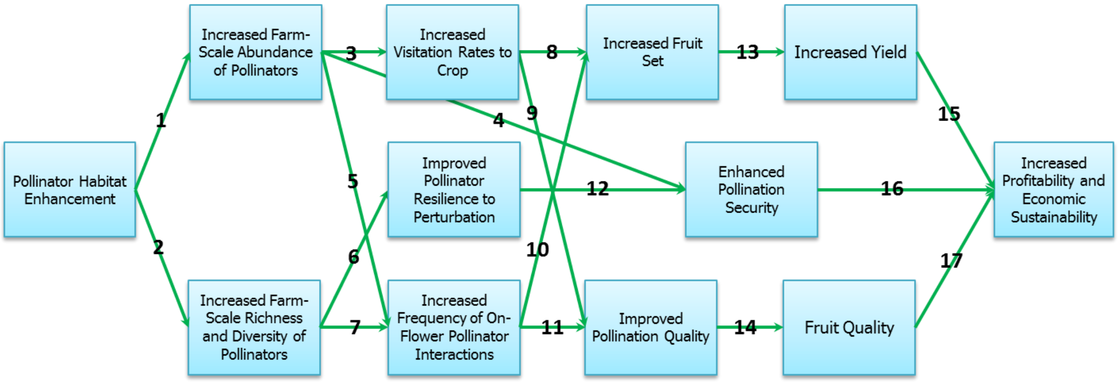

Table 1.1. Explanation and citations for cause and effect interactions in Figure 1.1.

Flowchart Interaction	Explanation and Supporting Research
1	If food is limiting in the environment, then providing more of it can increase the landscape's carrying capacity for pollinators (Blaauw & Isaacs 2014, Larsson & Franzén 2006, Scheper et al. 2015, Wood et al. 2015).
2	Pollinator plantings can increase both the species diversity and richness of pollinators (Kleijn et al. 2006, Klein et al. 2012, Saunders et al. 2013).
3	Although this relationship can be influenced by the abundance of alternative floral resources and other factors, pollinator abundance increases pollination services (Winfree et al 2015).
4	In the event of a scarce honey bee supply or cold wet weather during crop bloom, an abundance of wild pollinators acts as crop insurance, ensuring at least a baseline level of pollination when managed pollinators fail (Winfree et al. 2007).
5	Greater abundances of wild bees increase on-flower bee interactions, which increases the transfer of pollen between flowers (Greenleaf & Kremen 2006b).
6	Ecological theory links biodiversity with ecosystem resilience (Bender, Case, & Gilpin 1984). More diverse pollinator assemblages are more resistant to disturbance (Winfree & Kremen 2009).
7	Diverse assemblages of wild bees increase the interactions between bees on flowers, thereby increasing cross pollination (Greenleaf & Kremen 2006b).
8	Pollinator visitation rates are highly correlated with fruit set. This has been demonstrated in a number of studies and presented by Garibaldi et al. (2013) as a meta-analysis.
9	Insect-mediated pollination improves size, weight, and the number of seeds in fruit (Garratt et al. 2014, Greenleaf & Kremen 2006a).
10	Increased interactions between on-flower foragers lead to greater cross-pollination and fruit set (Greenleaf & Kremen 2006b, Klein, Cunningham, Bos, & Steffan-Dewenter 2008).
11	Increased interactions between on-flower foragers lead to greater cross-pollination and fruit quality (Garratt et al. 2014, Greenleaf & Kremen 2006a, 2006b, Klein et al. 2008).
12	A healthier and more diverse pollinator community provides an insurance against losses or failures of managed pollination systems (Winfree et al. 2007).
13	Field data clearly link fruit set and yield in lowbush blueberry (Bushmann 2013).
14	Greater quality of pollination (number of pollen grains deposited per stigma and the amount of cross pollination) results in larger, heavier fruits with more seeds (Greenleaf & Kremen 2006a).
15	Field studies suggest that the cost of bee pasture installation and maintenance can be recouped by resulting yield increases in 3-5 years (Blaauw & Isaacs 2014).
16	Increasing the proportion of natural habitat increases bee abundance, which raises crop yields and profitability. One estimate suggests that maintaining 30% of a landscape in natural habitat maximizes canola profitability (Morandin & Winston 2006).
17	High quality pollination increases not only fruit set, but also fruit quality, which is an often underappreciated aspect of wild bee pollination that results in increased profitability (Garratt et al. 2014, Sheffield 2014).

1.5. Choosing Plants for Pasture Based on Attractiveness

Before drawing conclusions about the relationship between flora and their pollinators, it is important to understand some of the mechanisms that guide these interactions. The glossa, or tongue length of bees is highly variable among species and even individuals in a single *Bombus* colony (Harder 1985, Peat et al. 2005). A long tongue allows access to nectar hidden deep within the corolla, whereas a short tongue only allows access to nectar in shorter corollas. Although short tongued bees cannot access the rewards in certain inflorescences, they can be much more efficient at handling shallow corollas. In one study, short-tongued *Bombus terrestris* individuals outperformed long-tongued conspecifics when handling flowers with short corollas (Peat et al. 2005). Likely due to corolla length, long- and short-tongued bees generally exhibit different floral preferences (Carvell et al. 2006b).

The relationship between the corolla of a flower and the tongue of a pollinator is relatively simple, but plant-pollinator relationships on the whole are not. Some flowers, particularly legumes, possess triggers, effectively limiting the diversity of bees capable of cross-pollinating them. Others, including Solanaceous species (Harder & Barclay 1994) and blueberries (Javorek et al. 2002), release much greater quantities of pollen with buzz pollination. Some flowers openly exhibit the competitive nature of many plant-pollinator relationships by mimicking the female con-specifics of the male pollinator, enticing the deceived male with visual and chemical stimuli, which ultimately benefits only the flower (Ayasse 2001). Floral evolution can be driven by selective pressure to limit the species richness of visiting pollinators, and at the same time increase the likelihood that a pollinator is carrying viable pollen—pollen recently collected from another flower of the same species (Waser & Ollerton 2006). This would tend to increase the level of specialization of these mutualisms over time. Specialization is however, a risky business. If a plant were to rely on a single pollinator it risks losing its reproductive capability when that pollinator is in short supply or goes extinct.

Instead, plant-pollinator interactions are often mismatched, with one of the co-evolved partners tending towards generalization and the other towards specialization. More specialized bees tend to visit more generalized plants and more generalized bees visit more specialized plants (Waser & Ollerton 2006). These relationships inform us that the diversity of pollinators in a landscape is not only strongly related to the diversity of the flora found there, but also vice versa.

Considering the complexity of plant-pollinator relationships, how can researchers hope to predict the effects of pollinator targeted landscape enhancements on wild bees? A first step is learning through experimental observation which pollinators visit which plants. In a seminal paper, Ayers et al. (1986) realized that the preference of honey bees for one flower over another is only a valid comparison when flowers are offered as a choice test. Visitation rates fluctuate greatly day to day and so comparisons should not be drawn between plants observed on different days. Inflorescences also vary greatly in size, shape, and spatial density making it difficult to draw conclusions based only on visitation rates. Should visitation rates be considered per inflorescence, per floral area, or per square meter? At what scale should the inflorescence be sampled, a floret, a flower-head, or a cluster? The authors' goal was to identify plants suitable for honey production and so by considering bee visitation on a per plot basis, they were also accounting for the ability of the plant to produce an abundance of resources within a limited space. They tested visitation of honey bees to 54 different species of plants and recommended 14 of them based on their ranking as "highly attractive." The flowering phenology of these 14 species forms a continuum of bloom that extends across Michigan's entire season. Their recommendations are not necessarily equally attractive to other bee species.

A similarly designed study in Michigan assessed native plant species' ability to attract both an abundance and diversity of pollinators. The authors recommended several native plant species based on their findings (Tuell et al. 2008). This was one of the first studies to test visitation rates to native plants. Native plants are at least as attractive as non-natives and are more likely to benefit native than non-native bees (Fiedler, Landis, & Wratten 2008, Morandin &

Kremen 2013, Tuell et al. 2008). Krewer et al. (1996) found that *Hibiscus syriacus, Abelia grandifolia, Vitex agnus-castus, Trifolium pratense, Cuphea hyssopifolia, Liriope muscari, Clethra alnifolia,* and *Helianthus giganteus* showed the greatest potential for use as alternative bumble bee forage in rabbit-eye blueberry. A Tennessee study conducted on small diverse farms used non metric multi-dimensional scaling (NMDS) ordination analysis to compare bee visitation rates across a range of bee pasture plants and cover crops, but did not draw major conclusions or make recommendations based on the findings (Wilson 2011). Numerous studies in Europe have compared the attractiveness of flowers to pollinators (Carvell 2002, Carvell et al. 2006b, Carvell et al. 2007, Fabian 2013, Haaland & Gyllin 2010, Kells et al. 2001, Lye et al. 2009, Pywell 2005, Pywell et al. 2006, Pywell et al. 2011). These studies are mostly focused on the conservation of bumble bees rather than enhancement of pollination services and may not be applicable beyond their respective study region or cropping system. Analysis of the proportion of flower pollens in bees' pollen loads may support visitation observations and it also provides a much more detailed accounting of resource utilization (Carvell et al. 2006b). It should be noted that many studies have found that patch size, density (Dauber et al. 2010, Isaacs et al. 2009, Tuell et al. 2008) and flower frequency (Smithson & Macnair 1996) were more strongly correlated with visitation than flower species. This casts doubt on the importance of selection based on flower species if the density of bloom or the total area of the planting is more important to bees. Likewise, the validity of bee visitation studies that do not consider or control for these confounding factors may be questioned.

One illuminating method of illustrating plant-pollinator interactions is through the use of quantitative visitation webs (Memmott 1999). A recent study established 25 wildflowers as bee pasture in Pennsylvania and by measuring both floral density and pollinator visitation constructed a quantitative bipartite visitation network that clearly depicts flower phenologies, pollinator phenologies, and the frequency of species-specific interactions (Russo et al. 2013). This type of plant-pollinator web is a frequent and useful component of plant-pollinator studies (Dicks et al. 2002, Campbell et al. 2011). Future bee pasture research should seek to construct these network maps for each pollinator-dependent cropping system so that farmers and habitat managers may use them to assess the utility of bee pasture plants.

While the findings of researchers in Michigan and elsewhere offer a starting point for the selection of habitat enhancement plants, their utility likely varies greatly from one system to another. Even where plants are native in both regions, it does not necessarily follow that what is attractive to Michigan bees is also attractive to those in Maine. Slight differences in flight periods, alternative forage, and climate may influence bees' flower choices. If habitat managers are going to successfully use native or naturalized plants to enhance bee communities, ecosystem-specific assessments of the attractiveness of regionally native plants are required. Replicated trials underway in Maine (Dibble et al. unpublished data) should generate a list of Maine native plants that could be used for pollinator habitat enhancement schemes in lowbush blueberry and will add to the list of suitable high value alternative forage for bees in Maine documented by Loose et al. (2005).

Although wildflower mixes for pollinator habitat enhancement should be tailored to the agroecosystem for which they are intended, these studies offer a starting point for the development of ecologically based agroecosystem specific flower mixes. Flowers that are demonstrated as highly visited by bees across multiple studies likely offer an abundance of food resources—pollen, nectar, or both. In Maine and the Canadian Maritimes the pollen and nectar content of many common and regionally native plants is well documented (Loose et al. 2005, Stubbs at al. 1992) and these records offer habitat managers important resources. Native plants or those that otherwise pose no risk of invasiveness or of attracting native pollinators away from rare or endangered plants (Menz et al. 2011) should be considered for use in bee pasture.

Several books list plants shown to attract bees and make regionally based recommendations (Mader et al. 2010, Mader et al. 2011). Many organizations have also compiled similar lists (Cane 2013, Sarver 2007a, 2007b, Webb 2008). The simple recommendations written in clear language often found in these publications offer a resource for individuals wishing to implement pollinator habitat enhancements and yet, due to a lack of research, necessarily fall short of offering agroecosystem-specific recommendations. Few reviews have drawn conclusions about specific plants suited for pollinator habitat enhancement (Carvell et al. 2001), but many have outlined the most important considerations when selecting wildflowers for pollinator habitat enhancement and conservation (Haaland et al. 2011, Menz et al. 2011, Nicholls & Altieri 2012, Vaughan & Black 2006, Vaughan et al. 2007).

1.5.1. Guidelines for Selecting Bee Pasture Enhancement Plants

1. Choose plants that bloom at different times of the year. Generally plan for at least three plants to be simultaneously in bloom at any point throughout the season. If certain bee taxa are targeted for enhancement, ensure that bloom of the chosen mix extends across their entire flight period (Menz et al. 2011, Nicholls & Altieri 2012, Vaughan et al. 2007).
2. Select a mix of annual and perennial flowers that encompass a variety of floral morphologies (Nicholls & Altieri 2012, Vaughan & Black 2006). Important aspects of floral morphology include corolla length, complexity (Vaughan et al. 2007), and pollen grain size (Thorp 2000).

3. Consider using native plants to eliminate the risk of introducing invasive species. Use seed sourced from your area so that plants are adapted to the local conditions (Tuell et al. 2008, Vaughan & Black 2006, Vaughan et al. 2007). Non-native plants may be appropriate in some situations (Schlaepfer et al. 2011).
4. If bee pasture is part of a cropping system, eliminate or otherwise control plant species that are, or could become weed problems. This can be considered on a crop-by-crop, and even farmer by-farmer-basis (Menz et al. 2011).
5. Choose only plants that are suited to your site and will establish successfully with the level of care you intend to provide (Vaughan et al. 2007).
6. Select a mixture of plants that will, after five years, continue to meet your goals (Vaughan et al. 2007).
7. Use plants that complement the crop. You may need to limit or eliminate flowers that would bloom simultaneously with the crop and supplement the diversity and number of plants blooming before and after it (Vaughan et al. 2007). In lowbush blueberry *Andrena spp.* and *Bombus spp.* demonstrate a high floral constancy and so in some cases the elimination of co-blooming species may not be necessary (Bushmann & Drummond 2015).

This list, based on the literature, offers a number of guidelines to consider when selecting plants for wild bee habitat enhancements. This list is not comprehensive. Other recommendations, for example choosing flowers based on color, are not included because they are not supported based on research. Another consideration is the use of both ‘framework’ plants that can provide abundant pollen and nectar resources to a wide range of bees and also ‘bridging’ plants that target phenological gaps in both the site and in the immediate landscape

(Menz et al. 2011). Bridging plants differ in suitability depending on the perspective of each bee species, or functional guild. A flower with long corollas like *Monarda fistulosa* may be a perfect bridge plant for long tongued *Bombus spp.* or Megachilidae at a site devoid of other mid-season plants with deep corollas. The same plant would not however, be available to most sweat bees whose tongues are too short to reach the nectar within. Not only should the mix as a whole bloom throughout the season, but each portion of the flower mix suited to each functional group of bees should also contain a set of plants that bloom throughout the season. This will help ensures that all bee functional groups in the landscape have access to suitable pollen and nectar resources at every point of the season.

As additional investigations explore the suitability of plants for pollinator habitat enhancement in specific cropping systems, new candidate plants should emerge and specific wildflower lists be developed for each agroecosystem with pollination insecurity. Breeding and artificial selection programs may even promote plant traits that increase their utility to pollinators, potentially allowing habitat managers to increase the per unit area efficiency of pollinator plantings.

1.6. The Impact of Floral Resources on Bee Communities

1.6.1. Wild Bee Communities

Oligolectic bees, those that are reliant on a small subset of related flower species for pollen and nectar, are the model organisms for studies of floral limitation. Because of the narrow niche occupied by specialist bees, their host plants can be readily identified and manipulated to facilitate experimentation. They offer a starting point for understanding the relationship between bee abundances and floral resources. One specialist bee, *Andrena hattorfiana,* is more abundant with increased abundance of its preferred plant species within its foraging range (Larsson & Franzén 2006) and for some solitary bees, abundant suitable blooming resources located within a short distance from the nest are crucial for reproductive success (Zurbuchen et al. 2010b). The reproductive success of female *Osmia lignaria* is correlated with distance to semi-natural habitat that contains its preferred flowers (Williams & Kremen 2007).

Flowering phenology of host plants exhibits a significant influence on associated pollinators. The phenology of the sunflower specialist, *Dieunomia triangulifera*, closely tracks the bloom of its primary host plant, *Helianthus annuus* (Minckley et al. 1994). A recent study of alternate year mass flowering resources found that while a social bee taxon (*Bombus* spp.) responded within-season to mass flowering resources by producing greater numbers of workers, a solitary bee taxon (*Anthophora* spp.) only exhibited population level increases in the following year (Crone 2013).

More difficult to assess, but also more applied considering agricultural demands, is the relationship between floral resources and bee communities as a whole. In Switzerland, Albrecht et al. (2007) assessed the effectiveness of a widely adopted agro-environmental scheme, Ecological Compensation Areas (ECAs), which consist of orchards, hay meadows, flower strips, and hedges. Higher species richness and abundance of both large and small-bodied bees was associated with the presence of ECAs more than the proportion of nearby intensively managed meadows. A paired study found that in Germany and Switzerland, agricultural fields incorporating agro-environmental schemes supported greater abundance and diversity of bees than similar fields without plantings (Kleijn et al. 2006).

The exact mechanics of what drives bee population responses likely varies between systems. One driver is floral diversity and nectar quality, which have an additive effect on bee species richness (Potts et al. 2003). Others have found that bee abundance and richness are best explained by differences in floral cover (Batáry et al. 2010) or floral diversity (Steffan-Dewenter & Tscharntke 2001). In almond orchards, flowering ground covers support a greater richness of wild bees (Saunders et al. 2013). Overall, surrounding landscape quality has a positive influence on bee populations. This effect is stronger at low quality sites (Kennedy et al. 2013).

Agro-environmental schemes aimed at enhancing pollinator populations do not always succeed in increasing bee diversity or species richness. While habitat enhancement schemes are associated with greater bee diversity in Germany and Switzerland, an international study did not find the same relationship in the Netherlands, Spain, or the UK (Kleijn et al. 2006) and Kleijn et al. (2001) found little evidence supporting the benefits of agro-environmental schemes in Dutch landscapes. Few studies have considered the influence of habitat enhancement quality on success but this author has found that successfully establishing small seeded perennial wildflowers is often outside of the realm of experience of farmers. Poorly established mixes are likely to exert less positive influence on the bee community.

The influence of habitat complexity and landscape context on bee communities has been studied extensively (Carvalheiro et al. 2010, Nicholls & Altieri 2012, Persson & Smith 2013, Smukler et al. 2010) but many of the underlying mechanisms are far from clear. One study counted the number of ground nesting bees on farms ‘near’ to natural habitat relative to those found nesting on farms classified as ‘far’ from natural habitat (Kim et al. 2006). Near farms had higher nest densities. This suggests either that nearby floral and nesting resources increase bee abundance, or that these areas are simply aggregating bees from the surrounding landscape and functioning as sinks in a source—sink dynamic. Likewise, the discovery that orchards in Wisconsin surrounded by a greater proportion of forest maintain higher wild bee richness and abundances (Watson et al. 2011) could be explained by either mechanism. According to one study, natural habitat without concurrent pollinator-friendly management practices does not result in greater bee abundances (Andersson et al. 2014), suggesting that in some areas intensively managed fields may act as negative sinks, such that enhancement activities are ineffective. The proportion of surrounding natural habitat is commonly thought to influence bee abundance and diversity, but an alternative explanation is that habitat homogeneity covaries with the intensity of management in agriculturally intensified landscapes where pesticide applications (Brittain et al. 2010) and tillage practices (Shuler et al. 2005) are destructive forces.

A number of meta-analyses have increased our basic understanding of bee communities and how they respond to habitat change. Overwhelmingly, fields with sown wildflower strips are associated with greater abundances of pollinators (Scheper et al. 2013); however, the methods of Kleijn et al. (2006) were used to vet studies suitable for inclusion in this meta-analysis and so described ‘abundances’ are may be the effects of aggregation rather than population increase. To support this further, Scheper et al. (2013) found that agro-environmental schemes did not affect local pollinator abundances in cleared landscapes, possibly because there were so few pollinators in the landscape that pollinators did not aggregate sufficiently for statistical detection.

A growing body of literature supports the general consensus that the proportion of natural habitat within 1-2000 meters is highly correlated with pollinator richness (Ricketts et al. 2008), although appropriate scaling varies with the typical foraging distance of the bee in question (Murray et al. 2009, Tscharntke & Brandl 2004). For example, in Indiana, visitation rates by wild bees on cucumber were highest when natural habitat within 250 m was maximized (Smith et al. 2013). The use of these map-based analyses of habitat components are effective tools for accurately predicting bee populations in agricultural areas (Lonsdorf et al. 2009) and some models can explain as much as 49% of the variation in bee abundance (Chapin 2014). The latter is based on an informed optimization INvest model that predicts bee abundance in Maine blueberry fields. These predictions of pollinator abundance can be overlaid with agricultural demand for pollination to identify areas that could benefit the most from pollinator habitat enhancements (Schulp et al. 2014).

A recent synthesis by Kennedy et al. (2013) suggests that high quality pollinator habitat is more important in large monocultures. As the number and size of monocultures increases around the country, pollinator communities [and pollination services] on farmland will be greatly reduced. Further work that examines the mechanisms influencing pollinator communities specific to each pollinator-dependent crop will provide farmers the tools necessary to make appropriate pollinator habitat management decisions on their farms.

1.6.2. Bumble Bees

In Europe, bumble bee declines are well documented (Carvell et al. 2006a, Goulson et al. 2008, Rasmont et al. 2005, Williams 1982). In North America pollinator communities are shifting, several *Bombus* species have declined catastrophically since the 1990s (Goulson et al. 2008) while other species are increasing in number (Bushmann et al. 2012). Eleven out of thirteen *Bombus* species in Ontario significantly decreased over a 35 year period ending in 2006 (Colla & Packer 2008) and bumble bee surveys in the United States report declines of *Bombus terricola, Bombus occidentalis* and the possible extinction of *B. franklini* (Spivak et al. 2011). Last, in January of 2013 the Xerces Society filed a petition to the USFWS seeking Endangered Species Act protection for the increasingly rare rusty-patched bumble bee (*B. affinis*).

In the face of these declines, lawmakers in Europe and more recently in the United States are taking steps to conserve this highly valued taxon. Partly due to this financial support, a large body of work has explored the influence of floral resources and habitat enhancements on bumble bees. Most have simply compared bumble bee abundances between grassy agricultural margins or other non-improved habitat to sown strips of pollen and nectar rich forage mixes (Carvell 2004, Carvell et al. 2006b, Pywell et al. 2006). Not surprisingly, the wildflowers strips attracted greater abundances of pollinators. This however, should not be taken as proof of conservation value. These resources may simply be attracting bees from the surrounding landscape instead of increasing their population size. Addressing this gap, Wood et al. (2015) used microsatellite loci and transect walks to compare the population sizes of common bumble bee species between farms with bee pasture (on average 13 acres, making up 2% of the farm area for at least 3 years) and farms with no bee pasture. They found that across all bumble bee species, nest densities were significantly greater at bee pasture sites.

Some researchers have found that bumble bees are influenced by floral abundances on a local scale. In several naturally occurring meadows, the number of *Bombus* gynes recorded was correlated with the overall floral abundance (Bowers 1986). Using commercial colony weight as a proxy for colony success, Goulson et al. (2002) found that *B. terrestris* gained more weight after foraging in suburban habitats with an abundance of forage than in 'enhanced' agricultural landscapes or conventional farmland. Bumble bee abundance in agricultural landscapes is tied to the floral resources that within them (Greenleaf & Kremen 2006a).

Bumble bee population level abundance is more strongly correlated with landscape level variables than floral resources on a local scale. Nearby mass flowering crops (MFCs) can enhance bumble bee densities (Heard et al. 2007, Westphal et al. 2003) especially immediately prior to or following the mass flowering event (Kovacs-Hostyanszki et al. 2013). Meaningful interpretations of these data are hindered by the relative paucity of floral resources in mass flowering landscapes; where resources suddenly become limiting, pollinators will aggregate around the only available food sources. Differences in observed density may be more attributable to great inter-seasonal fluctuations in flowering resources than the presence of

MFCs. Interestingly, a study using micro-satellite markers found that while *Bombus pascuorum* colony density did not increase near MFCs, the number of workers did (Herrmann et al. 2007). This may indicate that early flowering MFCs (samples were taken months after mass flowering events) can increase colony development, but not the production of gynes and drones. These findings are supported by Crone (2013) who found that bumble bees produced more workers in response to mass flowering but not more gynes or drones. Further, despite high rates of early season colony growth, bumble bees in simple landscapes with MFCs produced fewer reproductives than those in more complex landscapes (Persson & Smith 2013).

Goulson et al. (2010) used a micro-satellite technique to determine colony number and subsequent colony-level abundance and found that the area of gardens within 750 meters predicted the proportion of *B. pascuorum* colonies surviving into the late season. *B. lapidarius* nest survival was most strongly correlated to the area of gardens within 1000 meters. Their findings suggest that small areas of nearby floral resources can have a positive effect on colony survival that is likely a more important measure of colony success than colony size. Similar studies found that 72% of the variation in nest densities was explained by field bean, oilseed rape, and non-crop areas (Knight et al. 2009) and that the quantity of floral resources within 2 km of *Bombus vosnesenskii* colonies predicted worker and male but not gyne production (Williams et al. 2012). In analysis of the latter study, floral resources furthest from the colony were weighted less than those closer. None of these studies manipulate local floral abundances and so the bumble bee population studied presumably follows a relatively unpredictable dynamic equilibrium. As such, the bumble bee population in these landscapes is already established and has no experimentally controlled reason to increase or decrease. In such an environment, the greatest colony fitness may not be the production of more gynes. If a gyne fails to establish her colony—potentially highly likely in a colony-saturated landscape—she will confer zero fitness to the mother colony. The greatest chance of reproductive success, and an outlet for resource rich colonies, may be the increased production of drones.

There is a need to identify those factors that influence the number of gynes bumble bee colonies produce. Likewise, research into other aspects of bumble bee population success is needed. For example, what proportion of gynes overwinters successfully and establishes new colonies in the spring? Can a greater abundance of late season flowering plants alter their overwintering survival? What types of habitat manipulations have the greatest influence on the numbers of bumble bee colonies in the landscape?

1.7. The Impacts of Floral Resources on Pollination Services

1.7.1. Does Bee Pasture Increase Crop Yields or Profits?

Studies that directly link pollinator plantings or bee pasture to increases in yield or profits are rare. Carvalheiro et al. (2012) planted Native Flower Compensation Areas (NFCAs) and found that their presence in South African mango orchards significantly increased flower visitors and yields in adjacent mango fields, but they also found that distance to natural habitat was a stronger predictor. These findings are supported in part by Klein et al. (2012) who found that strips of natural vegetation in isolated almond orchards increased visitation frequency to almond flowers. They were not able to show a subsequent increase in fruit set or yield but attributed this to the possible poor quality of floral resources in the natural vegetation strips. While naturally regenerating margins can confer benefits (Kells et al. 2001), margins sown with pollen and nectar rich wildflowers are more attractive (Pywell et al. 2006) and offer a greater density of resources, thereby presumably conferring a greater benefit to bee populations per unit area. In another study, researchers installed flowering strips in highbush blueberry crop margins and found that yields were greater with increasing proximity to wildflower plantings but could not sufficiently determine if plantings aggregated pollinators or increased local populations (Blaauw & Isaacs 2014. These authors also considered the costs and benefits of pollinator habitat enhancement and concluded that the time to profit from bee pasture was 3 and 4-5 years with and without a government subsidy, respectively. The dearth of literature that links pollinator plantings to crop yields is disconcerting. It is possible that research has been completed and left unpublished that contradicts the hoped for hypothesis of most pollination biologists. The linkage between pollinator plantings and yield merits further study.

1.7.2. The Influence of Habitat Complexity on Pollination Services

A growing body of evidence supports the hypothesis that pollinator habitat on a landscape scale is more likely than local floral resources to influence pollination services (Gemmill-Herren & Ochieng 2008, Steffan-Dewenter & Tscharntke 1999). For example, the proportion of high diversity bee habitat within 1 km around cherry orchards is correlated with higher rates of wild bee visitation and fruit set (Holzschuh et al. 2012). A similar study in the tropics found a positive relationship between proximity to rainforest and fruit set (Blanche et al. 2006). Likewise in California, Kremen et al. (2004) found that crop pollination services were predicted by the proportion of upland natural habitat within 1-1.25 km of the crop field.

Reviews of the literature suggest that the proportion of natural habitat to crop field is strongly correlated with visitation rates and species richness, is more pronounced in tropical versus temperate climes, and has a greater effect on social than solitary bees (Ricketts et al. 2008). Furthermore, the inverse of the temporal and spatial variability of pollination services (stability)—often suggested as a factor limiting the practicality of using wild bees for crop pollination—also declines significantly in crop fields more isolated from natural habitats (Garibaldi et al. 2011a). Globally, increased acreages of pollinator-dependent crops do not cause proportional increases in yields. This is attributed to unstable pollination services (Garibaldi et al. 2011b). In fact, as acreages increase, habitat homogeneity and isolation of crop fields from natural sources of pollinators also increase, exacerbating the shortage of wild pollinators, decreasing stability and perpetuating a negative feedback loop. One study quantified marginal losses to coffee farmers from decreased pollination services due to deforestation and found that they ranged from $0 to $700 (U.S.) per ha (Ricketts and Lonsdorf 2013).

Some studies offer examples of exceptions to the general rule that greater pollination services are found where the proportion of natural habitat is greatest. Williams & Winfree (2013) found diverse assemblages of pollinators even in isolated forest fragments. The size and light levels of forest patches most accurately predicted the level of pollination services found there, suggesting that habitat arrangement and other factors may be useful tools for understanding the role of habitat complexity in crop pollination services. In Argentine grapefruit plantations, pollinator visitation, but not yields, decreased 50% when forest fragments were over 1 km distant (Chacoff et al. 2008). Winfree et al. (2008) were unable to relate the level of pollination services to any of their variables including proportion of surrounding natural habitat. Realistically, relationships between pollinator and landscapes are site-specific, although it is possible to generalize the dynamic within specific agroecosystems. For example Chapin (2014) used an INVEST model to reliably predict up to 48% of the variance in native bee abundance in Maine’s lowbush blueberry agroecosystem.

These findings indicate problems with the general assumption that the proportion of natural habitat in landscapes around crop fields is predictive of pollination services. First, the definition of “natural habitat” is an open one and changes drastically from system to system and from study to study. In temperate regions for example, ‘natural habitats’ of coniferous woodlands do not offer many floral resources but in the spring, wetland or deciduous patches could be associated with greater numbers of pollinators. In some areas, landscape heterogeneity may be great enough that it is not the most limiting factor (Winfree et al. 2008).

1.8. The Impact of Bee Communities on Pollination Services

The positive relationship between the pollinator community and pollination services in crop fields has also been well demonstrated (James & Pitts-Singer 2008). Some researchers have even found that the wild bee community alone offers much stronger links to fruit set and yield than abundance of honey bees (Garibaldi et al. 2013). Theory offers that interaction frequency between bees and inflorescences is more important than the diversity of flower visitors (Vázquez et al. 2005) but the reality is more complex. A clear link between diversity and fruit set has been repeatedly experimentally demonstrated (Garibaldi et al. 2013, Winfree et al. 2007). The honey bee is often considered the most important, the most abundant and often the most frequent flower visitor in agricultural systems. It does not however, provide the majority of pollination in world crops (Garibaldi et al. 2013) although there are many examples where it does. When we consider large and intensive agricultural systems alone, the honey bee may be responsible for a larger proportion of crop pollination.

Although some studies suggest that bee abundance is related to crop production (Morandin & Winston 2005), bee species richness often emerges as the key factor. Klein et al. (2003) illustrate the relationship between bee species richness and fruit set in coffee plantations. Over 24 study sites in Indonesia had fruit set measurements ranging from 60 to 90%. The proportion of set fruit was positively related to bee species richness that ranged from a low of three species to a high of twenty. Interestingly, twenty pollinating bee species also caused sufficient fruit set in California watermelon fields and higher species richness dampened inter-annual fluctuations in abundance (Kremen et al. 2002). Wild bee richness is linked to higher production in sunflower (Greenleaf & Kremen 2006b), coffee (Klein et al. 2003, Vergara & Badano 2009), blueberry (Bushmann & Drummond 2015) and a multitude of other crops (Garibaldi et al. 2013). However, true bee species abundance is more variable than species richness and much more difficult to experimentally measure. Richness may so often emerge as a significant factor in studies not because it is a stronger driver, but because it is more experimentally detectable.

More specialized crops probably rely on robust populations of a lower diversity of pollinators. Tomatoes, like many other Solanaceous crops, release much more pollen when buzz pollinated, a service that is provided by only a subset of the bee community. In California, the size of tomatoes was enhanced by wild bees (Greenleaf & Kremen 2006a), but only five genera comprised all of the wild bee visitors. Some evidence suggests that the interactions between bee species can increase pollination efficacy and fruit set (Brittain et al. 2013b, Greenleaf & Kremen 2006b). Once an inflorescence is visited by a buzz pollinator and has released a quantity of pollen, more pollen would be picked up and transported by less effective pollinators on subsequent visits (Drummond, personal communication). The findings of Hoehn et al. (2008) offer correlative evidence that the number of bee species and also functional guilds increase seed set of pumpkins. Mechanistic explanations of this common relationship include increased movement between capitula (Greenleaf & Kremen 2006), differences between bee usage of flower parts (Klein et al. 2009), spatially mediated resource partitioning (Brittain, Kremen & Klein 2013), decreased temporal and spatial variation in pollinator abundances (Hoehn et al. 2008, Kremen et al. 2002) or increased resistance to environmental disturbance (Klein et al. 2009). Healthier wild bee communities can increase fruit set directly, but also indirectly, by increasing the efficacy of rented or commercially managed pollinators through synergisms.

1.9. What is the Ideal Bee Pasture-to-Crop Ratio?

How much bee pasture is needed to sufficiently enhance pollinator populations? A number of pollinator planting fact sheets and bulletins recommend that 30% of farmland be maintained as natural habitat (Vaughan et al. 2007). When 25-30% of the landscape within 750-1000 m of the crop field is natural habitat, 100% of crop pollination needs are met in watermelon fields (Kremen et al. 2002), the profitability of canola is significantly increased (Morandin & Winston 2006), and bee populations are maintained over time (Banaszak 1992). While extremely useful, this estimate is based on "natural habitat" not enhanced floral patches, or bee pasture. Successfully established bee pastures should provide an unnaturally high density of floral resources. While the best ratio of bee pasture to crop is unknown, it is likely significantly lower than the above estimate. There is no empirically based recommendation for the proportion of bee pasture to crop, but appropriate size likely depends on the cropping system, the effectiveness of the planted flower mixture, the location and spatial distribution of flower patches in the landscape, the proportion of surrounding natural habitat, and a number of other unidentified factors. Future research should attempt to identify the appropriate sizes of bee pasture for effective pollinator habitat enhancement in a variety of pollinator-dependent cropping systems.

1.10. Methods for Surveying Wild Bee Populations

The language in many peer-reviewed studies implies a bee population-level dependent variable responding to a change in floral resources. In reality, many of these researchers use visitation rates or otherwise observe bees in enhancement plantings and use this metric as a proxy for population-level change or pollination services (Korpela et al. 2013, Varah et al. 2013). This approach is problematic. "Abundance," as measured by visitation rates or the numbers of bees observed during a transect walk within a planting, can estimate the attractiveness of a habitat enhancement to bees. It indicates less about landscape-level abundance or population-level change, which is the bottom line of most bee conservation schemes. The number of bees observed foraging on a given day varies with weather (Peat & Goulson 2005, Vicens & Bosch 2000), seasonal fluctuations in plant density (Persson & Smith 2013), and a number of other factors unrelated to absolute density. Also, when samples are taken or observations made from within planted bee pasture, results may be attributed to aggregation around a resource rather than population level responses. Visitation rates within plantings are important for "side by side" comparisons of which plants are most utilized by bees, but as stand-alone metrics they should not be construed as measures of the effectiveness of pollinator habitat enhancement. Other sampling methods, particularly those that quantify change over time, are more indicative of population-level responses. However, if researchers use these sampling methods to produce rarefaction curves of species richness that asymptote, conclusions about changes in diversity over time would be valid (Bushmann 2013).

1.10.1. Social Bees

Potentially a more direct method to estimate the number of reproductive units—not only a measure of population but of future population increases—is through the use of molecular data. This method only applies to social insects and has been employed to estimate bumble bee nest density (Herrmann et al. 2007, Rao & Strange 2012, Teruyoshi & Hiroki 2009, Wood et al. 2015) and honey bee hive density and genetic diversity (Jaffé et al. 2010). Genetic tests can estimate the number of genetically distinct colonies in a landscape, a unit of measurement that is directly related to effective population size for a social organism. This approach is also not without problems. These problems include queen multiple mating, incorrect assignment of sister-pair status, the amount of differential selection among years, genotypic dependent dispersal, and the low genetic diversity of some species (Rao & Strange 2012). Molecular techniques depend on the flight activity of workers that is influenced by weather, colony dynamics, and is likely described by an aggregate distribution. Goulson et al. (2002) measured the impact of floral resources on bumble bee colonies by quantifying the weight gained per commercial colony across a range of floral resource treatments. Colony weight is often used as a proxy for colony success (Gels et al. 2002, Whitehorn et al. 2012) but the weight of managed colonies may be a poor indicator of wild colony success and may or may not be related to the production of new gynes or fitness. Fitness is best captured by the number of successfully established colonies in the year following a habitat manipulation.

Another possible method for bumble bee colony counts is the use of scent detection dogs. Detection dogs have been used by the military to detect bombs and other threats. Their use in wildlife research is relatively recent and in many cases, extremely successful. Dogs have been successfully used to detect termite infestations, survey populations of grizzly, lynx, fishers (Long et al. 2007), and even egg masses of the invasive gypsy moth (Brooks et al. 2003). Use in bumble bee colony detection is only recorded in two related articles. One detection dog located 100% of buried nesting material with zero false positives (controls) in a trial and 33 nests in twelve 500-meter transects in the field—overall an excellent candidate for research use (Waters et al. 2010). In a related study, a second detection dog was much less effective with only a 62.5% success rate and 5 false positives. The authors concluded that human searchers are more efficient (O'Connor et al. 2012). Based on these studies, and the use of dogs in other wildlife research, scent-detection dogs can be used for bumble bee colony estimates, but with caution. Even the best wildlife surveys often provide only a relative density estimate. Provided that individual detection dogs are consistent within studies, and that care is taken when making comparisons across different detection dogs, they may be a promising tool in future bumble bee population estimates.

1.10.2. Solitary Bees

Mark-recapture is a well-established procedure for estimating wildlife populations. Considering the size limitations of mark-recapture study organisms, it is perhaps surprising that one of the first study subjects was the tsetse fly (Jackson 1933). This technique has since expanded and is now used on virtually every study organism large enough to mark. Bees are challenging subjects, but researchers are creative and a number of studies have successfully implemented mark-recapture techniques on bee populations (Bischoff 2003, Peakall & Schiestl 2014, Steffan-Dewenter & Schiele 2004, Zurbuchen et al. 2010a). If mark-recapture experiments are repeated on the same population multiple times, researchers can estimate not only population size, but also survivorship, dispersal, and even the flow of bee-mediated pollen transfer (Peakall & Schiestl 2014). Mark-recapture studies of bee populations are most informative and practical when flight ranges of the study subject are relatively small. It is much more difficult to re-capture bees in an unbiased manner, i.e. unrelated to distance from capture, as they may forage over several square kilometers (e.g., bumble bees) (Westphal et al. 2003).

Other authors have investigated the effects of habitat manipulations on the generally smaller-bodied solitary bees. Trap-nesting is a method commonly used to compare populations of stem-nesting bees (Baños-Picón et al. 2013, Gathmann et al. 1994, Klein et al. 2002). Using trap nests, Gathmann et al. (1994) concluded that naturally regenerating fallow fields exhibited much greater bee species richness than cropped fields. Also, older set-aside fields supported greater bee species richness and a wider variety of differently sized species, lending credence to the idea that areas of impoverished flora preferentially support large-bodied bees able to access resources at great distances. Similarly, wildflower strips containing greater floral diversity supported greater abundance and diversity of trap-nesting bees (Fabian 2013, Fabian et al. 2013). Stubbs & Drummond (2004) surveyed cavity nesters using trap nests and found that by providing artificial wooden blocks for nesting, populations of cavity nesters increased. This last study reveals a shortcoming of trap nest surveys. In habitats already rich with nest sites, trap nesting would represent a much smaller proportion of the population than in habitats where nest sites are limiting (Sheffield et al. 2012). Trap nesting can therefore only serve as an estimate of relative density that cannot easily distinguish between an abundance of cavity nesting bees and a paucity of nearby nest sites. As with any survey method, this one excludes certain parts of the bee community—in this case, ground-nesting and social bees. It is however, a method that offers scientists a non-invasive sampling technique (trapped bees can be released into the environment following a census) where other methods may decrease ability to detect population increases by collecting reproductive females. Trap-nesting also provides direct counts of the number of reproductive individuals produced per cavity.

In California, Kim et al. (2006) surveyed ground-nesting bees by placing floating row covers over randomly chosen patches at night. A similar method was tested by Drummond and Stubbs (1997) in lowbush blueberry. Bees leaving the nests in the morning to forage were captured under the row covers and sampled the following morning. The authors provide a graph of the relationship between bee species richness and sampling intensity of this method. This method is likely only applicable to areas with short and uniform vegetation (e.g., turfgrass and crop fields). It would be much more difficult to employ in forest or heathland habitats.

1.10.3. Bee Community Measures

This review of methods is primarily focused on techniques for measuring population level change, a metric not often included in pollinator habitat enhancement studies. This brief summary presents some of the methods used to measure not abundance, but richness, diversity, and evenness. To achieve the high level of species resolution required for community analyses these methods must necessarily involve collecting specimens to later be identified with a microscope. One of the best methods for easily collecting large numbers of wild bee specimens is the bowl trap, widely popularized and streamlined by Sam Droege's baseline wild bee monitoring programs (Droege et al. 2010). Bowl traps attract bees to pans of soapy water, where they climb in and drown. As such, they are limited to collecting only bees that are attracted to the traps. Colors, especially in the ultra-violet range, influence capture (Droege 2002) and so researchers use multiple colors or include equal sampling effort of other techniques (e.g., netting) to account for any sampling bias (Cane et al. 2000, Droege et al. 2003). Other methods of sampling bee communities include hand capturing directly into specimen tubes, malaise traps (Bartholomew & Prowell 2005, Drummond & Stubbs 1997), flight-intercept traps, canopy fogging, sweep netting (Noyes 1989), line-transect counts, emergence traps, and visual plot counts (Drummond & Stubbs 1997). Some of the methods here may also serve as proxies or estimators of abundance in some systems. For example, visual plot counts are thought to be the most efficient method for estimating the abundance of blueberry flower visitors during lowbush blueberry bloom (Bushmann & Drummond 2015, Drummond & Stubbs 1997). Most "bee sampling methods" papers recommend a combination of sampling methodologies to minimize the inherent bias of any one method.

Table 1.2. Application and shortcomings of selected bee sampling procedures.

Sampling Method	Application	Shortcomings
Visitation Rates/Visual Plot Counts	- In conjunction with species rarefaction curves, useful for comparing community data between sites or over time - An excellent choice when comparing the attractiveness of co-blooming floral resources - In some cases (within the crop field) is a proxy for abundance	- Neither an estimator nor an accurate index of abundance or population growth - Controls or corrects for floral density and patch size - Underestimates small fast flying species - Some observers are much more adept at bee ID than others
Genetic Markers	- Social bee population abundance, colony survivorship	- Expense - Availability of molecular markers - Less useful if population inbreeding is high
Detection Dogs	- Bumble bee population abundance, colony survivorship	- Has not been tested on any other types of bees. Detection accuracy and ability of individual dogs varies greatly
Mark-Recapture	- Single species abundance, population change over time, survivorship, flight period phenology	- Estimates the number of individuals, not just the number of colonies - Best used for solitary bees or spring nest-searching queens - Difficult to use for bees with large foraging range - May interfere with flight, or impact bees in other, unknown ways
Trap Nesting	- Index of cavity and stem nesters abundance, inter-annual population change, community composition of cavity and stem nesters	- Applicable only to those bees (*Osmia spp.*, *Megachile spp.,* limited Halictidae and Colletidae) which readily occupy trap nests - May be heavily influenced by the availability of natural nesting sites in the landscape
Floating Row Covers	- Community richness, diversity, and abundance of ground nesting bees, single species/functional guild population change over time - Could accurately assess survivorship in conjunction with mark-recapture studies	- Difficult in sparsely populated landscapes - Applicable only to ground nesters - Requires large sample sizes if community exhibits a highly aggregate distribution - Restricted to habitats with low growing or no vegetation
Bee bowls	- Baseline richness and diversity sampling, best in landscapes without an abundance of floral resources - Studies where high capture volume is required	- Selects for subsets of the bee population - For improved census, combine with other methods - Destructive sampling
Malaise and flight intercept traps	- Baseline richness and diversity in densely flowering landscapes - Studies using long-term monitoring	- Less efficient than pan trapping - Destructive sampling - Does not rely on attractiveness to capture bees

1.11. Conclusions and Limitations

Based on the literature, it seems likely that intentionally sown bee pasture in and around agricultural fields could result in greater pollination services provided by native and wild bees. Additional research to determine the impact of pollinator plantings on bee communities is needed (Carvalheiro et al. 2012, Gill 2013), but floral resources (Kennedy et al. 2013, Larsson & Franzén 2006, Williams & Kremen 2007) and natural habitat (Kim et al. 2006, Ricketts et al. 2008) can increase the abundance and diversity of pollinators. Greater abundances of wild and native bees often result in higher levels of pollination services (Garibaldi et al. 2013). Only one published study considered both the costs and benefits of bee pasture plants and presented their assessment of the time to reach positive profit (Blaauw & Isaacs 2014). A recent review highlights some of the same research gaps discussed here and recommends pollination strategies that combine single-species management and wild pollinator habitat enhancement (Garibaldi et al. 2014).

Pollinator species respond differently to floral resources. Some species increase in agricultural landscapes while others are more successful in natural habitats (Cariveau, Williams, Benjamin & Winfree 2013). Floral diversity benefits wild bees (Jha & Kremen 2013, Potts et al. 2003), but floral density and overall flower abundance might be the most important driver of pollinator abundance (Dauber et al. 2010, Herrmann et al. 2007, Power & Stout 2011, Westphal et al. 2003). Planted mixes should strive to incorporate a diverse mix of successional of bloom phenologies to ensure that plantings benefit bees across the whole season and address any gaps in site-specific bloom phenology. Flower morphology also selects for certain pollinator guilds. Most bee pasture strategies aim to include a diversity of floral morphologies to enhance a diverse assemblage of pollinators. An alternative strategy may be to target certain high-value pollinators by planting specific floral phenologies and morphologies to achieve crop pollination goals. Future reviews should compare and contrast flower species most appropriate for region and crop-specific habitat enhancement goals.

Bee populations exhibit a great degree of interannual variability. This inconsistency may limit the usefulness of pollinator habitat enhancements to growers. Ecological theory suggests that biodiversity buffers communities from perturbation (Bender et al. 1984); simulation modeling (Bartomeus et al. 2013) and applied pollination ecology research provides several examples (Brittain et al. 2013a, Ebeling et al. 2011, Rogers et al. 2014). However, is a biologically diverse pollinator assemblage sufficient to dampen severe interannual fluctuations in the pollinator community that may be due to weather, interannual floral dynamics, or other factors? Additional research that increases understanding of pollination population dynamics (Crone 2013) may help to shed light on this important topic.

A growing body of research supports the hypothesis that landsape level habitat types are a crucial component of pollinator population dynamics (Ricketts et al. 2008). The proportion of “natural habitat” (Carvelheiro et al. 2010, Greenleaf & Kremen 2006a, Holzschuh et al 2012), or areas rich with flowering resources (Williams & Kremen 2007) act positively on pollinator populations. Continued research on this topic should increase the resolution of our understanding of these dynamics. For example, which bee species or functional guilds are associated with each distinct habitat type? Further, some work suggests that the shape and arrangement of habitats in the surrounding landscape can influence population dynamics (Fabian et al. 2013). These types of relationships should be elucidated for specific agro-ecosystems so that bee conservationists and farmers alike can assess pollinator habitat within a landscape. Computer similation models (i.e. INvest) may offer useful tools (Chapin 2014) and may be improved by factoring in the effects of spatial arrangement. Models designed within the context of specific agroecosystems may also be very effective tools in pollinator habitat enhancement plans — optimizing size, location, and even the shape of bee pasture plantings within a landscape, prior to breaking ground.

Landscape alterations, such as planting areas into resource-rich flowering meadows for bees, impact fauna in a number of unintended ways, both positive and negative. As national policies continue to encourage these plantings, and as more farmers understand the benefits of bee habitat management, researchers should seek to understand the non-target impacts of habitat manipulations. The benefits of flowering strips for natural enemies for example, are already well documented (Landis, Wratten, & Gurr 2000) and it is highly likely that bee pasture would enhance populations of a diversity of beneficial insects. What is less understood however, is the potential for a bee pasture to also benefit pest insects. While a number of studies have documented the interactions between flower plantings and both pests and beneficials, and suggest that enhanced natural enemy populations cause a net decrease in pest pressure (Blaauw & Isaacs 2012, Letourneau et al. 2011), more research should aim to identifly those plants in specific agroecosystems that are more likey to be utilized by beneficial insects than pests. Another possible consequence of bee pasture plantings is increased pathogen transmission via dense aggregations of pollinators occuring in bee pasture, as implied by the work of Durrer and Schmid-Hempel (1994). Recent research suggests that infected honey bees may transmit pathogens to wild bees (Furst et al. 2014), and that managed bumble bees can likewise transmit pathogens to wild congenerics (Murray et al. 2013),. The extent to which pathogen transmission occurs as a result of high density flower plantings requires further research (Bushmann 2013).

Even the best understood pollinator-plant relationships can vary greatly from one site to another. Research needs to focus on regional and crop-specific plants suitable to local agroecosystems, empirically test establishment methodologies, and trial the effectiveness of bee pasture in each pollinator-dependent agroecosystem. Based on such findings, farmers, crop consultants and Extension personnel can develop best management practices that increase or provide stability to crop pollination security.

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CHAPTER 2

BEE PASTURES FOR WILD BEES (HYMENOPTERA: APOIDEA) ENHANCEMENT: A STUDY OF ESTABLISHMENT, BEE VISITATION, AND UTILITY

2.1. Chapter Abstract

The protection and conservation of wild pollinators is increasingly used as a strategy for enhancing crop pollination. Bee pastures, densely planted areas of pollen and nectar-rich flowers, offer farm managers a viable option for increasing pollinator populations. Several studies have measured the attractiveness of flowers to bees, yet few have been designed to assess crop- and region-specific bee pasture plantings. This two-year study of bee pasture plantings at four sites in Maine assessed (1) factors that influence bee pasture establishment success, (2) flower visitors (3) and comparative utilities of sown clover, sown wildflower, and unsown naturally regenerating strips adjacent to wild blueberry fields (*Vaccinium angustifolium* Aiton). Last, (4) we measured the contribution of bee pasture to bumble bee pollen loads by contrasting bumble bee pollen load composition between treatment and control fields. Similar patterns of visitation to bee pasture are apparent among years. Analysis of visitation in the second year alone suggests that sown treatments supported 3-4 times more wild bee pollinators than naturally regenerating agricultural margins ($\chi^2 = 5.808$, $P = 0.055$). These differences are significant when wild bees are parsed into social and solitary groups. Social bees utilize clover plantings at a significantly greater rate than solitary bees ($\chi^2 = 7.269$, $P = 0.026$) and solitary bees use wildflower plantings over clover and naturally regenerating plots ($\chi^2 = 7.423$, $P = 0.024$). On average, across all blueberry fields sown with bee pasture, bumble bee pollen loads contained 37% bee pasture pollen. Our findings suggest that in Maine wild blueberry fields (*Vaccinium angustifolium* Aiton), even relatively small sown flowering strips provide over 1/3 of

the dietary pollen for localized bumble bees, clover plantings are highly utilized by bumble bees, and wildflower plantings show great potential to provision resources for solitary native bees.

2.2. Introduction

Both managed and unmanaged (hereafter referred to as wild) bees pollinate a significant proportion of the world's crops. By weight, 35% of food produced globally directly benefits from pollination (Klein et al. 2007) and 75% of the world's most valuable and productive crops benefit from insect-mediated pollination (Garibaldi et al. 2011). Although estimates vary, approximately one-tenth of the annual value of global food production is attributable to pollinators (Gallai et al. 2009). Historically, honey bees (*Apis mellifera*) were assumed to provide the bulk of this service—and still do in many highly intensive large-scale cropping systems, but wild bees also play an important role (Goulson 2003; Greenleaf & Kremen 2006). Recent studies suggest that overall, wild bees contribute more to pollination than honey bees (Garibaldi et al. 2013, Asare 2013).

In 2006 apiculturists in the United States experienced drastic hive losses, which scientists now largely agree is caused by a synergism of pests, diseases, pesticides, and overly intensive management practices (Drummond et al. 2012, Neumann & Carreck 2010, Kielmanowicz et al. 2015). These challenges make apiculture increasingly costly to both beekeepers and pollinator-dependent farmers. The problem is aggravated by higher demands for managed pollinators as more land is put into pollinator-dependent crops (Aizen & Harder 2009).

Maine's wild blueberry is a pollinator-dependent crop. Wild blueberry contributes $250 million to Maine's economy every year (Smith 2004) and is an important source of revenue for rural communities. On average, in 2014 wild blueberry growers stocked 1.34 honey bee hives per acre at a cost of $98.44/hive (Hoshide et al., In Review), compared to $40.00/hive in 2000 (Stubbs & Drummond 2001). When stocked at the recommended rate, honey bee rentals account for 35% of wild blueberry growers' total variable costs (Hoshide et al., In Review)**.**

These costs are causing growers to consider alternative modes of pollination. Some install nesting blocks around field perimeters to increase populations of leaf-cutter (*Megachile* spp.) and mason bees (*Osmia* spp.) (Stubbs et al. 1997; Stubbs & Drummond 2004, Rose et al. 2013), and roughly 30% purchase commercial colonies of bumble bees (*Bombus impatiens*) (Hanes et al. 2013). Although both methods enable growers to diversify their pollination portfolio, nesting blocks enhance only a small subset of wild pollinators, and commercially purchased bumble bee quads may vector diseases to wild populations (Colla et al. 2006, Graystock et al. 2013), outcompete native bumble bees, and possibly dilute the genetic diversity of wild conspecifics (Ings et al. 2006). See Bushmann et al. (2012) for a discussion of these possible interactions in wild blueberry.

Another alternative is increasing reliance on wild native, instead of alternative managed, pollinators. The wild bees associated with Maine's wild blueberry agroecosystem have been extensively documented. Stubbs et al. (1992) found 38 species of bees associated with wild blueberries. More recently, Jones et al. (2014) and Bushmann and Drummond (2015) suggest that this number is greater than 100 bee species (including kleptoparasites).

Farmers across the country are attempting to increase their wild bee populations by planting mixes of wildflowers, or bee pasture. Studies in the United Kingdom (Scheper et al. 2013) and continental Europe (Haaland et al. 2011) provide evidence that pollinator strips are attractive to bees and at least one study presents evidence that they can increase populations of bumble bees (Wood et al. 2015). Most pollinator habitat enhancement schemes to date are generalized, attempting to provide resources to wild bees as a whole. However, any set-aside strategy likely benefits only certain components of wild bee communities – which may or may not be crop pollinators (Sardinas & Kremen 2015). Seed mixes marketed for pollinator conservation are easily obtained from most seed companies but are not tailored to a specific crop's pollinators, phenology, and soils. Is a "Northeast Pollinator Mix" equally suitable for planting in shady apple orchards, fertile annual cropping fields, and in the acidic soils of blueberry barrens?

This paper presents the results of two related studies. The first assesses three different bee pastures for their use in one specific agroecosystem: the wild blueberry barrens of Maine. The second compares establishment methodologies for one of those bee pastures, a wildflower mix, in the same system. The primary objectives of this research were to (1) compare planting methodologies for a wildflower seed mix, (2) contrast the attractiveness of three different bee pastures (clovers, non-leguminous wildflowers, and natural regeneration flora from the existing seed bank) to wild and managed bees, (3) compare pollinator visitation rates to the most abundant sown wildflower species, (4) determine the proportion of sown bee pasture pollen in bumble bee pollen loads in treatment versus control fields, and (5) discuss the implications for pollinator habitat enhancement considering the establishment potential, floral density, and attractiveness of plantings.

2.3. Methods

2.3.1. Wildflower Mix Establishment

The wildflower mix establishment site was located at the University of Maine's wild blueberry research facility, Blueberry Hill Farm in Jonesboro, Washington Co., ME. To achieve a soil pH of 6.0 from a starting pH of 4.7 at the establishment site, on 18 May 2012, we applied 7846 kg/ha of lime using a Gandy^{TM} T36 drop spreader and incorporated with tillage to a depth of 7.5 cm. Shallow tillage was repeated on 31 May. On 8 July we raked the seedbed and broadcasted seed using an Earthway^{TM} hand crank seeder. Seeds were bulked with vermiculite to ensure an even distribution. Immediately after broadcasting, all plots were rolled with a 1.5 m wide 1,180 kg compacter. Plots were irrigated to receive 2.5 cm of rain per week. If rain fell equal to or in excess of 2.5 cm in a given week, no additional irrigation was applied.

Each of four replicates (statistical blocks) contained five treatment plots (4x8 m). Treatment 1 was an unsown rototilled control. All other treatments were seeded to the same mix of wildflowers. In addition to wildflower seed, treatment 2 was mowed monthly during the first year, and again once annually in October, treatment 3 was sown with a low density of sheep fescue, treatment 4 included both mowing and sheep fescue (*Festuca ovina*), and treatment 5 was seeded to the wildflower mix alone. Each treatment plot was split into two sub-plots. One sub-plot in each treatment plot was also sown with oats (*Avena sativa*). See Table 2.1 for a list of seed and seeding rates. Mowing was carried out with a line-trimmer, always cutting plants at 6-8 inches in height.

In September 2013, we randomly selected 0.5 m^2 from each sub-plot for cutting to assess plant biomass. All above-ground plant material in each sub-plot was cut, bagged by species, and dried for 2 weeks in a drying room (40-45 ºC) at the University of Maine Analytical Laboratory and Maine Soil Testing Service in Orono, ME. All plant material was identified, labeled as sown or unsown, and weighed. Opened, unopened, and past inflorescences were identified to species and recorded.

Table 2.1. List of sown species and seeding rates for wildflower and clover treatments.

Common Name	Species	Habit	No. live seeds/ sq foot	No. live seeds per acre
Wildflower Treatment				
Plains Coreopsis	*Coreopsis tinctoria*	Annual	9.55	416,000
Indian Blanket	*Gaillardia pulchella*	Annual	7.66	333,600
Sunflower	*Helianthus annuus*	Annual	2.75	120,000
Lavender Hyssop	*Agastache foeniculum*	Perennial	5.29	230,400
Lance-Leaved Coreopsis	*Coreopsis lanceolata*	Perennial	5.79	252,000
Canada Tick Trefoil	*Desmodium canadense*	Perennial	1.82	79,200
Purple Coneflower	*Echinacea purpurea*	Perennial	4.69	204,400
Common Boneset	*Eupatorium perfoliatum*	Perennial	3.53	153,600
Bergamot	*Monarda fistulosa*	Perennial	4.01	174,720
New-England Aster	*Symphyotrichum novae-angliae*	Perennial	4.52	196,800
		Total Wildflower →	**49.60**	**2,160,720**
Clover Treatment			**lbs/acre**	**Price $/lb**
Crimson Clover	*Trifolium incarnatum*	Annual	7.00	7.95
Medium Red Clover	*Trifolium pratense*	Perennial (short-lived)	5.00	9.50
Sweet Yellow Clover	*Melilotus officinalis*	Biennial	6.00	8.20
		Total Clover →	**18.00**	**25.65**

The number of live seeds/ft^2 is unavailable for clover seeds. Not shown is a nurse crop of *Avena sativa*. Clover pricing is from Johnny’s Selected Seeds 2012 prices. Wildflower statistics shown are supplied by Diane Wilson at Applewood Seed Company. All seeds are organically certified.

2.3.2. Wildflower Mix, Clover, and Naturally Regenerating Bee Pasture

2.3.2.1. Site Location and Preparation

In June 2012, we established bee pastures at four sites in Maine. Two are owned and operated by commercial wild blueberry growers in Blue Hill, Hancock Co., Maine. The third, Blueberry Hill in Jonesboro, Washington Co., Maine, is the University of Maine’s Wild Blueberry

Research Farm. A fourth site, the University of Maine's Rogers Farm Forage and Crop Research Facility in Stillwater, Penobscot Co., Maine, is comprised of hay pasture, annual grains and mixed vegetables. Rogers Farm characterizes the landscape that surrounds wild blueberry fields in the central coast blueberry production region of Maine (Yarborough 2009). All treatment site blueberry fields (n=3) excepting Rogers Farm were paired with a control blueberry field (n=3); a nearby (<20 km), similarly managed wild blueberry field without bee pasture treatments.

Between 18 May and 1 June 2012, we prepared seed beds using the methods of Mader et al. (2011) and Blaauw and Isaacs (2014). Lime was applied to raise pH to 6.0 according to the recommendations of the University of Maine's Soil Testing Service. We implemented a "stale seedbed" practice to all plots. Seeds were broadcast over a smoothly raked seedbed using an Earthway^{TM} hand crank seeder. We bulked wildflower seed with horticultural grade vermiculite 6:1 and clover seed to vermiculite 14:1. Oats were hand broadcast as a nurse crop in the wildflower treatment only. After sowing, we compacted the soil in plots with a weighted roller. Planting dates ranged from 8 June to 20 June 2012. During establishment, plots were watered as needed. Weeds were controlled during the first year with a line-trimmer when weeds were significantly taller than seedlings, except in regeneration plots.

The planted area at each treatment site included three treatments: natural regeneration, clovers, and wildflowers. Each of the three bee pasture treatments within a site measured 3.3 x 50.0 m. Natural regeneration treatments were established and maintained following the same methodology as the other two treatments except they were not sown with seeds or mowed, and all emerging flowering plants originated from the existing seed bank. For a list of sown species and seeding rates see Table 2.1.

2.3.2.2. Bee Visitation

Bee pasture plots were sown in 2012, but did not fully establish until 2013. Bee visitation sampling was initiated late in 2012 when flowers started to bloom. Observations in 2012 were limited to Rogers Farm and Blueberry Hill Farm (two of four treatment sites). Rogers Farm was sampled on 20 and 23 August; Blueberry Hill Farm was sampled on 23 July, 6 August, and 13 September. In both years, we observed flower visitors on the three most dominant blooming species within each treatment. Three representative 1.0 m^2 patches of each flower species were observed for 1-minute periods, for a total of nine minutes per treatment per sampling date. To avoid edge effects, all 1.0 m^2 quadrats were 1.0 meter from the plot edge. When treatments contained fewer than three blooming species, we apportioned observations according to floral abundance. For example, when *Melilotus officinalis* was the sole species blooming in the clover treatment, we conducted nine separate 1-minute observations on *M. officinalis*. In 2013, trained observers recorded bees visiting bee pasture flowers every 2-3 weeks from June to September 2013, except during wild blueberry harvest in mid-late August.

Flower visitors were identified to morpho-species that included bumble bee, orange-belted bumble bee (*Bombus ternarius*), Megachilidae, honey bee, small black bee (usually *Lasioglossum*), metallic green bee (usually *Augochlora, Augochlorella,* and *Agapostemon*), medium striped abdomen (often *Halictus* or *Lasioglossum*), cuckoo bee (*Sphecodes* or *Nomada*), other bee (identified but not belonging to other categories), hoverfly (*Syrphidae*), and unidentified bee. We collected voucher specimens to estimate accuracy of on-the-wing identification (Table 2.2). To limit collections, bumble bee pollen load specimens were used as vouchers. The same voucher collection was used for morpho-species groups, bumble bee and *B. ternarius*, as *B. ternarius* is an almost unmistakable species. Although possible to mistake *B. ternarius* for the rarer *B. rufocinctus*, *B. rufocintus* was never identified in our 235 specimen voucher collection. We did not distinguish commercial bees from wild conspecifics as it is usually not feasible. The identities of all collected species were confirmed or corrected by Sam Droege at the Patuxent Wildlife Research Center, Beltsville, MD.

Floral density can be a primary driver of bee visitation (Dibble & Drummond 1997, Ohashi and Yahara 2001, Bushmann and Drummond 2015); therefore we recorded floral density within each quadrat. When inflorescences were too numerous to count, absolute density was estimated by subsampling (Venturini 2015, Appendix D). The flowering unit varied with plant species. For example, although *C. tinctoria* is an Asteraceae with capitula, each floret was not counted on each flower head, instead, the sampling unit for both floral density and flower visitation was the flower head. Hereafter, the sampling unit used for each flower species is referred to as inflorescence.

For each site visit in 2013 only, the number of bees/inflorescence/min was multiplied by the number of inflorescence/m^2 (as estimated by transect counts) to estimate the number of bees/m^2/min. This metric was calculated for the treatments as a whole and also for each plant species observed. Values were pooled to evaluate bee usage of treatments across the entire season. Across-year comparisons were completed using bees/m^2/min, and unlike the independent analysis of 2013 visitation data, did not include floral density.

2.3.2.3. Estimating Floral Density

Floral density was assessed 2-3 times per week from June to September in 2013 using a transect survey method adapted from Karem et al. (2010). A randomly placed 3.3 m string was secured diagonally across the plot excepting a 1.0 m buffer from the plot edge. If any part of a blooming plant crossed the string’s vertical plane, we counted the number of blooming inflorescences. Methodology varied depending on the arrangement and size of the inflorescence

(Venturini 2015, Appendix D). During each site visit, this was replicated 3 times within each treatment for a total of 9 transects per site visit. Floral density estimates were not used in 2012. To convert the linear transect to an absolute estimate of inflorescence /m^2 we measured the diameter of five representative plants of each species. These were averaged and used to calculate the sampled area of each plant species using the formula, $(3.33 * 2d) + (\pi d^2)$, where d = average diameter of the plant species.

2.3.2.4. Bumble Bee Pollen Loads

At all sites, two collections were made each year (2012 and 2013), totaling 30 bumble bee workers per site per year (n=240). Collections were made immediately following blueberry bloom (late June) and in late August. Bumble bee workers were suitable for capture when pollen loads were visible. We intentionally avoided capturing queens. At sites with few bumble bees it was not always possible to collect 15 specimens. Workers were often found concentrated in one, two, or more densely flowering areas and were simply caught where they were found. When possible, paired sites were sampled on the same day. Bees were captured by hand using 50 mL centrifuge tubes. Each tube was labeled with the date, the site, the collector, and the flower the bee was caught on. If the flower was unidentifiable, it was collected and pressed for later identification. Specimens of all blooming flowers were collected from each site during each collection, processed and used as pollen reference samples.

Both reference samples and pollen loads were processed using acetolysis according to the methods of the University of Maine Palynology Laboratory (Venturini 2015, Appendix A). Acetolysis procedures were similar to the methods of Erdtman (1960) and Jones (2014). Pollen loads were separated from the scopa by washing in 10% HCl, cutting off the legs, or manually removing with forceps. Each pollen load was suspended in a 10 mL centrifuge tube with 5 mL of 10% HCl. Reference sample pollen was processed in a similar fashion.

Processed pollen samples were mounted on slides and examined with light microscopy under 40X magnification. Pollen grains were identified to the level possible and binned into taxa groups (Table 2.4). At least 100 pollen grains were identified from each specimen. Grains were identified and counted in transects across slides (Jones, 2014) but counting ceased upon transect completion if the cumulative pollen count met or exceeded 300 grains. When a slide contained fewer than 300 grains, we remounted the sample on a new slide. Cumulative pollen counts from both slides were used for analysis. If the sum of two slides was less than 100 grains, the sample was discarded.

2.3.3. Data Analyses

2.3.3.1. Wildflower Mix Establishment

We used a RCB split-plot ANOVA to analyze treatment effects on bee species richness. Our response variables were sown species richness and unsown species richness. Main model effects were Treatment, Split-plot oats, and the interaction term Treatment x Split-plot oats. Block and Treatment x Block were included in the model as random effects.

We also analyzed the response of the four most common sown wildflower species to treatments. The four most common species in study in the fall of 2013 were *Coreopsis lanceolata*, *Coreopsis tinctoria*, *Monarda fistulosa*, and *Symphiotrichum novae-angliae*. Analyses used the same model as above. Our response variables were the number of open inflorescences, total inflorescences (open, unopened, and past), and dry matter recorded in the sampled area of each sub-plot (0.50 m^2). Analyses were performed on JMP version 12 (SAS Institute Inc., Cary, NC).

2.3.3.2. Bee Visitation by Treatment

We analyzed differences between years using visitation by “wild bees” (inclusive of all bees except honey bees) as the response variable and considered only two sites visited in both years (Rogers Farm and Blueberry Hill Farm). We analyzed the square root transformed metric (bees/m^2/min) using a repeated measures two-way MANOVA with site as the blocking term and natural regeneration, wildflower mix, and clover as treatments.

To better understand differences between treatments, we also considered the more robust 2013 bee visitation dataset independently. Floral density influences bee visitation rates independent of other factors (Dibble and Drummond 1997; Smithson and Macnair 1996). To consider its effects we included only those observations with a paired floral density estimate (transect method). Rare flowers were typically not captured by floral density transects. Paired density-visitation observations were pooled by sampling date, leaving 91 different bee density measurements, each of which is comprised of three or more visitation observations.

We pooled bee utilization of bee pasture (bees/m^2/min) over time by treatment across the 2013 season and blocked by site. Bees were grouped as wild bees (inclusive of all wild bee categories), solitary bees, honey bees, hoverflies, or bumble bees. Two nested groups within the solitary bee category, small black bees and medium striped abdomen bees, were also analyzed. Voucher specimens were collected during sampling and identified to species (Table 2.2). Due to the low number of replications in our RCBD (4 sites) and the possible low statistical power, we used blocked nonparametric Kruskal-Wallace tests for the overall model analyses and for pairwise comparisons, nonparametric Wilcoxon Block tests. Analyses were performed on JMP version 12 (SAS Institute Inc., Cary, NC).

2.3.3.3. Bee Visitation by Flower Species

Pollinator visitation data were ordinated using non-metric multi-dimensional scaling (NMDS). Similar approaches have been used to illustrate bee-flower relationships (Scriven et al. 2013, Wilson 2011). To reduce the effect of low occurrence visits we omitted plant species comprising less than 5.0% of all observations. Flowers that dominated sites and established well were more likely to be observed. Therefore, those flowers comprising > 5.0% of all observations were limited to *C. lanceolata*, *C. tinctoria*, *M. officinalis*, *M. fistulosa,* and *T. pratense*.

The ordination's main matrix contained insects/m^2/min observational data partitioned into the bee groups: honey bee, small black bee, medium striped abdomen, hoverfly, bumble bee, and other. These data were logarithmically transformed to allow for randomized testing of the data with a Monte Carlo test (Barnard, 1963). The second matrix included the following log (x) transformed environmental gradients: number of inflorescences within a 1.0 m^2 quadrat, wind speed, temperature, and relative humidity. The second matrix also included the two categorical grouping variables, site and flower species.

NMDS ordinations were performed using PC-ORD according to the methods of Mather (1976) and Kruskal (1964). Distances were measured using a Sorensen (Bray-Curtis) approach, starting with a maximum of 6 dimensions and stepping down by 0.20 per iteration with 50 runs using real data. Pairwise comparisons of grouping variables were conducted using a Multi-Response Permutation Procedure (MRPP) in PC-ORD version 6.0.

2.3.3.4. Bumble Bee Pollen Loads

The proportion of pollen species abundance within each sample was calculated by volume, which is a more direct measure of utility to bees than the number of grains (Da Silveira 1991). Polar and equatorial pollen grain diameters were averaged from measurements of 30 reference pollens for each species. When reference samples were not available, we used previously published average diameters (Kapp et al. 2000, Reille and Pons 1990).

To analyze the pollen load species composition we used unbounded traditional EMS standard least squares regressions (JMP version 12, SAS Institute Inc., Cary, NC). Dependent variables included pollen diversity, richness, evenness, and the volume corrected relative abundance of pollen within each load, square root transformed. These data were pooled by pollen type (bee pasture, unsown, and overlap). Bee pasture pollens are those produced by our experimentally sown flowers, unsown pollen is produced by naturally occurring flowers, and overlap pollen is *Trifolium pratense* and *T. incarnatum,* which occur as both sown and unsown plants in our study sites. The main model effects were year, season (early and late), treatment (control and treatment), treatment x season, treatment x year, field size, and field size x treatment. Random effects were season x year and treatment x season x year. We used a Student's T-test of LS means to determine specific patterns in the interaction.

Volume corrected pollen counts were also ordinated using NMDS with a Sorensen (Bray-Curtis) distance measure. To decrease ties we log transformed all pollen species data and deleted species occurring in <2.5% of pollen loads. These pollen species data (main matrix) were ordinated using land cover data (proportion of land cover types and area of land cover types within both 500 and 1000 m. Land cover classes at the 500 m scale emerged as stronger predictors for pollen counts than the larger buffer. Therefore, our final NMDS ordination included land cover classes within 500 m such as agricultural lands, blueberry crop land, conifer forest, deciduous forest, urban, and emergent scrub/shrub wetland (Venturini 2015, Appendix B). We also used weather data at time of collection (such as air temperature, relative humidity, wind speed, and cloud cover), pollen measures (total, diversity, evenness, richness), plant collected on (which flower species bees were foraging on when collected), plants visited, year, and season (spring, summer, fall). We included the grouping variables, season, year, treatment, site, predominant pollen, and plant. Pollens were classified into 18 morpho-species taxonomic categories. For tables of ordination factors see Venturini (2015) Appendix B. All ordinations were completed using PC-ORD version 6.0 (McCune & Mefford 2011).

2.4. Results

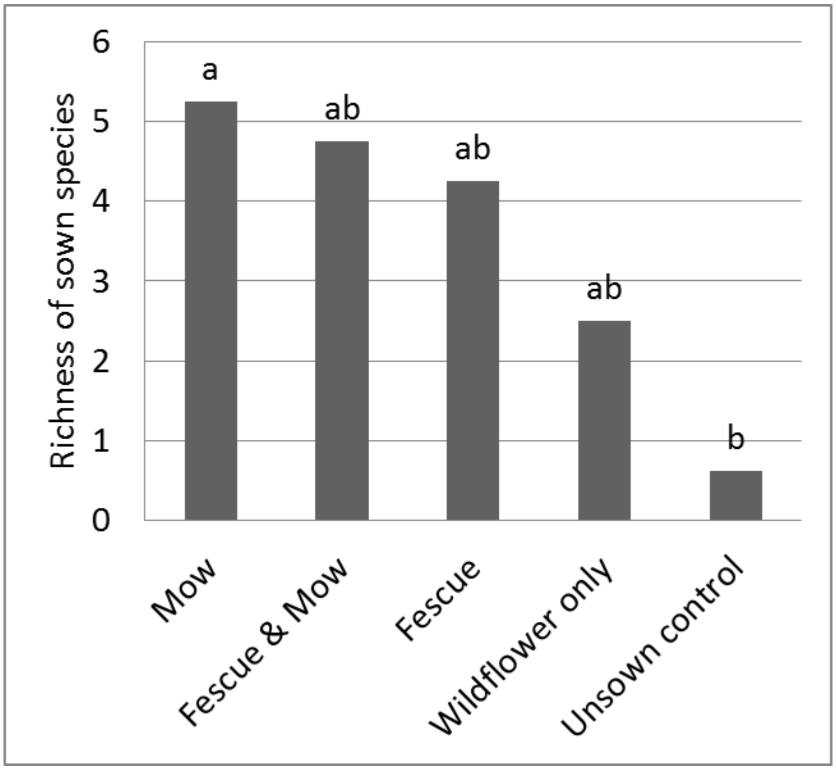
2.4.1. Wildflower Mix Establishment

In September 2013, the second year after plot establishment, we cut, dried, and weighed a total of 7,123 g of plant material, counted 747 open inflorescences and a total of 10,928 open, unopened, and past flowers. Throughout the summer and early fall in our establishment plots an average of 527 inflorescences/m^2 bloomed and 340 g of plant dry matter/m^2 was produced.

Plant richness was affected by both treatment ($F_{(4,12)}$ = 13.3321, P = 0.0002) and the split-plot factor oats ($F_{(1,15)}$ = 5.2326, P = 0.0371). Sub-plots sown with oats had greater richness of sown plant species than those without, 6.30 species/0.50 m^2 vs 5.55 species/0.50 m^2, respectively. Comparison of treatment means revealed that control plots were significantly different from other treatments. No other significant effects on total plant species richness were found.

Treatment significantly influenced the species richness of sown species ($F_{(4,12)}$ = 3.6894, P = 0.0351), mowing had the greatest effect on sown species richness (LS mean = 5.25). However, mowing was only significantly different from control plots. All treatments except wildflower seed alone had a significantly greater richness of sown species than the control.

Figure 2.1. Treatment effects on the richness of sown wildflower species.



Mowing has the greatest effect, but is significantly different from only the unsown control ($F_{(4,12)}$ = 3.6894, P = 0.0351). Tukey HSD used for LS means comparison.

Coreopsis lanceolata, *C. tinctoria*, *M. fistulosa*, and *S. novae-angliae* were the four most common plants in samples. There were no significant treatment effects on *C. lanceolata* dry matter weight, open or total number of inflorescences. *Coreopsis tinctoria* finished flowering by the time of our sampling, explaining why there was no treatment or split plot effects on the number of open inflorescences. However, both *C. tinctoria* dry matter weight ($F_{(4,12)}$ = 4.7615, P = .0156) and total inflorescences ($F_{(4,12)}$ = 4.4261, P = 0.0199) were affected by treatments. Means comparison (Tukey HSD) revealed that when the wildflower mix was seeded alone, *C. tinctoria* produced significantly more inflorescences (443.50 inflorescences/m^2) and plant material (31.52 g/m^2) than any other treatments except when seeded with fescue (94.75 inflorescences/m^2 and 5.91 g/m^2, respectively). *Monarda fistulosa* was also not significantly affected by treatment or split plot effects. However, when wildflowers were sown alone and not mowed, *M. fistulosa* produced more dry matter (LS mean = 70.91 g/m^2, $F_{(4,12)}$ = 2.4427, *P* = 0.1036). *Symphiotrichum novae-angliae* was in bloom during our sampling. Although neither treatments nor split plot effects influenced *S. novae-angliae* at the 0.05 level, the interaction term treatment x split plot significantly influenced the number of open inflorescences produced at the α = 0.10 level ($F_{(4,15)}$) = 2.4515, *P* = 0.0911).Treatments involving fescue and mowing consistently resulted in greater numbers of open *S. novae-angliae* inflorescences than wildflower seed alone, though these results were not significant.

2.4.2. Wildflower Mix, Clover, and Naturally Regenerating Bee Pasture

2.4.2.1. Bee Visitation by Treatment

To compare bee visitation rates to different treatments, we observed flower visitors in quadrats. In 2012, the bee pasture establishment year, we completed 69, 1-minute observations in 1.0 m^2 quadrats at two different sites and observed a total of 64 insect visits to flowers from July 23rd to September 13th. These observations were distributed over nine different plant species. In the second year of establishment, from June 18th to September 17th, 2013, we completed 570, 1-minute observations in 1.0 m^2 quadrats in clover, wildflower, and natural regeneration treatment plots and recorded 1325 insect visits comprised of 221 solitary bees, 101 honey bees, 259 bumble bees, and 744 wasps, hoverflies, and other insects.

Table 2.2. Accuracy and species composition of 2012 and 2013 voucher specimens.

Group	Accurate IDs	N	% Accuracy	Species composition of Accurate IDs
Andrena	12	14	85.7%	58.3% *Andrena carlini*, 16.7% *A. rufosignata*, 8.3% *A. crataegi*, 8.3% *A. forbesii*, and 8.3% *A. rugosa*
Beetle	5	5	100.0%	Not identified to species
Bumble bee	235	244	96.3%	35.3% *B. ternarius*, 26.0% *B. bimaculatus*, 17.0% *B. impatiens*, 14.5% *B. vagans*, 3.4% *B. perplexus*, 2.1% *B. terricola*, 0.9% *B. griseocollis*, 0.4% *B. fervidus*, and 0.4% *B. vagans/sandersonii*
Cuckoo bee	4	4	100.0%	75.0% *Sphecodes davisii* and 25.0% *Nomada* sp.
Fly	6	6	100.0%	Not determined to species
Honey bee	12	12	100.0%	100.0% *A. mellifera*
Hoverfly	5	5	100.0%	Not determined to species
Megachilidae	2	2	100.0%	50.0% *Megachile melanophaea* and 50.0% *M. inermis*
MGB*	11	11	100.0%	72.7% *Augochlorella aurata*, 18.2% *Agapostemon virescens*, and 9.0% *Augochlora pura*
MSA**	10	12	83.3%	40.0% *Halictus. ligatus*, 20.0% *H. confusus*, 20.0% *H. rubicundus*, 20.0% *Lasioglossum leucozonium*
SBB***	10	12	83.3%	20.0% *Lasioglossum cressonii*, 10.0% *L. cinctipes,* 10.0% *L. davisii*, 10.0% *L. leucocomum*, 10.0% *L. pectorale*, and 10.0%, 10.0% *L. smilacinae,* 10.0% *Lasioglossum sp.*, 10.0% *H. confusus,* and 10.0% *H. rubicundus*
Unk bee	1	1	100.0%	*Melissodes subillata*

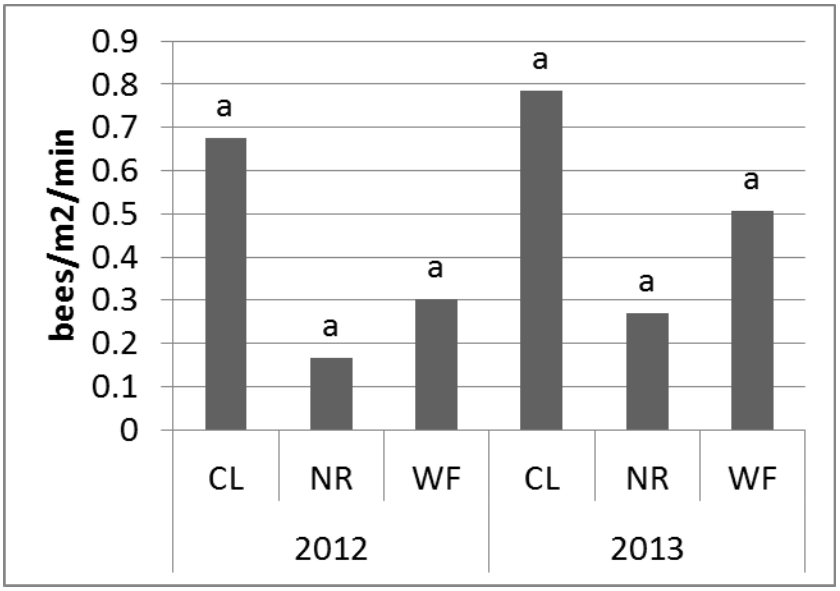
*MGB includes any bees identified on the wing as medium green bee

**MSA includes any bees identified on the wing as medium striped abdomen

***SBB includes any bees identified on the wing as small black bee

We found no significant differences in total wild bee visitation rates between years or among pollinator planting treatments ($F_{(3,2)}$ = 1.4263, P = 0.4374). However, the pattern among pollinator plantings was similar in both years (Fig. 2.2). Clover was visited at high rates in both years, even in 2012 when the only blooming species was the annual clover, *T. incarnatum*. The wildflower treatments in both years were visited less than clover. In both years, natural regeneration treatments were visited the least.

Figure 2.2. Wild bee visitation rates to treatments in 2012 and 2013.

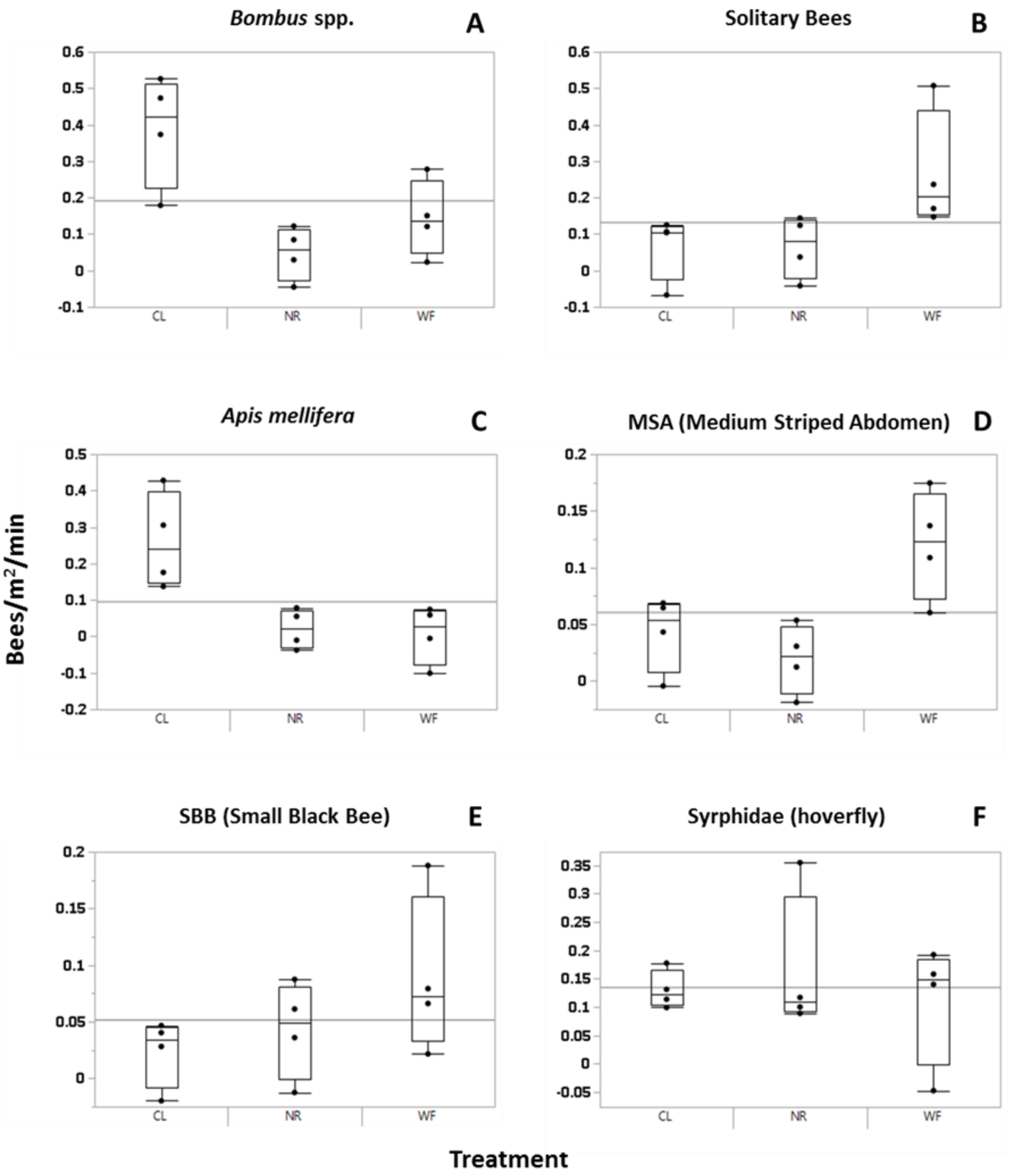


Data were square root transformed to meet normality assumptions.

In 2013 wild bees (solitary and social) visited the three plantings at different rates (oneway Wilcoxon/Kruskal-Wallis test, $\chi^2 = 5.808$, df = 2, $P = 0.055$). Clover was used more than natural regeneration (pairwise comparison, P=.030), but not more than wildflower ($P > 0.05$) and there was no difference among the natural regeneration treatment and the wildflower mix ($P > 0.05$). Bumble bees used clover the most ($\chi^2 = 7.269$, df = 2, $P = 0.026$). Nonparametric rank comparisons of bumble bee visits revealed a significantly greater use of clover than natural regeneration ($P = 0.030$). Further comparisons of bumble bee utilization were not significant.

We performed the same tests on the category, “solitary bees” (Halictidae, Andrenidae, Megachilidae, Colletidae, and others). These are illustrated in Figure 2.3. The wildflower mix was used most, followed by natural regeneration and then clover (χ^2 = 7.423, df = 2, *P* = 0.024) and ranked Wilcoxon comparisons were significant between wildflower and clover (*P* = 0.030), and between wildflower and natural regeneration (*P* = 0.030). There was no difference between clover and natural regeneration treatments. Honey bees exhibited use similar to bumble bees (χ^2 = 7.385, df = 2, *P* = 0.025,) and used clover at a much greater rate than either wildflower (*P* = 0.030) or natural regeneration (*P* = 0.030). However there was no difference between their use of wildflower and natural regeneration treatments. Medium striped abdomen bees, primarily Halictidae (83.33%), and mostly *Halictus* spp. (66.66%) used the wildflower mix more than natural regeneration (*P* = .030) and clover. Small black bees, primarily Halicitidae (91.66%), mostly *Lasioglossum* spp. (66.66%) exhibited no difference among treatments (χ^2 = 2.462, df = 2, *P* = 0.292). Hoverflies were frequently observed in all treatment types and exhibited no significant differences among treatments (χ^2 = 0.2692, df = 2, *P* = 0.8741).

Figure 2.3. Average 2013 bee visitation in bee pasture treatments.



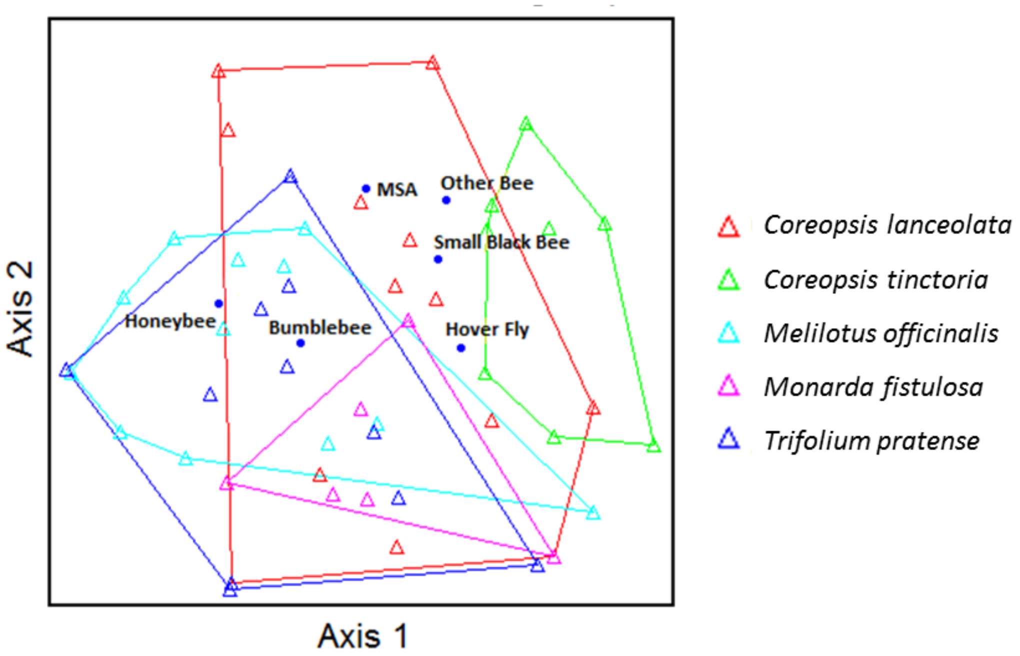
Data represented by box plots, 75th percentile are edges of boxes, horizontal line within box is mean bee density.

2.4.2.2. Bee Visitation by Flower Species

The NMDS ordination of bee visitation to flower species in 2013 resulted in a 3-dimensional solution after 96 iterations, and when compared to a randomization of the data (Monte Carlo test) was significant (P = 0.0196) with mean stress of 0.150. Three axes explained 71.5% of the pollinator community variance, with the 1st, 2nd, and 3rd accounting individually for 26.9%, 21.8%, and 22.7% variance, respectively. Pairwise comparisons using a Multi-Response Permutation Procedure revealed that flower visitor communities differed between the following pairs of plants: *C. lanceolata* and *M. officinalis* (P = 0.0327), *C. tinctoria* and *M. officinalis* (P = 0.0004), *C. tinctoria* and *M. fistulosa* (P = 0.0005)*, C. tinctoria* and *T. pratense* (P = 0.0001), and *M. officinalis* and *M.fistulosa* (P = 0.0018).

These results support our findings at the bee pasture treatment level. Bumble bees and honey bees used flowers similarly, and were separated from other insect visitors in ordination space (Fig. 2.4). They were most exclusively associated with the clovers: *M. officinalis* and *T. pratense*. Solitary bee species group designations medium striped abdomen, small black bee, and other bee were similar to hoverflies and all were centrally located on the ordination axis. These groups were most exclusively associated with *C. tinctoria* and *C. lanceolata* (Fig. 2.4).

Figure 2.4. NMDS ordination graph of axes 1 and 2 grouped by flower species.



Bee species groups are distributed in species space according to the 1st and 2nd axes.

Examination of correlations with the second matrix (environmental gradients) revealed the most likely environmental associated variates for each axis. The first and most significant axis was primarily associated with floral density (r^2 = 0.133), signifying that both honey bee and bumble bee visits, which were associated with higher axis 1 values, tended to visit dense patches of inflorescences. Other studies report similar findings (Dauber et al. 2010 and Scriven et al. 2013). Other insect groups were more centrally located on all axes. This may indicate that these solitary bees are generalists, but is more likely attributed to the course resolution of this species group. It contains a large number of species and foraging behaviors. The main predictors associated with axis 2 included wind speed (r^2 = 0 .034), relative humidity (r^2 = 0.018), and air temperature during observed foraging ($r^2 = 0.013$). Temperature and relative humidity were positively associated with insect visitation rates while wind speed was negatively associated.

2.4.2.3. Bumble Bee Pollen Loads

Our least squares regression of pollen loads tested the influences of bee pasture on bumble bee pollen loads. With "Season x Year", and "Season x Year x Treatment" included as random effects in the model, the Random Effect, Season x Year x Treatment & Random interaction was significant ($F_{(1,286)} = 16.909$, $P = 0.0001$). The greatest proportion of bee pasture pollen in bumble bee pollen loads was found at treatment sites (fields with bee pastures) in early summer of 2013 (mean proportion = 0.486) and was significantly greater ($P \leq 0.05$) than the proportion of bee pasture pollen found in any other combination of year and treatment. The second greatest proportion of bee pasture pollen was found late in the season at treatment sites in both 2012 (mean = 0.196) and 2013 (mean = 0.258). In 2012 there was no significant difference between treatment and control sites (Table 2.3).

Pollen diversity and evenness were most significantly influenced by field size but were not associated with any bee pasture treatment effects ($F_{(1,286)} = 4.160$, $P = 0.042$). Species richness of pollen was influenced by year ($F_{(1,11.314)} = 46.298$, $P = <0.0001$), season ($F_{(1,.969)} = 523.017$, $P = 0.031$), and treatment ($F_{(1,3.088)} = 13.732$, $P = 0.033$). The least squares estimates of species richness increased from 2012 to 2013, from 3.420 ± 0.068 (se) to 4.047 ± 0.065, respectively.

Table 2.3. Relative abundance of pollen among collected bumble bee pollen loads.

Level	Student's T-test[1]	Sample Size	Mean (Standard Error)	Effect Test (Prob > F)
Relative Abundance of Pollen from Sown Bee Pasture Plants				
Treatment, Early, 2013	A	38	0.48550450 (.03321012)	<0.0001
Treatment, Late, 2013	B	46	0.25804101 (.03099263)	
Treatment, Late, 2012	B	37	0.19567039 (.03483845)	
Treatment, Early, 2012	C	32	0.05099665 (.03726468)	
Control, Late, 2013	C	46	0.05038096 (.03563786)	
Control, Late, 2012	C	20	0.01768373 (.04584931)	
Control, Early, 2013	C	40	0.00100209 (.03758208)	
Control, Early, 2012	C	37	0.00074446 (.03397265)	
Relative Abundance of Pollen from Sources Other than Sown Bee Pasture				
Control, Early, 2012	A	37	0.9995241 (.02791594)	0.0017
Control, Early, 2013	A	40	0.99917905 (.03088187)	
Control, Late, 2012	A	20	0.99851396 (.03767521)	
Control, Late, 2013	A	46	0.99104899 (.02928427)	
Treatment, Early, 2012	A B	32	0.94935538 (.03062106)	
Treatment, Late, 2012	B C	37	0.88707051 (.02862739)	
Treatment, Late, 2013	C	46	0.83327752 (.02546720)	
Treatment, Early, 2013	D	38	0.64599799 (.02728936)	
Relative Abundance of Overlap Pollen[2]				
Treatment, Late, 2013	A	46	0.13550028 (.02440408)	0.6826 ns
Treatment, Late, 2012	A B	37	0.11366631 (.02743235)	
Treatment, Early, 2012	B C	32	0.05224270 (.02934279)	
Treatment, Early, 2013	C	38	0.03146727 (.02615017)	
Control, Late, 2013	C	46	0.01644135 (.02806181)	
Control, Early, 2012	C	37	0.00760075 (.02675060)	
Control, Early, 2013	C	40	0.00756059 (.02959272)	
Control, Late, 2012	C	20	0.00558636 (.03610247)	

[1] Student's T-tests of LS Regression (traditional, unbounded, EMS) effect levels. Letters that are different denote significance. Sample size (N) denotes the number of bumble bee pollen loads within each level. Pollen grain counts are multiplied by average pollen grain size for a volume-corrected metric of proportion.

[2] Overlap pollen is defined as pollen from plants that were growing both in the pollinator plantings and also in non-planted adjacent habitats.

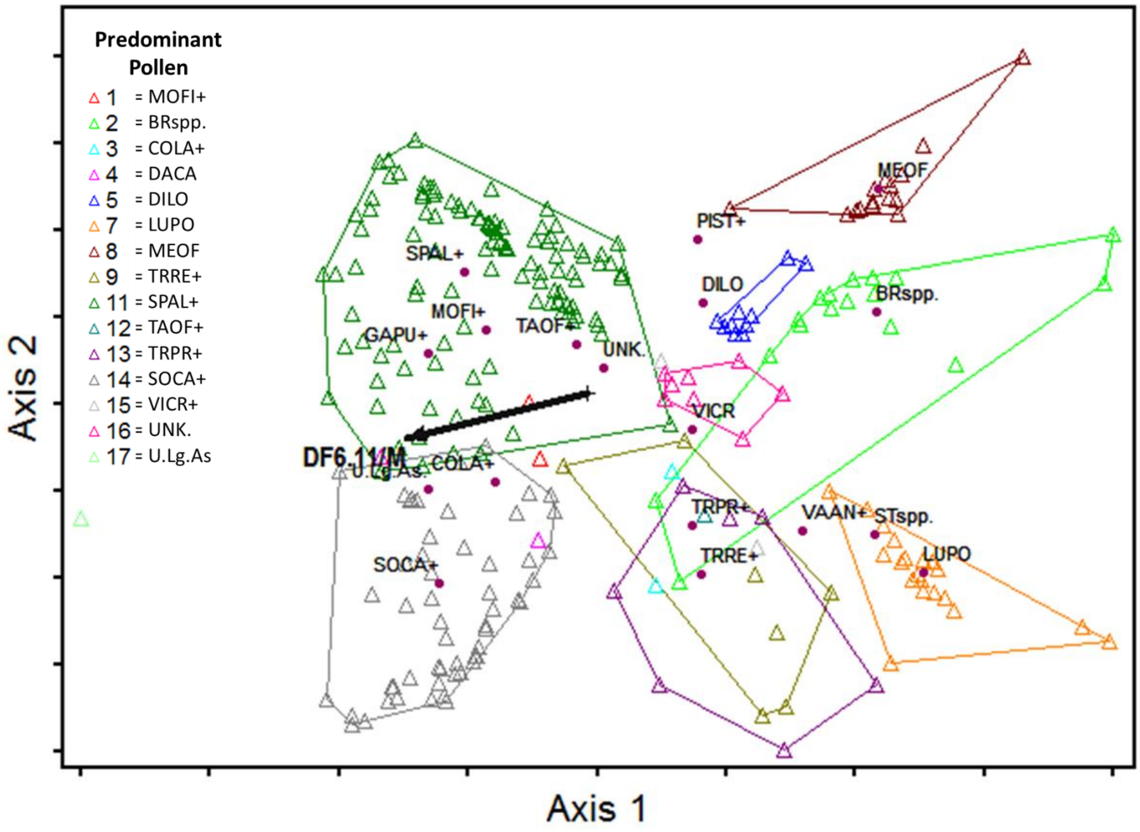
2.4.2.4. Pollen Load Ordination

We performed non-metric multi-dimensional scaling of pollen load composition data to better understand the factors that affect their distribution. The final stress for a three-dimensional solution was 0.163 suggesting a good fit to the three dimensional solution of this ordination. The first 3 axes explained 73.0% of the total variance in pollen load composition, with the first, second and third individually making up 31.8, 21.6, and 19.6% of the variance, respectively. We assessed stress in relation to dimensionality using a Monte Carlo randomization test (first 4 axes, $P = 0.020$).

Pearson and Kendall correlations between second matrix factors and the 1st three axes revealed the primary associated environmental factors with each axis. On the first axis, seasonality was the strongest associate ($r^2 = 0.350$). Contributing the most to the second axis were the following: area of land within 500 m that is managed for blueberry production ($r^2 = 0.099$), proportion of land within 500 m that is managed for blueberry production ($r^2 = 0.088$), and days since first sample date, a measure of the progression of the flowering season ($r^2 = 0.089$). The third and final axis was described by relative humidity, field size, and area of land within 500 m that is managed for blueberry production (r^2 = 0.103, 0.060, and 0.066; respectively).

Grouping the data by the predominant pollen taxon within each sample resulted in a greater degree of separation than any other classification variable assessed (Fig. 5). These findings are supported by a nonparametric Spearman's ranked linear correlation of the plant species that bumble bees were collected on versus the predominant pollen type within each pollen load ($r = +0.858$, $P = .0001$). Several other grouping variables are included in the ordination. Season (early or late) showed clear separation (Fig. 6), while treatment did not, likely because its effects are largely determined by season and year.

Figure 2.5. Two dimensional representation of the separation of pollen species groups according to predominant pollen grain within each sample.

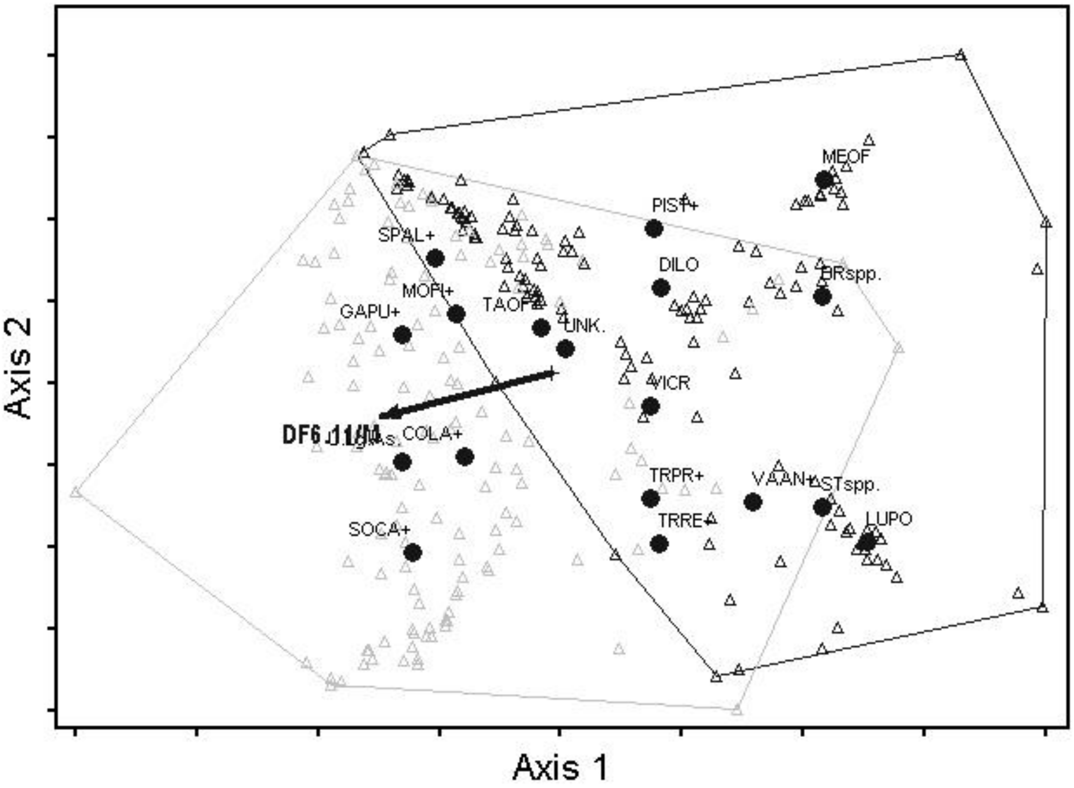


Each pollen load is represented by a colored triangle. Samples comprised predominantly of the same pollen are framed by a colored polygon. Pollen species that were predominant in <2 samples are represented by colored triangles alone. The black arrow (joint biplot) is a measure of seasonality (days since 6/11/2013). Values to the left are later in the season. Brown solid circles indicate the location of each pollen species group in species space. Greater degrees of separation between points indicate greater differences. Plant abbreviates are provided in Table 2.4.

Table 2.4. Description of pollen types within each species group designation.

Species Group	Common Name	Predominant Taxon	Pollen Description
BRspp.	Mustards	*Brassica* spp.	Small to medium tricolpate and reticulate. Grains very uniform.
COLA+	Coreopsis and coneflower	*Coreopsis lanceolata*, *Coreopsis tinctoria*, and *Echinacea purpurea*	Large, spheroidal, and echinate. Spines especially long and sharp.
DILO	Northern bush-honeysuckle	*Diervilla lonicera*	Large, tri-porate
GAPU	Indian blanket	*Gaillardia pulchella*	Very large, spheroidal, and echinate. Spines short and broad at base.
LUPO	Big-leaved lupin	*Lupinus polyphyllus*	Medium to large, prolate, tricolpate, perforate, and reticulate
MEOF	Yellow sweet-clover	*M. officinalis*	Medium, tricolporate, prolate, and slightly reticulate.
MOFI+	Hyssop and bee balm	*Agastache foeniculum* and *Monarda fistulosa*	Large, oblate, and reticulate with 6 furrows
PIST+	Pine family	*Pinus strobus* and other Pinaceae	Very large and saccate
SOCA+	Small aster pollens	*Solidago* spp., *Euthamnia* spp., assorted small grained Asteraceae	Small, echinate and spheroidal. Spikes are relatively short.
SPAL+	Rose family and similar	Rosaceae (*Rubus* spp. and *Spiraea alba*), *Hypericum perforatum*, and *Linaria vulgaris*	Small, psilate to slightly reticulate, and tricolpate.
STspp.	Chickweed	*Stellaria media* and other Caryophyllaceae	Medium, spheroidal, poly-porate pollen (12 aperatures). Spaceship-like.
TAOF+	Dandelion family	*Taraxacum* spp., *Hieracium* spp. & *Leontodon* spp.	Fenestrate
TRPR+	Large clover pollens	*Trifolium pratense* and *Trifolium incarnatum*	Large *Trifolium* pollen, heavily reticulate
TRRE+	Small and smooth legume pollens	*Trifolium repens* and *Lotus corniculatus*	Small, prolate, and psilate to slightly perforate
U.Lg.As.	Unidentifiable large Aster pollens	Asteraceae	Large - very large, spheroidal, Asteraceae pollen. Spines relatively short.
UNK.	Unk.	Any	Varied
VAAN+	Heath family	*Vaccinium angustifolium*, *Vaccinium myrtilloides*, *Vaccinium corymbosum,*and *Kalmia angustifolia*	Tetrad
VICR	Cow vetch	*Vicia cracca*	Large, prolate, and remarkably psilate

Figure 2.6. Two dimensional representation of the partitioning of pollen taxon groups according to the season collected.



Each pollen load sample is represented by a colored triangle (see Table 2.4 for pollen type descriptions). The dark framed polygon frames all pollen samples collected early in the season. The light gray-polygon frames samples collected late in the season. The black arrow (joint biplot) represents the increasing no. of days since 6/11 (first sample date), a measure of seasonality. Solid black circles indicate the location of each pollen species group in species space. Greater degrees of separation between points indicate greater differences.

2.5. Discussion

2.5.1. Wildflower Mix Establishment

A growing number of researchers recommend that farmers and pollinator conservationists install mixes of permanent flowering set asides (Kevan et al. 1990, Goulson 2003, Garibaldi et al. 2014, Kremen and M'Gonigle 2015). As this study and others suggest, these resources are heavily utilized by pollinators (Carreck and Williams 2002). The addition of flowering resources to the landscape can enhance bumble bee populations (Wood et al. 2015), and increase crop pollination (Blaauw and Isaacs 2014). However, no studies have explored the factors that influence their establishment success in an agricultural context. Wild blueberry, our focal agroecosystem, presents an especially challenging environment in which to establish long-term flowering set-asides. Wild blueberry fields are managed at a pH range between 4.0 - 4.5, whereas most flowers recommended for pollinator plantings are expected to grow best at pH 5.5-7.0. Each agroecosystem is different, and establishing flower mixes within each type presents unique challenges. The continuing increase of pollinator plantings and pollinator friendly farming methodologies depends, in part, on the availability of crop-specific wildflower seed mixes. When planted in their target cropping system these mixes should (1) be easy to establish, (2) not become weedy, (3) target those pollinators most crucial to the system, and (4) present few flowers during bloom of the target crop.

We explored the effects of mowing and of oats and fescue as nurse crops on the species richness and bloom of a wildflower mix that we designed for use in the wild blueberry agroecosystem. Although flower species responded differently to treatments, our findings suggest that the establishment of slow growing perennials, especially *S. novae-angliae*, may benefit from both mowing and nurse crops. The annual flower *C. tinctoria* did not benefit from mowing or nurse crops but occurred in significantly higher densities when wildflowers alone were seeded to the plot. All twenty plots were divided by a split-plot factor: seeding oats as a nurse crop. Although the presence of oats significantly increased the richness of species, it did not have a significant influence of the richness of sown species, suggesting that the presence of oats may have increased weed pressure or native flowering plants, depending upon one's perspective.

Mowing is often recommended as a strategy for weed control during the first year of establishment (Pywell et al. 2011). The timing of mowing is important, and flower species respond differently to various mowing regimes (Aldrich 2002). Although we detected no effects of mowing on species richness over the two years of the study, it is possible that an annual program of late-fall mowing will increase the useful life of the planting for the longer term. A late-fall mow allows pollinators to use the planting during the foraging season while still reducing competing vegetation to encourage spring germination of wildflower seeds. Further research in wild blueberry should determine whether the biennial fall burning of the blueberry field could also be used to effectively manage weeds in an adjacent pollinator planting as it does in wild blueberry (Drummond et al. 2009).

2.5.2. Wildflower Mix, Clover, and Naturally Regenerating Bee Pasture

Bees exhibited markedly different use of the three bee pasture treatments. Although not significant in comparisons across both years, patterns of use were similar in both 2012 and 2013. Clover was used the most, followed by a wildflower mix, and natural regenerating agricultural margins were used the least. Social bees, including both managed and unmanaged honey bees and bumble bees, used clover at much higher rates than either wildflower or natural regeneration treatments. On average across the season, 63.2 bumble bees and 43.6 honey bees foraged in the 166.67 m^2 clover planting per minute compared to only 11.20 solitary bees.

Legumes are generally considered excellent bee forage (Decourtye et al. 2010), are frequently cited in regard to honey bees (Campana and Moeller 1977), and are often major components of bee flower mixes (Pywell et al. 2011, Wilkerson et al. 2014, Woodcock et al. 2014). Our analysis of bumble bee pollen loads lends further support to the importance of legumes for social bees. Of the three sown species of clover, *T. pratense*, *T. incarnatum*, and *M. officinalis*, the easiest to establish at our sites and the most heavily used was *M. officinalis.* During peak bloom ithis species presented 2,459 inflorescences/m^2 and attracted a maximum of 450 foraging wild bees to the 166.67 m^2 plot per minute (2.70 bees/m^2/min). *Trifolium pratense* and *T. incarnatum* presented 1,387 and 162 inflorescences/m^2, respectively and attracted a maximum of 216.67 and 100.00 wild bees per min in the 166.67 m^2 plots, respectively. Bumble bees captured on *M. officinalis* had pollen loads predominantly consisting of *M. officinalis* pollen, indicating a high degree of floral constancy (Fig. 2.5).

We attribute this to both the degree of learning that complex floral morphologies require of pollinators and also the greater use of high density and mass-flowering resources by honey bees and bumble bees. Social bees have a greater capacity for learning than solitary bees (Dukas and Real 1991). This makes complex floral morphologies more accessible to social bees and provides an explanation of the differences in use observed in this study. Further, the storage capacity of honey bees—and to lesser extent bumble bees—allows them to take greater advantage of mass-flowering crops than solitary bees (Rollin et al. 2013). Pollinator habitat enhancement strategies that include plantings of clover and other legumes may benefit social bees more than other pollinators. In agroecosystems that depend primarily on social pollinators, pollinator habitat modifications that include clover plantings could be useful for targeted enhancement strategies. These ideas are supported by the abundance of bumble bees in the clover-rich Willamette Valley of Oregon (Rao and Stephen 2010) and a five-fold increase in male bumble bees found in the Swedish landscapes that contained even a small proportion of late-season red clover (Rundlöf et al. 2014). Wood et al. (2015) also describe increased densities of common bumble bee colonies found on farms implementing clover-rich habitat enhancements (Wood et al. 2015).

During an average minute, any one of the 166.7 m^2 wildflower strips contained 44.2 foraging solitary bees and 23.9 foraging bumble bees. A mixture of ten different plant species, the wildflower treatment included Asteraceae, Fabaceae, and Lamiaceae with a diversity of floral morphologies. Plant diversity is generally associated with greater diversity of pollinators (Kennedy et al. 2013). Our more diverse wildflower mix attracted a greater diversity of pollinators (Shannon 1-D = .821) than the less morphologically diverse clover treatment (Shannon 1-D = .750). The diverse, but resource poor naturally regeneration treatment attracted a greater diversity of insects than even the clover treatment (Shannon 1-D = .774).

As a whole, wildflower mixtures can offer habitat managers a "shotgun approach" to pollinator conservation. A single planting of a diverse mixture of flowering plants representing different floral morphologies benefits a diversity of beneficial insects (Haaland et al. 2011, Blaauw and Isaacs 2012, 2014; Campbell et al. 2012, Fabian 2013, Gill 2013, Korpela et al. 2013). However, with careful design and planning, a custom-designed wildflower planting can include flowers that target specific pollinator groups, and provide resources during the most critical times. Of the wildflower species planted in this study, several stood out as especially promising for inclusion in future pollinator habitat enhancement efforts. Both species of *Coreopsis*, *C. tinctoria* and *C. lanceolata* were quick to establish at all sites, bloomed prolifically, and were used extensively by solitary bees. Other studies report similar findings for *Coreopsis* spp. (Buckley 2011; Tuell et al. 2008). *Monarda fistulosa* also established well at a wide range of sites. It was attractive to a diversity of bees, but especially bumble bees—as is indicated by the abundance of Lamiaceae pollen in their pollen loads at treatment sites. *Symphiotrichum novae-angliae* was a prolific bloomer at many sites, but did not begin flowering until after sampling was complete and so it is not sampled in this study. Based on our observations, it was one of the only plants blooming from late September to early October and was so heavily visited by bumble bees during that time that 5-15 individuals were typically foraging on each plant at any given time. Other studies confirm the importance of this aster (Russo et al. 2013).

The natural regeneration strategy is a cheap, simple way to enhance pollinator habitat in farmland. This technique however, is appropriate only if opportunity costs are low and if the seedbank at a given site is especially rich in flowering plants (Carvell et al. 2001). In this study, the natural regeneration treatment was used less by bees than either wildflower or clover. While some flowers in the natural regeneration treatment were visited at high rates (i.e. *Solidago* spp. and *Rubus* spp.), they were less dense than flowers in the planted treatments, and therefore bee densities (per m^2) in natural regeneration plots were also less. On average, 11.0 solitary bees and 8.0 bumble bees foraged in the 166.7 m^2 plot area per minute. Wild blueberry growers in Prince Edward Island, Canada create similar naturally regenerating habitat for pollinator habitat enhancement by cutting back coniferous forest rather than tilling (Byers 2014). Where growers do not perceive land as limited, large areas of naturally regenerating agricultural margins (whether tilled or untilled) can still offer floral resources and habitat to native pollinators. Based upon the average visitation rates of both solitary bees and bumble bees in this study, wildflower treatments supported 3.6 times the density of foragers as natural regeneration and clover supported 3.9 times the density of foragers as natural regeneration. Natural regeneration strategies may require 3-4 times the land base of clover or wildflower plantings in order to support the same numbers of wild bees. As an added risk, volunteer plants in naturally regenerating margins are likely to be aggressive agricultural weeds (Wratten et al. 2012).

In this study floral density and bee visitation observations were conducted only in 2013. This limits our understanding to a relatively short window in the longer-term dynamics of bee pasture and pollinators. Observations in 2013 represented the second year after sowing and the year in which clover (esp. *M. officinalis*) bloomed most prolifically. Few sown clovers bloomed in the clover treatment in 2014 and the dynamics of flowering species in the wildflower mixture continued to shift. Continued monitoring of the bee pasture plots established for this study should provide further conclusions regarding the longer term dynamics of bee pasture treatments. Flowers that establish over a longer period (*Echinacea purpurea*, *Desmodium canadense*, *Eupatorium perfoliatum*) were not highlighted by our methods. *Echinacea purpurea* bloomed in year two, but at low densities in most sites. As the species composition of the wildflower mix changes over time, plants with the longest time to bloom become more dominant and, as their densities increase, potentially more attractive to pollinators.

The success or failure of bee pasture depends on the establishment of its component species. All three treatments varied between sites with some flowers establishing well at some sites and not at others. Natural regeneration treatments exhibited the greatest degree of variability, as the composition of species depends entirely on the site-specific seedbank. The measured densities of sown wildflowers were also highly variable between sites (e.g., maximum *M. fistulosa* inflorescences/m^2 ranged from 0 – 230.7 over 4 sites), although some species (*C. lanceolata* and *C. tinctoria*) established consistently across all sites. Relating site differences to plant species-specific establishment success was not a part of this study. However, we can make some recommendations based upon our observations. First, the lowest pH soils, even when amended with lime, prevented an even germination of clovers. Both white-tailed deer

(*Odocoileus virginianu*) and groundhog (*Marmota marmax*) herbivory had a deleterious impact on clover stands where these species were uncontrolled.

Floral phenology is a major consideration in bee pasture visitation studies. At any given point in the season the flowers in anthesis are in competition for pollinators only between co-blooming heterospecifics. Bee pastures do not function alone, but are nested within a unique landscape. If the goal of a bee pasture is to enhance crop pollination, habitat managers need to consider alternative plant phenology, crop phenology, and the periods at which floral resources most limit wild bee population growth. In practice this is complicated. Actual phenologies of sown species vary considerably from region to region, and from site to site. Some species require 2 or 3 years to bloom and others last only 2-3 years.

The metric we used to compare use of treatments by bees (bees/ inflorescence x inflorescence /m^2) is an absolute density estimate, and we suggest that it provides a practical metric for the comparison of bee pastures. This method requires that quantification of per flower bee visitation rates and flower density in the planting as a whole. – an important factor that greatly influences bee visitation rates (Dibble and Drummond 1997; Smithson and Macnair 1996).

There is a need continue to assess the effectiveness and profitability of pollinator habitat enhancement strategies for farmers. This study was designed in part to measure pollination services as a function of bee pasture, but we did not find significant differences over only two field seasons. Continued monitoring may help to increase understanding of the effectiveness of bee pasture enhancements on pollination services and the bee community. See Venturini (2015) Appendix C for methods and results on this topic.

2.5.3. Bumble Bee Pollen Loads

Bumble bees are highly efficient pollinators and an important part of wild blueberry pollination (Javorek et al. 2002, Bushmann and Drummond 2015). During blueberry bloom overwintered new queens regularly forage in blueberry fields, dusting blueberry flowers with pollen via buzz pollination and synergistically increasing the pollination efficacy of future flower visitors (Drummond 2014). Other studies have used comparative analysis of pollen loads to estimate foraging preferences (Kleijn and Raemakers 2008, O'Neill et al. 2012, O'Neill and O'Neill 2011, Pearce et al. 2012, Stubbs et al. 1992). In this study, we assessed the contribution of clover and wildflower bee pastures to a surrogate of bumble bee fitness by analyzing the contribution of bee pasture to pollen loads in treatment fields in contrast with control fields. Across all wild blueberry treatment sites in 2013, on average bee pasture pollen comprised 37.2% of bumble bee pollen loads (excluding *T. pratense* pollen). This estimate is based on two collections each year, and each collection is a snapshot of the resources that bee pasture provides bumble bees. These plantings were located near fields surrounded by 7 – 25% wild blueberry land within 500 m and ranged in size from 3.5 to 21.8 ha. The high proportion of bee pasture pollen found in pollen loads suggests that in our study system, small dense plantings can effectively supplement floral resources, and possibly enhance bumble bee populations.

This idea is supported by other studies. A study of *Osmia lignaria* found that populations increased at a greater rate with access to a post crop bloom foraging resource, *Lupinus polyphyllus*. This species comprised >90% of post crop bloom pollen loads in their study (Sheffield et al. 2008).

Alternatively if bee pasture was not installed, bumble bee workers may have collected equal quantities of other pollen. In our study, locating bumble bees with full pollen loads was much more difficult in control fields (personal observation). This suggests that bee pasture pollen at treatment sites is both replacing and supplementing wild pollen sources in the landscape.

The proportion of land cover classes surrounding crop fields is increasingly recognized as a major correlate of wild bee abundance, diversity, and richness (Kremen et al. 2004, Kennedy et al. 2013). To date however, no one has explored the effects of land cover class on the proportion of pollen in bumble bee pollen loads. Based upon ordination analyses of pollen loads, we found that coniferous and deciduous forest act inversely on pollen load composition. Also, proportion of blueberry land surrounding the crop field and field size covary; these factors influence pollen loads in a similar way. Our most significant ordination factor was seasonality. Overall, early (June) floral resources (*L. polyphyllus*, *V. angustifolium, Kalmia angustifolia*) were related to increasing proportions of conifer forest in the surrounding landscape. Inversely, the late season pollen groups (mostly Rosaceae, small aster pollens, and *Solidago* spp.) were associated with greater proportions of deciduous forest.

2.6. Conclusions

Our findings suggest that densely flowering bee pastures can significantly influence the composition of pollen collected by bumble bees, even when the planted area is only a small proportion of the total crop field. Landscape factors are also major correlates of bumble bee foraging density. The interaction between landscape and bee pasture is an important component of site-specific pollinator habitat enhancement decisions.

In this study, clover plantings were used primarily by social bees, whereas a perennial wildflower mixture attracted a more diverse assemblage of pollinators. Annual, biennial, and short-lived perennial clovers can provide fast and abundant resources for social bees, but if farmers wish to install a long-lived planting, the clovers tested here may not be appropriate.

These clovers can provide short-term (1-2 year) resources for honey bees and bumble bees while perennial wildflower mixes become established. Alternatively, clover plantings can provide an integral piece of an annually or biennially sown pollinator habitat enhancement strategy.

It is important to note that no treatment provided early spring bloom. This is an important period for pollinators that systems-based pollination enhancement strategies need to include. The wildflower mix tested in our study also had phenology gaps between the end of crop bloom and July 1st, and for a short period around August 7th. Future plantings that use the wildflower mix tested here should include species that fill these gaps. Bee pasture plantings need to consider floral resources as they are available to each functional guild (e.g., social vs. solitary bees), and ensure that throughout the season, each pollinator guild has access to suitable resources. For flower mix recommendations in wild blueberry see Venturini et al. (2015).

As system-based management of agroecosystems and farmland pollinators becomes more prevalent, the demand for crop- and region-specific wildflower mixes for pollinator habitat enhancement will continue to increase. Future studies should test suitable crop- and region-specific bee pasture plantings for their ability to establish and to boost pollinator populations in crops most at risk of pollinator shortages.

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APPENDIX A

BOMBUS SPP. POLLEN ACETOLYSIS PROCEDURES

A.1. Introduction

The analysis of pollens, especially that of wild bee pollens is a versatile tool that provides researchers with the ability to probe the foraging behaviors of bee specimens in historical collections, understand foraging behaviors in response to environmental change and assess the impact of specific floral resources on bee fitness. While an uncommon method in ecological entomology, as the study of wild bees continues to blossom, more researchers are putting these techniques to use. In the interest of future studies on bee foraging behaviors, I include here a thorough accounting of the pollen processing procedures that I used in the University of Maine's Palynology Laboratories in Orono, ME.

The following techniques were compiled by Andrea Nurse at the University of Maine and adapted by the author. A. Nurses' original processing technique was adapted from Faegri and Iverson (1989) and Bryant (2013), personal communication.

A.2. Equipment

80^0C water bath

Laminar flow hood

Vortex mixer

15 ml centrifuge tubes

Teflon stirring rods

Centrifuge tube racks

Centrifuge

Centrifuge bucket covers

½ dram glass vials

Glass microscope slides

22 mm sq cover slips

A.3. Reagents

Deionized water

10% Hydrochloric acid

Ethyl alcohol (removes residual H_2O)

Glacial acetic acid (dehydrates organic material)

Acetic anhydride

Concentrated sulfuric acid (acid hydrolysis (aka: acetolysis) removes lipids and proteins to reveal cell wall structure of pollens)

Silicon oil

A.3. Processing Procedure

Safety note: Wear a lab coat and closed-toed shoes, eye goggles, and nitrile gloves throughout processing. Work under the hood, wear chemical gloves and centrifuge with bucket covers in place when using glacial acetic acid and acetolysis.

- Start water bath at 80^0C
- Sample size is limited by centrifuge capacity
- Label the appropriate number of 15-mL centrifuge tubes with wax marking pen, pencil, or removable labels affixed with Scotch tape
- All centrifuging done for 5 minutes at 3500 rpm. Do not fill tubes beyond 13 mL.

1. Transfer pellet to labeled 15-mL centrifuge tubes. Wash forceps, probes, and other tools used to transfer pollen prior to each sample to avoid cross-contamination.
    a. Pollen is electrically charged and will leap between plastic vials. To control this add 10% HCl to collection vial and mix or suspend pollen prior to transferring to a 15-mL centrifuge tube.
    b. If pollen load is still attached to a bee, you may wash the entire specimen in 10% HCl to dislodge pollen, then remove bee specimen with forceps.
2. Add any additional 10% HCl required in order to fill all test tubes to the 5.0 mL mark. Place in hot water bath for 5 minutes. Centrifuge and decant into sink.
3. Wash with deionized water, vortex to mix, centrifuge, and decant into sink. Repeat at least 3 times until supernate is clear.
4. Under hood, wash samples with 5.0 ml glacial acetic acid. Vortex to mix. Centrifuge with bucket covers in place. Decant into a prepared glacial acetic acid waste bottle.
5. Work under the hood and avoid all contact with water. First add 4.5 mL acetic anhydride and then add 0.5 mL concentrated sulfuric acid to each tube. Vortex gently to mix. Place in 80^0C water bath for 3 minutes. Centrifuge with bucket covers in place. Decant into acetolysis waste bottle.
6. Under the hood, wash samples with glacial acetic acid. Vortex gently to mix. Centrifuge with bucket covers in place. Decant into glacial acetic acid waste bottle.
7. Wash samples with deionized water 3 times to remove the acid and acetolysis mixture. Centrifuge, decant, and vortex after each wash. Decant the first wash into glacial acetic acid waste bottle.
8. Dehydrate samples by adding 5.0 mL ethanol (ETOH). Centrifuge and decant into sink.

9. Re-suspend sediment in small amount of ETOH and transfer to pencil-labeled, ½ dram vials. Centrifuge and carefully decant excess ETOH into sink.
10. Suspend sediment in silicone oil. Use 1-3 parts silicone oil for each part pollen sediment. Stir each vial thoroughly with a new toothpick. Leave uncovered overnight at 50^0C in a vented incubator to allow ETOH to evaporate.
11. Mix well with a new toothpick and mount on slides for analysis.

APPENDIX B

ADDITIONAL FIGURES

Table B.1. MRPP pairwise comparisons of insect visits to flower species in ordination matrices.

	MRPP Statistics		
Pairwise Comparisons	**T**	**A**	**p-value**
COLA vs. COTI	-1.0926955	0.02162194	0.13665288
COLA vs. MEOF	-2.14688326	0.03238677	0.032734*
COLA vs. MOFI	-1.85715749	0.04734345	0.05108912
COLA vs. TRPR	-1.14177524	0.0201523	0.12567566
COTI vs. MEOF	-5.28170892	0.10612512	0.0004184**
COTI vs. MOFI	-5.16183004	0.17853182	0.00050857**
COTI vs. TRPR	-6.47734541	0.12876291	0.00010787**
MEOF vs. MOFI	-3.90160044	0.08894398	0.00189217**
MEOF vs. TRPR	-0.95522634	0.01589235	0.15752791
MOFI vs. TRPR	-0.7923188	0.02013739	0.18908559

COLA = *C. lanceolata*, COTI = *C. tinctoria*, MEOF = *M. officinale*, MOFI = *M. fistulosa*, and TRPR = *T. pratense*. T is the test statistic. A = 1 when all items are identical between groups, A = 0 when heterogeneity within groups is likely due to chance alone, and A < 0 when heterogeneity within groups is greater than that expected by chance alone. Note: p-values not corrected for multiple comparisons. Includes flowers occurring in >5.0% of sample units.

Table B.2. Pearson and Kendall correlations with bumble bee pollen load ordination axes.

	Axes								
	1			**2**			**3**		
Factor	**r**	**r-sq**	**tau**	**r**	**r-sq**	**tau**	**r**	**r-sq**	**tau**
log(# FW)	-0.375	0.141	-.257	-.041	.002	-.006	-.290	.084	-.204
log(WS)	.046	.002	.079	-.168	.028	-.147	-.030	.001	-.012
log(Temp)	-.110	.012	-.048	.280	.078	.202	-.092	.009	-.020
log(RH)	.235	.055	.170	.242	.058	.144	-.259	.067	-.169

R denotes directionality and relative contributions of explanatory factors to each synthetic axis. N = 52.

Table B.3. Pearson and Kendall correlations with second matrix of NMDS ordination of bumble bee pollen load data.

Land cover classes (within 500 m)	**Axis 1**			**Axis 2**			**Axis 3**		
	r	**r-sq**	**Tau**	**r**	**r-sq**	**tau**	**r**	**r-sq**	**Tau**
Area_ha	0.157	0.025	0.012	0.223	0.050	0.148	-0.183	0.033	-0.212
Ag_area5	-0.181	0.033	-0.126	0.076	0.006	0.103	-0.112	0.012	-0.024
Ag_pct5	-0.186	0.035	-0.133	0.066	0.004	0.090	-0.087	0.008	-0.013
Bl_area5	0.047	0.002	0.001	0.314	0.099	0.212	-0.257	0.066	-0.196
Bl_pct5	0.000	0.000	-0.050	0.297	0.088	0.223	-0.241	0.058	-0.163
Co_area5	0.360	0.130	0.207	-0.046	0.002	-0.057	-0.086	0.007	-0.089
Co_pct5	0.394	0.155	0.231	-0.200	0.040	-0.095	-0.053	0.003	-0.030
De_area5	-0.315	0.099	-0.210	0.123	0.015	0.082	-0.056	0.003	-0.044
De_pct5	-0.205	0.042	-0.231	0.130	0.017	0.102	-0.071	0.005	-0.014
Ur_area5	0.130	0.017	0.065	0.192	0.037	0.122	-0.088	0.008	-0.143
Ur_pct5	0.087	0.008	0.043	0.189	0.036	0.095	-0.083	0.007	-0.120
Em_area5	0.021	0.000	-0.018	-0.083	0.007	-0.039	0.215	0.046	0.122
Em_pct5	-0.004	0.000	-0.001	-0.135	0.018	-0.058	0.237	0.056	0.173
We_area5	-0.136	0.019	-0.079	0.198	0.039	0.139	0.005	0.000	0.029
We_pct5	-0.200	0.040	-0.142	0.150	0.023	0.162	0.050	0.002	0.030
FS (ha)	0.040	0.002	-0.041	0.248	0.061	0.191	-0.244	0.060	-0.161
FS disparity	-0.047	0.002	-0.007	0.049	0.002	-0.026	-0.226	0.051	-0.079
Temp	0.171	0.029	0.109	-0.076	0.006	-0.005	-0.138	0.019	0.000
RH	-0.086	0.007	0.016	0.152	0.023	0.099	0.322	0.103	0.135
WS	-0.097	0.009	-0.021	0.231	0.053	0.156	-0.192	0.037	-0.121
CC	0.000	0.000	0.008	0.208	0.043	0.105	0.163	0.027	0.048
St. T	0.073	0.005	0.052	-0.156	0.024	-0.117	-0.082	0.007	0.012
Ed. T	0.106	0.011	0.045	-0.097	0.009	-0.034	-0.201	0.040	-0.103
DF6.11	-0.591	0.350	-0.397	-0.298	0.089	-0.153	0.053	0.003	0.088
TPG	-0.248	0.062	-0.173	0.108	0.012	0.069	-0.140	0.020	-0.075
H'	-0.231	0.053	-0.103	-0.023	0.001	-0.074	-0.143	0.021	-0.108
S	0.027	0.001	0.035	-0.186	0.035	-0.173	0.088	0.008	0.112
E	-0.231	0.053	-0.103	-0.203	0.001	-0.074	-0.143	0.021	-0.108

High r^2 values indicate a greater contribution to the synthetic ordination axis. R values indicate strength and directionality. For explanation of factors see Tables A.4 and A.5.

Table B.4. Description of land cover types used in main matrix of pollen count ordinations.

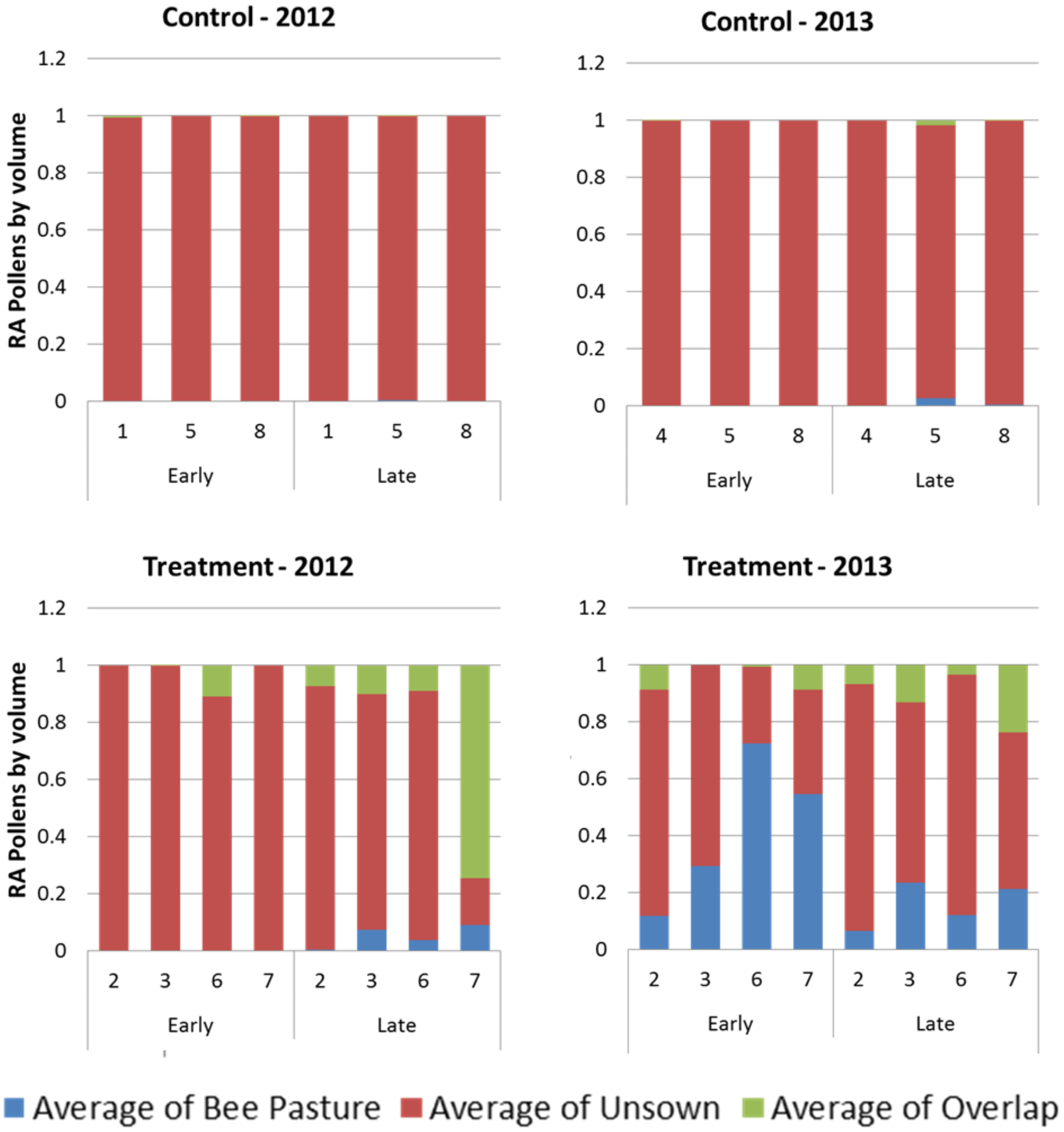
Land Cover Classification	Description
Area_ha	Area of crop field
Ag_area5	Area of agricultural land
Ag_pct5	Percentage of agricultural land
Bl_area5	Area of wild blueberry
Bl_pct5	Percentage of lowbush blueberry
Co_area5	Area of coniferous forest
Co_pct5	Percentage of coniferous forest
De_area5	Area of deciduous forest
De_pct5	Percentage of deciduous forest
Ur_area5	Area of urban land
Ur_pct5	Percentage of urban land
Em_area5	Area of emergent scrub/shrub wetland
Em_pct5	Percentage of emergent scrub/shrub wetland
We_area5	Area of wetland
We_pct5	Percentage of wetland

All classifications are of land cover types within a 500 m buffer around the field perimeter. Land classifications are based on GIS land cover datasets and methodology used by Chapin (2014).

Table B.5. Description of factors used in second matrix of pollen load composition ordination.

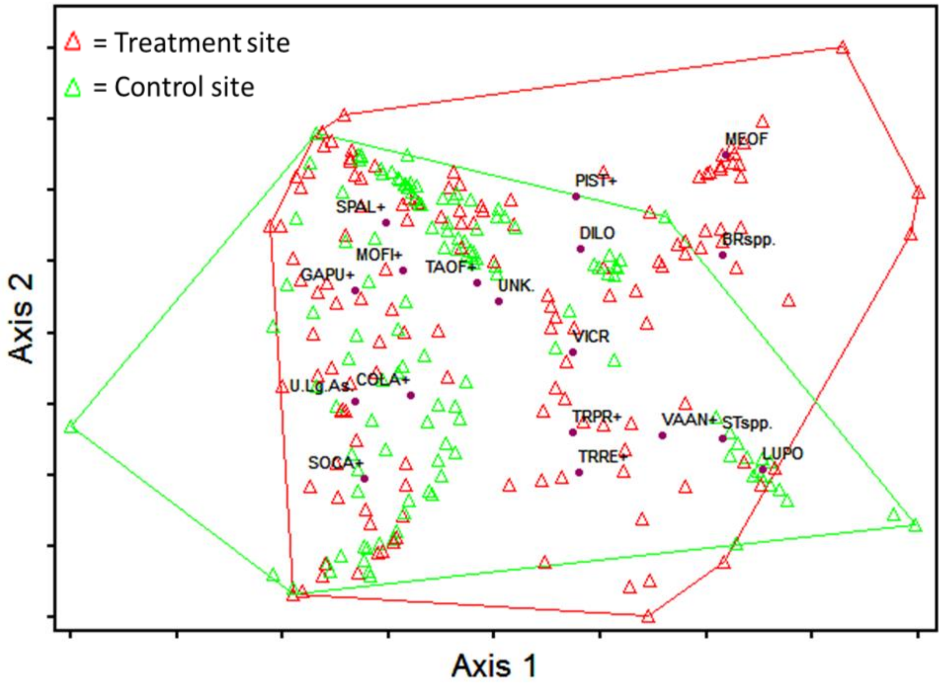
Factor	Type	Description
Land Cover Classes	Quantitative	See Table A.4
FS (ha)*	Quantitative	Size of wild blueberry fruiting field in 2012 (ha)
FS disparity*	Quantitative	Difference between "FS (ha)" and size of 2012 lowbush blueberry prune field
Temp/MAX*	Quantitative	Temperature (C) at time of bumble bee specimen collection
RH/MAX*	Quantitative	Relative humidity (%) at time of bumble bee specimen collection
WS/MAX*	Quantitative	Wind speed (m/s) at time of bumble bee specimen collection
CC/MAX*	Quantitative	Cloud cover (%) at time of bumble bee specimen collection
St.T/MAX*	Quantitative	Starting time of bumble bee specimen collection
Ed.T/MAX*	Quantitative	End time of bumble bee specimen collection
DF6.11/MAX*	Quantitative	No. of days between 6/11 (date of first specimen collected) and date of specimen collection
TPG/MAX*	Quantitative	Total number of pollen grains counted in each pollen load
H'/MAX*	Quantitative	Shannon-Weiner species diversity of each pollen load
S/MAX*	Quantitative	Species richness of each pollen load
E/MAX*	Quantitative	Species evenness of each pollen load
PCF	Categorical/Grouping	Plant group bumble bee specimen was captured on (binned into 18 possible groups, see Table 2.4)
PP	Categorical/Grouping	Plant group of predominant pollen grain observed in each pollen load (binned into 18 possible groups, see Table 2.4)
Cntrl/Trt #	Categorical/Grouping	Specimen collection location (Control or Treatment site)
Site #	Categorical/Grouping	Site bumble bee specimen collected from (1-6)
Year #	Categorical/Grouping	Year of collection (2012 or 2013)
Seas.	Categorical/Grouping	Season of collection (early summer or late summer)

Figure B.1. Histograms of the relative contributions of bee pasture pollen, unsown pollen, and overlap (TRPR+) pollen to bumble bee pollen loads.



Numbers on the x-axis designate sites. We present here also the proportion of pollen at Rogers Farm, an uncontrolled, non-blueberry field, treatment site (Field no. 7, not included in analysis). All pollen data is presented as relative abundance of pollen within a pollen load. Pollen grain counts are multiplied by average pollen grain size for a volume-corrected metric of proportion.

Figure B.2. NMDS ordination graph of axes 1 and 2 grouped by treatment.



Each pollen load sample is represented by a colored triangle. The red polygon frames all pollen samples collected at Treatment sites (with bee pasture). The green polygon frames those collected at control sites (without bee pasture). Brown dots indicate the location of each pollen species group in species space. Greater degrees of separation between points indicate greater differences.

APPENDIX C

THE INFLUENCE OF BEE PASTURE ON POLLINATION SERVICES

C.1. Methods

In the summer of 2012 we established pollinator plantings at four sites in Maine to assess any influence on native bee pollination services over time. Three of four sites are commercial blueberry operations with several acres of biannually harvestable wild blueberries. Rogers farm, a University of Maine research farm, grows mostly wheat, corn, and mixed vegetables. Treatment sites are located in Old Town, Jonesboro, and Blue Hill. We paired each of the three commercial wild blueberry treatment sites with a nearby control field. Rogers Farm has no control field. Control fields were selected on the basis of proximity to treatment sites, similarity of management, presence of a split field crop rotation, and willingness of the grower to participate. At all sites except Rogers Farm (six fields total), I sampled fruit set by flower and berry counts, yield by stratified sampling, and visitation to blueberry flowers by 1-minute observations of 15, 1 m^2 quadrats per field (with one exception). In 2012 excessive rain made it impossible to sample visitation to wild blueberry flowers at Blueberry Hill Farm.

Each of the four treatment sites consisted of plots with three different treatments—natural regeneration, clovers, and wildflowers. Both the clover and the wildflower mixes were planted with a nurse crop of oats, *Avena sativa*. The natural regeneration treatment was prepared with lime and tilling but no seeds were sown. Each treatment measures 3.3 x 50.0 m. At all sites but one, total plot area for all three treatments is 500 m^2. At one private farm in Blue Hill, Maine, space restrictions only allowed 100 m^2 of wildflowers, 100 m^2 of clover, and 25 m^2 of natural regeneration. Detailed labor and expense records were kept at every stage of the planting process in order to develop an enterprise budget model.

Relationships between field yields, fruit set, and bee community parameters (genus diversity, richness, abundance, and evenness) were assed using regression analysis. Site level means comparisons were performed with Student's T-tests. All statistical analyses were performed using JMP version 12 (SAS Institute Inc., Cary, NC).

C.1.1. Wild Blueberry Flower Visitation Observations

Bee visitation to wild blueberry flowers was measured as a function of distance from bee pastures (inclusive of all three treatments) at treatment sites. At control sites bee visitation was measured as a function of distance from the field edge. Sampling was conducted at 4 predetermined and marked distances, edge, edge + 10 m, edge + 20 m, and field interior (40 – 60 m from edge). Higher blueberry flower visitation rates closer to wildflower plantings would indicate either that the plantings aggregate pollinators or that they increase the local populations. We sampled across four transects in each field. Each transect was at least 15 m apart to increase the independence of observations.

C.1.2. Fruit Set

Fruit set in the fields was recorded at 4 points on each transect (same transects as above). Fruit set samples were taken 2 meters to the right of each plot used for flower visitor observations.

C.1.3. Diversity Samples

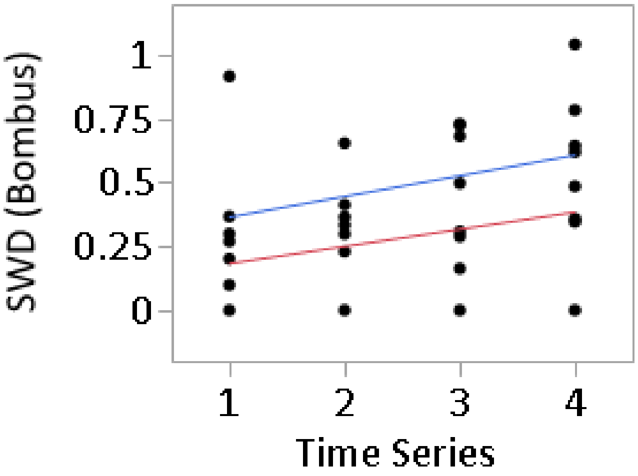
Fields were visited two times each year (2012 and 2013) to collect specimens for diversity indices. Samples were taken once in June and once in August. Specimens were collected by trained student workers for a total of 1 man-hour per field, twice per season.

Specimens were captured and stored using snap-seal 50 mL Corning Ware plastic vials. Honey bees and queen *Bombus* spp. were not collected. Sampling was only done in sunny conditions between 9:30 am and 4 pm with temperatures between 15 and 30 C. Workers collected bees using plastic flip-top vials. Samples were stored in a cooler with ice packs until they could be placed in a freezer for storage.

In the lab, occasionally vials were found empty. We assume these bees were considered caught in the field but had actually escaped. These samples were excluded from analysis. Occasionally observers in the field mistook flies and wasps for bees. All flies and wasps collected were removed from analysis. Bees were pinned and identified under microscope in the lab using the online key to genus at www.discoverlife.org. Shannon-Wiener diversity indices and richness were calculated using an online diversity calculator at http://www.changbioscience.com/genetics/shannon.html. All species determinations were verified by Sam Droege at the Patuxent Wildlife Research Center, Beltsville, MD.

C.2. Results

Figure C.1. Shannon Diversity Index (1-D) of Bombus spp. captured at treatment and control sites over 2 years.



The blue line of best fit represents treatment fields, the red line represents control fields. Time Series 1 – 4 represents Spring 2012 through Late summer 2013, respecitively. The change in the bee communities over time was not significantly different between control and treatment fields ($F_{(1,\,1)}$ = .0283, *P* = .8676).

Figure C.2. Residuals for Figure C.1.

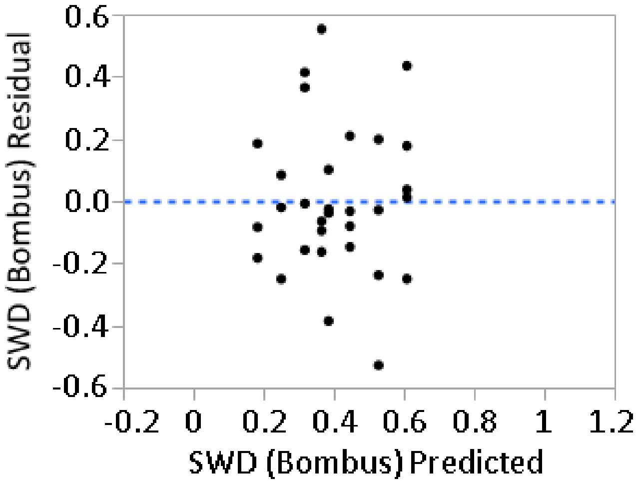
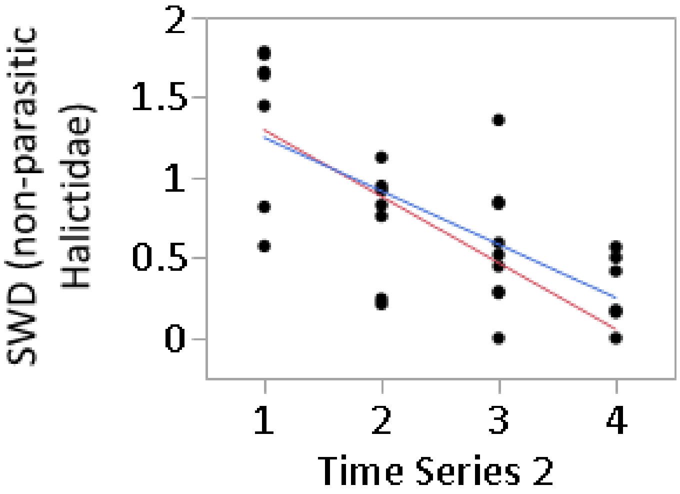


Figure C.3. Shannon Diversity Index (1-D) of non-cleptoparasitic Halictidae. captured at treatment and control sites over 2 years.



The blue line of best fit represents treatment fields, the red line represents control fields. Time Series 1 – 4 represents Spring 2012 through Late summer 2013, respecitively. The change in the bee communities over time was not significantly different between control and treatment fields ($F_{(1,\ 1)}$ = .0639, P = .5186).

Figure C.4. Residuals for Fig. C.3.

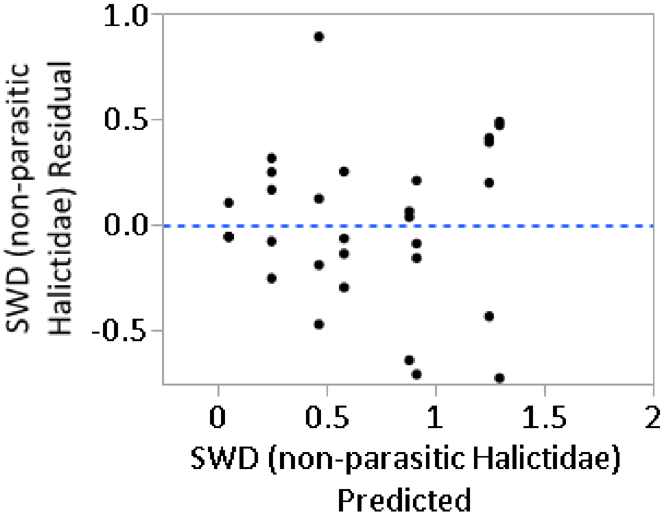
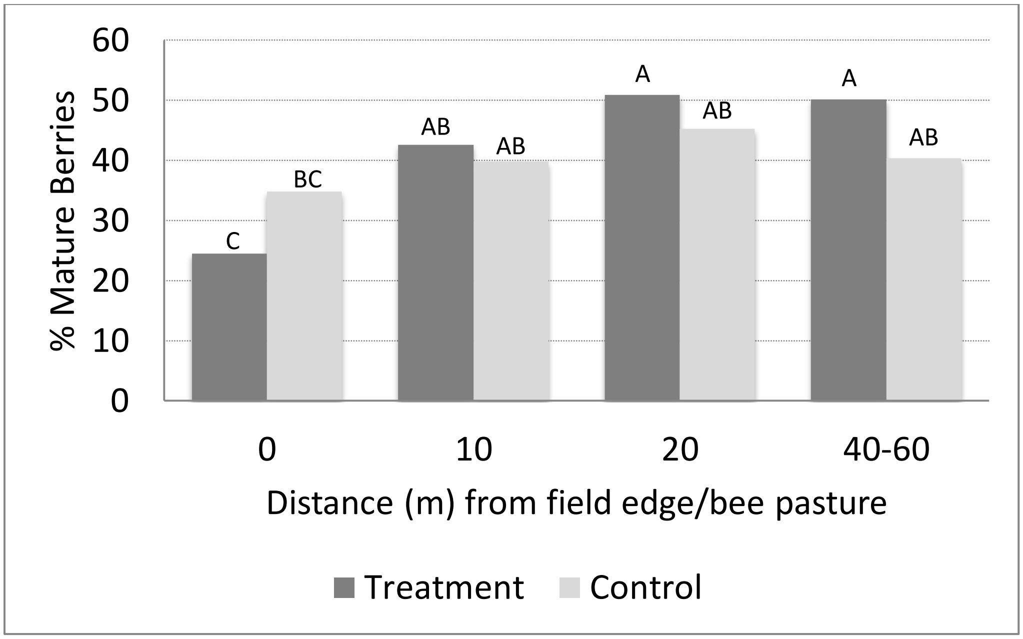


Figure C.5. Fruit set in 2013 as a function of distance from the field edge (control) and bee pasture at field edge (treatment).



Results of a LS Regression with the main effects distance sampled from field edge, cntl/tmt, and distance sampled from field edge x cntl/tmt. Whole model ANOVA ($F_{(7, 239)}$ = 2.3881, *P* = .0224). Letters denote significant differences according to Student's T-test. Levels not connected by same letter and significantly different.

Table C.1. List of all species captured at all sites in diversity sampling.

Genus	species	no. of specimens
Andrena	*algida*	1
	asteris	2
	barbilabris	1
	biscalis	2
	braccata	2
	bradleyi	2
	carlini	43
	carolina	14
	crataegi	1
	cressonii	1
	hirticincta	6
	imitatrix	5
	milwaukeensis	1
	miranda	1
	nida	10
	nivalis	1
	placata	3
	rufosignata	8
	sp.	1
	thaspii	1
	vicina	19
	vicini	1
	virginiana	7
	wilkella	24
Apis	*mellifera*	3
Augochlorella	*aurata*	63
	pura	2
Bombus	*bimaculatus*	18
	borealis	1
	griseocolis	4
	impatiens	88
	perplexus	1
	sp.	1
	ternarius	100
	vagans	58
Ceratina	*calcarata*	10
	mikmaqi	8

	sp.	1
Colletes	*simulans*	3
Epeolus	*scutellaris*	7
Halictus	*confusus*	12
	erythronii	1
	ligatus	36
Heriades	*leavitti/variolosus*	1
Hylaeus	*affinis/modestus*	15
	annulatus	1
	mesillae	5
Lasioglossum	*acuminatum*	7
	admirandum	1
	cinctipes	2
	coriaceum	1
	cressonii	53
	ephialtum	4
	ephialutm	1
	heterognathum	5
	imitatum	2
	inconditum	2
	leucocomum	13
	leucozonium	1
	macoupinense	6
	nigroviride	1
	pectorale	14
	perpunctatum	13
	quebecense	2
	smilacinae	1
	smilacrinae	1
	sp.	10
	tenax	1
	timothyi	1
	versans	10
	versatum	3
	verstum	1
	viridatum	1
	zonulum	3
Megachile	*gemula*	1
	latimanus	1
Melissodes	*druriella*	18
	illata	1
	sp.	2

	subillata	6
	trinodis	1
Nomada	*bidentate sp. A*	1
	cressonii	2
	luteoloides	5
	white setae sp. A	4
Osmia	*bucephala*	1
	inspergens	1
Peponapis	*pruinosa*	2
Pseudopanurgus	*andrenoides*	16
Sphecodes	*atlanticum/cressonii*	2
	coronus	1
	ranunculi	1
	solinus	2
	sp.	2
	townesi	1
SUM		**827**

Total no. of species (including unidentifiable species) is 95. All species determinations were verified or amended by Sam Droege at the Patuxent Wildlife Research Center, Beltsville, MD.

APPENDIX D

METHODS USED FOR ESTIMATING FLORAL DENSITY IN BEE VISITATION QUADRATS

D.1. Floral density within bee visitation quadrat

Flower visitation observations were made in 1 m^2 quadrats. We determined floral density independently within each sampled quadrat. The most appropriate scale for considering inflorescences was based upon both our ability to quantify inflorescences at that scale. For example, although flower visitors perceive the bloom of each floret within a capitulum, we only considered the number of capitula for ease of sampling. While daisy-like flowers were often displayed in a mostly two dimensional space, some flowers occurred in great densities within a three dimensional space. For these species (i.e.: *M. offinalis*), it was necessary to extrapolate in order to estimate the number of flowers per quadrat.

The estimates obtained with these methods were used to determine the number of flower visitors on a per flower basis within each quadrat. This metric was multiplied by our estimates of floral density within each treatment to compare use of treatments, and flower species, by flower visitors (see Ch. 2).

Table D.1. Extrapolation methods used to estimate floral density within flower visitor quadrats.

Flower Category	Examples	Sampling unit	Method*	Calculation
Daisy-like Asteraceae	*C. tinctoria* *C. lanceolata* *E. purpurea*	Capitulum	Count all capitula within quadrat	none
Goldenrod-like Asteraceae	*Solidago spp.*	Capitulum	Break 1 m^2 quadrat into four equal squares, count all capitula on a single stem in the center of each square (four total), count all stems in quadrat.	Av. capitula/stem x absolute stem count
Clustered flowers	*M. officinalis*	Flower	Break 1 m^2 quadrat into four equal squares, count the number of clusters on a single stem in the center of each square (four total). Count the number of flowers per cluster on a single cluster in the center of each square (four total). Count all stems in quadrat.	Av. flowers/cluster x av. clusters/stem x absolute stem count
Trifolium spp.	*T. repens* *T. incarnatum* *T. pratense*	Flower head**	Break 1 m^2 quadrat into four equal squares, count all flower heads within the most representative square.	flower heads/quadrat x 4
All low density samples	All species	Varied with flower category	Count total number of inflorescences in quadrat	none

* Only flowers that appeared to be in bloom were counted.

**The sampling unit for *Trifolium* spp. was a single inflorescence comprised of multiple florets. The number of florets per inflorescence was not quantified.

BIOGRAPHY OF THE AUTHOR

Eric Venturini was raised in Wallingford, PA on December 6^{th} 1983. He attended Strath Haven High School until 2002 when he started his undergraduate degree at the University of Maine in Orono. There he met his eventual wife, Julia McGuire. Eric graduated college with a B.S. in Ecology and Environmental Science in 2006. He studied fisheries for several years, working in Ireland, Alaska and Hawaii and spending long periods of time at sea. In 2010 he changed course to pursue his interest in agriculture and worked on farms in the west. In 2012, he was accepted as an M.S. student at the University of Maine in Orono. Eric now works at Johnny's Selected Seeds in Fairfield, Maine. He plans to continue working in the field of agriculture to help enable today and tomorrow's growers to create solvent businesses that they believe in. Eric is a candidate for the Master of Science degree Ecology and Environmental Science from the University of Maine in August, 2015.