THE IMPACTS OF HABITAT MANAGEMENT ON BENEFICIAL INSECTS IN LOWBUSH BLUEBERRY AGROECOSYSTEMS

by

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Submitted in partial fulfilment of the requirements

for the degree of Doctor of Philosophy

at

Dalhousie University

Halifax, Nova Scotia

August 2017

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ABSTRACT

Insect pollinators and natural enemies deliver vital pollination and pest control services in agricultural ecosystems (‘agroecosystems’), yet reported population declines threaten the production of many global food crops. The efficacy of various habitat management techniques to promote pollinator and natural enemy communities in agroecosystems were tested, using lowbush blueberry (*Vaccinium angustifolium* Aiton) as the model crop.

Artificial trap nests were evaluated as nesting substrates for cavity-nesting bees (Hymenoptera: Megachilidae). Megachilidae nesting occupancy was highest in milk carton trap nests, while nesting occupancy in wooden trap nests and overturned clay lids was low. Emergence after overwintering was low for all trap nests, and parasitism from wasps (Hymenoptera) and flies (Diptera) was observed.

Buckwheat plantings along blueberry field margins were compared to unenhanced ‘control’ blueberry field margins for impact on wild bee and natural enemy abundance and diversity after blueberry bloom. Higher bee abundance in buckwheat transects was only detected during mid-August. Bee fauna during blueberry bloom was documented to determine if the same bees visiting buckwheat were also involved in blueberry pollination. All bee genera recorded during blueberry bloom were also collected in buckwheat transects. Bee diversity was found to be significantly greater during late blueberry bloom than early or mid-bloom. Bee abundance was also higher during late blueberry bloom, although not significantly so. Aerial netting and pan trapping provided complementary collections of bees. Natural enemy abundance was generally higher in buckwheat transects than in control transects for many groups evaluated, although not significantly so.

Six forage crops were seeded to monitor their attractiveness to bees. Sweet clover, red clover, alsike clover, and birdsfoot trefoil were visited most frequently by bees. Red clover, birdsfoot trefoil, and sweet clover bloomed for the longest period. Based on these findings, red clover, sweet clover, alsike clover, and to a lesser degree, birdsfoot trefoil, are attractive forages to use for habitat management for pollinators.

My findings demonstrate that lowbush blueberry agroecosystems host a diverse and abundant beneficial insect fauna when alternative nesting substrates and flowering resources are present, and floral enhancements may be beneficial at certain times during the season.

LIST OF ABBREVIATIONS AND SYMBOLS USED

AIC	Akaike's Information Criterion
AES	agri-environmental scheme
ANOVA	analysis of variance
cm	centimetre
CRD	completely randomized design
df	degrees of freedom
di'	specialization asymmetry
e.g.	for example
F	*F*-value, Fisher's statistic
H_2'	the level of specialization within the network
ha	hectares
hr	hours
i.e.	that is
Inc.	Incorporated
IQR	interquartile range
kg	kilogram
km	kilometre

m	metre
min	minute
mL	millilitre
mm	millimetre
n	sample size
no.	number
P	*P*-value, probability
RCBD	randomized complete block design
SD	standard deviation
SE	standard error
U.K.	United Kingdom
U.S.	United States of America
USD	United States dollar
$\chi 2$	chi-square statistic
%	percent
~	approximately
°C	degrees Celsius
>	greater than
<	less than

≤	less than or equal to
≥	greater than or equal to
±	plus or minus

ACKNOWLEDGEMENTS

I am grateful to my family and friends who supported and encouraged me throughout this project. To my family who inspired my love for agriculture and my role in this industry: thank you for planting the seed and nourishing my growth in this sector. As I continue my own path in agriculture, I am grateful to the incredible mentors I have to inspire and encourage me.

Ryan: thank you for being with me on this journey from start to finish. I am grateful for your support and encouragement during the ups and downs. Thank you for providing the perfect distractions through farming and showing horses. I am blessed to call you my partner and share Barley Soup with you. Barley: you may be the first dog to be mentioned in a thesis acknowledgements section, but you deserve it. Thanks for sticking by my side throughout university.

My research path started with the New Brunswick Department of Agriculture (Tracadie Office). Thank you to Maurice Basque and Etienne Theriault for giving me the opportunity to learn about native bees in lowbush blueberry fields. Thank you also to Michelle Robichaud for inspiring my love for bees and nurturing my curiosity, and to Gilles Savoie for sparking my interest in buckwheat and alternative flowering resources for bees.

I am thankful I was able to continue my graduate studies at the Agriculture Campus. At the AC, I had so many inspiring women to look up to. I am thankful to Keltie and Joy for their care and concern, delicious cookies, home cooked meals, and conversations of inspiration. Thank you for showing me what powerful and compassionate female leaders can achieve. Another important mentor at the AC was Pat Jeffcock. Pat: thank you for teaching me about balance, self-care, and asserting myself. I appreciate all that you did to develop me professionally through the Students' Association. Your friendship and guidance are a big part of my life.

Thank you to the many growers who allowed me to use their fields for research, answered my many questions, and were genuinely interested in the results: D. Archibald, A. Bonnyman, B. Davison, V. McCully, A. Sargent, J. Slack, J. Smith, and D. Wyllie. I especially enjoyed sampling at Vernon and Carrie McCully's farm not only for their delicious garden produce, but for their connections to New Brunswick and their storytelling. Thank you to all the growers for taking me under their wing, introducing me to industry contacts at meetings, and following up with field progress. Thank you also to J. Geldart and M. Mills from the NS and NB blueberry associations, respectively, for welcoming me into the associations to develop my presentation and networking skills.

Thank you to the best field team possible, especially Kathleen Glasgow and Cody Chapman. Kathleen: your edits, support, and friendship are so important to me. I'm excited to watch your own journey in science. Cody: thank you for your curiosity about bee identification and bee photos. You both made field work fun. Thank you to Colin Chapman for arriving at the AC at the perfect moment to push identification forward, ask tough questions, and plan for the next field season. I am very grateful for your identification skills and pursuit for the correct ID! Thank you to C. Garden, J. Baak, E. Vance, D. Augustine Joseph, and A. Loureiro for sampling help in the field. Thank you to Sawyer Olmstead for helping me plan field studies, debate *Osmia* in blueberry fields, and learn about bee flowers. Thank you also for introducing me to the world of honey bees. Thank you to both J. Sproule and S. Dhadi for your help as lab managers, and A.

Melathopoulos for helping me talk things through. I am grateful to Deirdre Loughnan and Meghan Marriot for their help in the lab, and their unique perspectives on plant-pollinator interactions. Deirdre: I am inspired by your knowledge of R, your ability to encourage others, and your positive views on academia and science. Thank you to Paul Manning for encouraging me throughout this journey and always being available to help with problem-solving, technology, and statistics.

I am grateful for the good friends I am surrounded with. Thank you Rosalie Madden and Carolyn Marshall for stirring the pot with me throughout grad school, debating the role of women in agriculture and science, and strengthening my communication skills. Thank you Carolyn Wilson for your highly entertaining friendship, and sharing my love for NB agriculture, farming, and agricultural communication. Thank you to Katie for being the best sister anyone could ask for, and to E. Davis, S. Harding, and B. Ross for supporting and encouraging me throughout this project.

Thank you to the funding sources who made this project possible, including NSERC, Syngenta's Operation Pollinator, and Nova Scotia Department of Agriculture. I am also grateful to Paul Hoekstra from Syngenta who gave me many opportunities to broaden my pollinator knowledge and communication skills.

I am very thankful to both of my supervisors, Dr. Nancy McLean and Dr. Chris Cutler. Their unique perspectives strengthened the project and helped me grow as a student. I was fortunate to be able to incorporate insects and their interactions with plants in this project because of the expertise of my supervisors. Thank you both for your support along the way. Thank you also to Dr. Randy Olson and Dr. Derek Lynch for supporting me as committee members and providing valuable feedback throughout the study.

Thank you to Perennia for giving me the opportunity to enter the world of honey bees while finishing my thesis. This new perspective helped me greatly with my writing and allowed me to further consider the impact of my research.

CHAPTER 1: INTRODUCTION

1.1 BENEFICIAL INSECTS IN AGROECOSYSTEMS

Essential pollination and pest control services are provided by insect pollinators and natural enemies in many agricultural ecosystems (‘agroecosystems’), but declines of these beneficial insects have been widely reported (Allen-Wardell et al. 1998; Biesmeijer et al. 2006; Colla and Packer 2008; Potts et al. 2010; Colla et al. 2012b; Koh et al. 2015). Insect pollinators play an integral role in the perpetuation of flowering plants and pollination of agricultural crops (Klein et al. 2007; Ollerton et al. 2011). Bees (Hymenoptera: Apoidea) are the most significant pollinators due to their foraging behaviour and morphological adaptations, including pollen-carrying capacity (Free 1993; Michener 2007), although other insects including wasps (Hymenoptera, Apoidea), beetles (Coleoptera), and flies (Diptera) also pollinate flowers by moving pollen from anthers to stigmas. Wild (unmanaged) pollinators may provide more than $3 billion USD annually in pollination services for agricultural crops in the United States (Losey and Vaughan 2006). Natural enemies, including parasitoids and predators, provide biological control services through killing or limiting damage caused by insect pests. Predators including ground beetles (Coleoptera: Carabidae) and ladybird beetles (Coleoptera: Coccinellidae) attack and kill insect pests (Lovei and Sunderland 1996; Obrycki and Kring 1998; Kromp 1999) while parasitoids, including tachinid flies (Diptera: Tachinidae) and ichneumonid wasps (Hymenoptera: Ichneumonidae), parasitize and feed on insect pests. Natural enemies have been estimated to prevent nearly $4.5 billion USD in agricultural crop losses each year in the United States (Losey and Vaughan 2006).

Beneficial insect enhancement has struck a chord with the general public and researchers alike, and troubling population declines have motivated a plethora of research in the past decade on potential causes and solutions (Spivak et al. 2011; Gill et al. 2016). Multiple contributing factors have been identified for declining beneficial insect populations including habitat and landscape modification (Goulson et al. 2008; Brown and Paxton 2009; Westphal et al. 2009; Chaplin-Kramer et al. 2011; Kennedy et al. 2013; Koh et al. 2015), pest and disease pressures (Colla et al. 2006; vanEngelsdorp and Meixner 2010), pesticide use (Brittain and Potts 2011; Park et al. 2015), and climate change (Kerr et al. 2015; Ziska et al. 2016). Although multiple factors may be involved in population declines, I focused on habitat management, and tested different techniques for their effect on boosting beneficial insect communities in agroecosystems. Different treatments of habitat management, a component of conservation biology, were implemented to test their efficacy in enhancing lowbush blueberry (*Vaccinium angustifolium* Aiton) agroecosystems through provision of food and nesting resources.

Habitat management has been implemented for wild pollinators (Hopwood 2008; Wratten et al. 2012; Blaauw and Isaacs 2014a; M'gonigle et al. 2015; Venturini et al. 2017) and natural enemies (Landis et al. 2000; Thomson and Hoffmann 2009; Walton and Isaacs 2011) in various agroecosystems, but few enhancement techniques have been implemented in lowbush blueberry. Lowbush blueberry is among the most pollinator-dependent crops, and conceivably the most able to rely on wild bees for pollination in North America (Eaton and Nams 2012; Cutler et al. 2015b; Melathopoulos 2015). Additionally, lowbush blueberry faces significant insect pest challenges, is typically cultivated in relatively small fields, and is a perennial crop with minimal soil disturbance, factors which can facilitate beneficial insect conservation (Landis et al.

2000). These challenges and opportunities support my contention that lowbush blueberry agroecosystems are well suited for habitat management studies.

1.2 LOWBUSH BLUEBERRY AGROECOSYSTEMS

Lowbush or ‘wild’ blueberry (Ericaceae) is an agricultural crop that is managed commercially in Eastern Canada and Maine, U.S. (Vander Kloet 1988). Blueberry fields are developed after forest is cleared or burned, and blueberry plants spread into the cleared land by underground stems called rhizomes (Yarborough 2012). The crop is typically managed on a two-year cycle consisting of vegetative growth (“sprout” year) and fruit production (“crop” year). The vegetative year involves plant growth, spreading of rhizomes, and initiation of flower buds for the following fruit-bearing year. In the fruit-bearing year, blueberry plants bloom, and, if they are pollinated, set fruit. Following harvest in late summer, blueberry plants are pruned by burning or mowing in the autumn or spring (Barker et al. 1964), which stimulates growth and development for the following vegetative year.

Canada and the United States dominate lowbush blueberry production. More than 79,000 ha are cultivated in Canada alone (Statistics Canada 2016). A growing export market, particularly in Europe and Asia, and health benefits associated with rich antioxidants in the fruit, have driven increased production of this crop in recent years (Agriculture and Agri-Food Canada 2015). In order to facilitate an increase in production, pollination and pest control must be optimized (Kinsman 1993; Yarborough 1997, 2004).

1.3 HABITAT MANAGEMENT FOR BENEFICIAL INSECTS

As agricultural practices intensify to maximize food production, suitable habitat and floral resources for beneficial insects can be lost to monoculture crop fields and intensive management of weeds, diseases, and pests through chemical and cultural means (Kearns and Inouye 1997; Isaacs et al. 2009; Spivak et al. 2011; Rusch et al. 2016). Despite these practices, agriculture may benefit from incorporating conservation efforts (Tscharntke et al. 2005; Spivak et al. 2011), as many crops are dependent upon beneficial insects for pollination and biological pest control (Losey and Vaughan 2006; Klein et al. 2007). Furthermore, agricultural land use represents a significant land mass globally, and could therefore have substantial impacts on beneficial insect communities.

Crop field margins can provide key resources to beneficial insects, particularly before and after crop bloom (Kearns and Inouye 1997; Morandin et al. 2007; Isaacs et al. 2009; Kennedy et al. 2013; Bell et al. 2016). Providing adequate floral and habitat resources is especially important for beneficial insects with limited foraging ranges (Ricketts et al. 2008; Garibaldi et al. 2011; Rao and Strange 2012). Enhanced field margins can serve as stable habitats and have even been shown to positively impact crop fruit set and mitigate the harmful effects of pesticides applied in the adjacent crop. In almond orchards in California, U.S., increasing proportions of surrounding natural habitat facilitated increased wild bee visitation and greater fruit set (Klein et al. 2012). As the area of natural habitat surrounding apple orchards increased, the impact of pesticides on wild bee abundance and species richness diminished (Park et al. 2015), and perennial floral resources implemented in mango orchards buffered the negative effects of pesticide use and isolation from natural habitat on pollinators (Carvalheiro et al. 2012). Positive impacts on both pollinators (Kennedy et al. 2013; Blaauw and Isaacs

2014a) and natural enemies (O'Neal et al. 2005b; Walton and Isaacs 2011; Woltz et al. 2012; Blaauw and Isaacs 2015) have been documented with increased natural habitat and floral resources in agricultural landscapes.

There are challenges to ensuring pollinators have access to floral resources before and after the principal crop bloom and perhaps even during bloom, in order to supplement nutritional needs (Stubbs et al. 1992). The problem of insufficient floral and nesting resources is further exacerbated by a lack of awareness and understanding for practical on-farm techniques to conserve beneficial insects without hindering crop production. Negative relationships between intensive fruit cultivation and wild bee abundance have been detected in sweet cherry (*Prunus*) systems (Eeraerts et al. 2017), but when agroecosystems supply adequate food and nesting resources throughout the season, wild pollinators can contribute pollination services to nearby crops (Westrich 1996; Kearns and Inouye 1997; Carreck and Williams 2002; Morandin and Winston 2006; Morandin et al. 2007; Ricketts et al. 2008; Tuell et al. 2009; Blaauw and Isaacs 2014a). Another advantage of habitat management is that productive land does not need to be set aside; Blaauw and Isaacs (2014a) demonstrated that land used for floral plantings can be marginal and along the field edge. Similarly, floral enhancements in mango orchards occurred on non-productive field margins and did not negatively impact crop production (Carvalheiro et al. 2012). Other potential benefits of habitat management include erosion control, soil nutrient cycling, chemical runoff reduction, and aesthetic beauty (Isaacs et al. 2009; Wratten et al. 2012), rewards that could be used to promote greater producer adoption.

Despite documented success, recent research has highlighted the variable results of agri-environmental schemes (AES) in Europe (Scheper et al. 2013; Wood et al.

2015a; 2017). AES seek to enhance agroecosystems for services such as pollination and biological pest control, and deliver financial incentive to farmers willing to implement some form of habitat management (European Commission 2016). The drawbacks include variability of surrounding landscape and agricultural intensity, as well as the vast diversity and subsequent differing responses of various pollinator groups (Scheper et al. 2013; Wood et al. 2015a). A recent U.K. study found only 23.3% of pollen collected (by volume) by solitary bees was from flower-rich AES, and instead pollen was mainly collected from plants persisting elsewhere in the agroecosystem (Wood et al. 2017). More research into suitable floral resources is therefore needed. For example, phacelia (*Phacelia tanacetifolia*) is commonly added to AES mixtures due to its high pollen protein content, yet a study in New Zealand found that only 1 pollen pellet out of more than 23,000 pellets in nearby honey bee hives contained phacelia pollen, suggesting bees may not be accessing the high nutritional quality of this plant (Sprague et al. 2016). Honey bees were observed foraging on phacelia for nectar, however (Sprague et al. 2016). The diversity in needs among wild pollinators and natural enemies, including differences in nesting sites, food resource utilization, and emergence, can hinder enhancement measures, as these measures must also be diverse (Westrich 1996; Rollin et al. 2013). Yet another possible challenge with planting flowering borders or margins is the concern that floral plantings will concentrate beneficial insects rather than boost their populations in nearby target crops (Obrycki and Kring 1998). Various studies have demonstrated, however, that beneficial insects migrate to nearby crop fields to contribute to pollination and pest control, reinforcing the value of field edge habitat management (Morandin and Kremen 2013; Blaauw and Isaacs 2015).

The testing of augmentative plantings near agriculture fields has increased in the past decade, with variable findings. Benefits from floral plantings in agroecosystems have been documented in coffee (*Coffea* spp.) (Peters et al. 2013) and almond (*Prunis* spp.) agroecosystems (Saunders et al. 2013; Norfolk et al. 2016), but recent studies have also indicated the limitations of augmentative plantings (Wood et al. 2015a; Sardinas and Kremen 2015). Given the disparity of results from floral plantings for bees, I tested habitat management techniques in lowbush blueberry in Nova Scotia, Canada. I specifically planted buckwheat along blueberry field edges to provide food for bees after blueberry bloom. In order to be of economic benefit, however, floral plantings must be attractive to crop pollinators. As such, I also evaluated the bee fauna during blueberry bloom to determine whether the same genera involved in crop pollination also visited buckwheat. In addition to buckwheat, I evaluated six forage crops for their attractiveness to bees.

A greater understanding of the wild bee community and its specific habitat requirements is needed to best enhance and support these communities. These requirements are likely to vary depending on the family or genus in question. For instance, *Bombus* require food resources before, during, and after blueberry bloom, in order to sustain growing colonies. Unlike colonial *Bombus*, solitary *Andrena*, *Halictus,* and *Lasioglossum* typically actively forage only a few weeks (Michener 2007). Thus, solitary bees involved in blueberry pollination may only need alternative floral resources just before or immediately following crop bloom to complete their life cycles. Understanding which bees are present in blueberry agroecosystems could inform proper enhancement and management practices to best support the bee fauna, and the pollination services they provide. Accurate sampling techniques are needed, however, to precisely measure the bee community, its subsequent needs, and pollination potential (Russo et al. 2015; Wood et al. 2015b).

Habitat management must lead to subsequent increases in beneficial insect abundance in adjacent crop fields in order to impact pollination and pest control. Often this translates to a female beneficial insect having sufficient forage and habitat resources to provision for offspring, leading to future generations that will contribute to these vital ecosystem services. An on-farm habitat restoration study in California, U.S. found pollinator diversity to be higher in mature hedgerows (established more than 10 years ago) than control sites, but maturing hedgerows (1-10 years post-implementation) did not contain significantly more pollinators than control sites (Ponisio et al. 2016). Habitat management is therefore not an instant remedy; instead, it seeks to build communities of beneficial insects through supply of immediate resources. The challenges stemming from the variable results of AES and other habitat management endeavours demonstrate the need for further research in different agroecosystems. Despite more than two decades of habitat management research, the ‘optimal’ enhanced agricultural field edge has not been established, nor is research on this topic simple or straight-forward (Gill et al. 2016). Furthermore, enhancements may boost pollinators and natural enemies for a year or two, but long-term data on population trends are lacking (Gill et al. 2016).

1.4 WILD POLLINATORS IN LOWBUSH BLUEBERRY

Lowbush blueberries require insect pollinators for fruit production (Wood 1968; Aras et al. 1996; Cutler et al. 2012a), and although numerous insects are involved in pollination, bees are considered the most important (Free 1993; Michener 2007). Blueberry growers historically relied on wild pollinators for adequate pollination (Boulanger et al. 1967), but a combination of increased pesticide use, larger fields, and more blossoms per field have made pollination from wild pollinators less reliable, and has driven the use of managed bees, particularly honey bee (*Apis mellifera* Linnaeus) colonies (Boulanger et al. 1967; Kevan 1977; Stubbs et al. 1992; Free 1993; Eaton and Murray 1997).

Although not as well adapted to blueberry flower morphology as certain wild bees, honey bees can provide adequate pollination of blueberries (Whidden 1996; Yarborough 1997; Eaton and Nams 2012). As blueberry production continues to increase in eastern Canada and the northeastern U.S., demand for honey bee colonies is also increasing, but challenges such as disease and pest pressures, rising hive rental costs, and a limited supply of hives have arisen in recent years (Kinsman 1993; Kevan and Phillips 2001; Stubbs and Drummond 2001; Kremen et al. 2007; Potts et al. 2010; vanEngelsdorp and Meixner 2010). Furthermore, there is concern of relying on a single bee species for pollination (Winfree et al. 2007, 2011; Winfree 2010). In order to combat these issues and maintain adequate pollination, interest is turning to wild pollinators. Wild pollinators, especially bees, are efficient and effective, and some species have co-evolved with the blueberry crop. Common wild bees include mining bees (Andrenidae), bumble bees (Apidae), sweat bees (Halictidae), and mason bees (Megachilidae). More than 100 wild bee species and numerous fly pollinators have been recorded in lowbush blueberry agroecosystems (Sheffield et al. 2003; Moisan-Deserres et al. 2014b; Bushmann and Drummond 2015; Cutler et al. 2015b), and more than 75 species of bees have been documented visiting blueberry flowers in Eastern Canada (Sheffield et al. 2003; Moisan-Deserres et al. 2014b). Complementary pollination among different pollinator groups has been shown to enhance overall pollination in agroecosystems including almonds (*Prunus dulcis* (Mill) Webb) (Brittain et al. 2013), pumpkins (*Cucurbita* spp.) (Hoehn et al. 2008), and sunflowers (*Helianthus annuus* L.) (Greenleaf and Kremen 2006). Conserving a diversity of wild bees could therefore have beneficial impacts on lowbush blueberry pollination.

Many wild bees are also highly effective pollinators of lowbush blueberry. In Nova Scotia, Canada, bumble bees (*Bombus*) visited significantly more blueberry flowers per minute than any other bee recorded, and pollen-collecting mining bees (*Andrena*), *Bombus*, and *Halictus* bees had significantly greater rates of successful pollination than honey bees (Javorek et al. 2002). Wild pollinators native to the region are well-adapted to weather conditions typical of blueberry's early spring bloom (mid-May to mid-late June in Eastern Canada) as well as the floral morphology of blueberries (Free 1993; Kearns and Inouye 1997; Stubbs and Drummond 2001; Javorek et al. 2002; Michener 2007). Both bumble bees and mining bees are capable of buzz-pollination, and these two genera were also found to carry the largest blueberry pollen loads in Quebec, Canada (Moisan-Deserres et al. 2014b). Buzz pollination is particularly beneficial for lowbush blueberry due to its poricidal anthers, whereby pollen from anthers is released through a small opening and requires vigorous shaking to be released (Kearns and Inouye 1997; Delaplane and Mayer 2000; Michener 2007). Wild bees are also considered useful "insurance policies" during cool, wet weather (Hanes et al. 2013) while honey bees are more likely to forage during fair weather conditions (sunny and warm), wild bees native to the area have adapted to forage during poor weather conditions (e.g. light precipitation and wind). If a pollination season is rainy, wild bees may be needed to pollinate blueberry flowers when honey bees are unable to forage. Despite these qualities, wild bee communities are highly variable with natural year-to-year fluctuations (Kinsman

1993; Roubik 2001; Hanes et al. 2013; Bushmann and Drummond 2015), and face pressures from pesticide use, loss of natural habitat, and insufficient season-long food resources. Focus is therefore shifting to maximizing wild bee populations by managing the habitat to be conducive to these beneficial insects (Hanes et al. 2013).

Developing enhancement techniques for wild pollinators in lowbush blueberry presents an opportunity to study a rich insect fauna. Bees are the most important insect pollinators (Free 1993; Kearns and Inouye 1997) and focus was thus placed on this group, although other aforementioned pollinators (wasps, beetles, butterflies, moths and flies) were considered in a natural enemy study. Wild pollinators provide over $2.3 million USD in pollination services for lowbush blueberries in the U.S. alone (Losey and Vaughan 2006), yet knowledge gaps still exist regarding useful enhancement measures for wild pollinators (Delaplane and Mayer 2000; Michener 2007; Gill et al. 2016). With natural adaptations that allow them to thrive in the region, wild pollinators are invaluable to production of many of our food crops and represent a more sustainable and a potentially more effective means of pollination than managed honey bees (Javorek et al. 2002; Garibaldi et al. 2013). I therefore examined habitat management techniques for their ability to boost existing bee communities in lowbush blueberry agroecosystems, specifically through providing nesting habitat and flowering resources. I hypothesized that these habitat management techniques could provide the basic requirements of food and nesting within the crop vicinity, potentially encouraging bees to remain and reproduce in the area. I expected techniques to vary in their efficacy and impact groups of bees differently.

Artificial nesting substrates for bees have been implemented and encouraged in several cropping systems including apples (*Malus*) (Sheffield et al. 2013), alfalfa

(*Medicago sativa*) (Pitts-Singer and James 2008), almonds (*Prunus*), and blueberries (*Vaccinium*) (Drummond and Stubbs 1997; Sheffield et al. 2014). I was interested in different nest designs and placement within the blueberry field to best suit the cavity-nesting bee species found in Nova Scotia. The unique fruit-bearing and vegetative development stages of lowbush blueberry may potentially impact nesting success, as reproducing females must have adequate nesting materials and food sources for their offspring. Nesting occupancy was therefore compared between fruit-bearing and vegetative fields for different nest designs, as well as along the field edge and into the field for one trap nest design. Previous studies have highlighted concerns with parasitism and poor emergence from trap nests (Drummond and Stubbs 1997; Stubbs et al. 1997; Frankie et al. 1998; Pitts-Singer and James 2008; Sheffield et al. 2008; MacIvor and Packer 2015). Different nest designs and placement strategies were therefore evaluated in Nova Scotia lowbush blueberry fields to determine the efficacy of boosting cavity-nesting bees, and parasitism and emergence were also examined.

Buckwheat (*Fagopyrum esculentum* Moench) and six different forage crops were evaluated as potential floral resources for bees. My interest in evaluating buckwheat as a floral resource first began when I was studying wild bees in lowbush blueberry as a summer student with the New Brunswick Department of Agriculture. During this position, I met a blueberry grower who planted a variety of floral resources around his lowbush blueberry fields to support bees after blueberry bloom had finished. One of these plants was buckwheat, an annual with accessible, white flowers known to be attractive to bees. After observing the heavy presence of various pollinators in the buckwheat plantings, I was interested in further exploring this practice and determining its effect on wild bee communities. In addition to my interest in buckwheat, I wished to compare other flowering plants for their attractiveness to bees. Forages, particularly legumes, are known to be nutritious for other livestock (e.g. cattle and sheep), and many forages are naturalized to Atlantic Canada. Farmers are generally familiar with these plants, easing their concern of ‘bee plants’ becoming weed pressures within crop fields. The interest in forages led to an experiment comparing different forages, particularly legumes, for bloom period, floral density, bee visitation, and plant-pollinator interactions.

Effective and accurate sampling methods are required to study the bee fauna of any given agroecosystem, as different sampling methods can result in different bee taxa being collected (Popic et al. 2013; Meyer et al. 2017). Previous studies in lowbush blueberries tended to use single collection method (Hicks 2011; Moisan-DeSerres et al. 2014a; Cutler et al. 2015b; Melathopoulos 2015). Each method contains its own inherent bias, and the bee community structure is potentially misrepresented if only a single collection method is used. In Quebec, Canada, aerial netting was used to survey the pollinator fauna during blueberry bloom (Moisan-Deserres et al. 2014a). The study found *Bombus frigidus* to be the most abundant pollinator, followed by *Andrena* spp. (Moisan-Deserres et al. 2014a). In a Nova Scotia survey using pan trapping, *Lasioglossum* was the most abundant genus recorded, followed to a much lesser degree by *Andrena* (Cutler et al. 2015b). Recent studies in other crops have also implemented single sampling methods to determine the bee community structure including highbush blueberry (*Vaccinium corymbosum* L.) (Tuell et al. 2009; Isaacs and Kirk 2010; Blaauw and Isaacs 2014a) and apple (*Malus domestica* Borkh) (Russo et al. 2015). By using aerial netting to survey bee fauna in apple orchards, less than 75% of expected species richness was documented in over half of the study sites, despite intensive sampling efforts (Russo et al. 2015). In Uganda, pan trapping was found to be complementary to aerial netting for recording wild bee fauna (Theodore Munyuli 2013), indicating the value in implementing multiple collection methods. In Switzerland, a comparison of pan trapping and sweep netting demonstrated that different bee fauna can be captured when different sampling methods are utilized (Meyer et al. 2017). Utilization of multiple collection methods may therefore allow for a more representative survey of bees during blueberry bloom. I implemented two bee sampling techniques in lowbush blueberry agroecosystems: aerial netting and pan trapping.

1.5 NATURAL ENEMIES IN LOWBUSH BLUEBERRY

Similar to pollinator enhancement biological pest control using insect natural enemies has received much attention in recent years. Pesticides, including insecticides, are used on a number of agricultural crops, and can facilitate increased production required to feed the growing human population. Although widely used in agriculture, insecticides have the potential to cause detrimental effects on beneficial insects including bees and natural enemies (Desneux et al. 2007; Brittain and Potts 2011; Pettis et al. 2013; Frazier et al. 2015). Negative effects on bees from insecticides commonly used within lowbush blueberry fields have also been documented (Gradish et al. 2012a; Gradish et al. 2012b). A critical management challenge for agriculture is determining how best to protect beneficial insects while also protecting the crop from harmful pests. Amidst concern for misuse and harmful effects of pesticides, and increasing market pressure for ‘spray free’ and organic products, interest in biological pest control is growing.

Lowbush blueberry agroecosystems are home to numerous insect natural enemies that provide biological pest control, including wasps and beetles that prey upon or parasitize insect pests of this crop. In this dissertation, I focused on six natural enemy groups: ground beetles (Coleoptera: Carabidae), hover flies (Diptera: Syrphidae), ladybird beetles (Coleoptera: Coccinellidae), robber flies (Diptera: Asilidae), tachinid flies (Diptera: Tachinidae), and wasps (Hymenoptera). Certain ground beetles are known to predate upon blueberry maggot (*Rhagoletis mendax* Curran) (Renkema et al. 2012) and blueberry spanworm (*Itame argillacearia* Packard) (Renkema et al. 2013), both of which are significant lowbush blueberry pests (Wood et al. 1983; Kinsman 1993). In Nova Scotia blueberry fields, Ichneumonidae wasps and Tachinidae flies parasitized blueberry spanworm, and parasitism rates among fields ranged from 0 to 36.8% (Loureiro and Cutler 2016), while Cutler et al. (2015a) found rates as high as 50-60%, indicating biological control can be unique among fields. Biological pest control is not only limited to insect pests. In Nova Scotia, carabid beetles (*Harpalus rufipes* Degeer) and field crickets (*Gryllus pennsylvanicus* Burmeister) were found to consume seeds of sheep sorrel (*Rumex acetosella* L.) and hairy fescue (*Festuca tenuifolia* Pourr), prominent weeds in lowbush blueberry fields (Cutler et al. 2016). Studies in the last five years have highlighted the potential of natural enemies to provide important biological pest control services in lowbush blueberry, and enhancement techniques to boost these communities could significantly benefit pest management.

Beneficial insects require adequate food and shelter resources to thrive in agroecosystems, and these requirements vary based on life history and feeding patterns. For example, ground beetles typically lay their eggs on the surface of the soil or just below, suggesting undisturbed soils may be best for reproduction (Kotze et al. 2011). This could explain why a diverse and abundant ground beetle fauna has been detected in lowbush blueberry agroecosystems previously, due to its perennial growth and undisturbed soils (Cutler et al. 2012b). Although ground beetles are known to consume larvae of insect pests, certain ground beetles also consume seeds and plant material (Kotze et al. 2011; Cutler et al. 2016), suggesting that floral resources could increase available food resources for ground beetles. The installation of flower strips near crop fields to provide refuge and a location for breeding and overwintering could also increase the communities of beneficial ground beetles (Goulet 2003). With nearly 290 species of ground beetles known to occur in Nova Scotia (Majka et al. 2007; Majka and Bousquet 2008), efforts to conserve and enhance this group could have significant impacts on biological pest control. Ladybird beetles are well known biological control agents of agricultural crops, and 41 species are known to occur in Nova Scotia (Majka and McCorquodale 2006). Like ground beetles, ladybird beetles are known to predate upon insect pests, particularly aphids, but may also consume plant material such as pollen during their life cycle (Sloggett and Majerus 2000; Lundgren 2009). Provision of flowering strips or borders has also been suggested to conserve this group of natural enemies, although Obrycki and Kring (1998) cautioned these enhancement areas could act as 'traps' and keep ladybird beetles from performing pest control services in adjacent crop fields. Recent studies have revealed, however, that flowering hedgerows created in agricultural landscapes export bees into adjacent crop fields (Morandin and Kremen 2013), and the same may be true for natural enemies.

Many solitary wasps nest in the soil and, like other ground-nesting beneficial insects, potentially benefit from undisturbed soils. Most adult solitary wasps consume nectar, honeydew, and pollen but collect other insects to feed to their developing offspring, and parasitize insect pests and utilize them as hosts (Kevan 1973; Spradbery 1973; Hunt et al. 1991; Loureiro and Cutler 2016). Certain wasp families, including

Vespidae, are restricted to plants with shallow corolla tubes, limiting their ability to access nectar unless they ‘rob’ by chewing a hole through the corolla tube (Spradbery 1973). In Maine, U.S., a number of ‘weedy’ flowering species have been positively correlated to wasp abundance in lowbush blueberry fields (Karem et al. 2010), perhaps due to food provision and shelter. Due to their similar life histories, enhancement techniques for bees could conceivably also benefit wasps.

Hover fly larvae are known to consume insect pests, including aphids and thrips, but the adults generally consume pollen and nectar from flowers (Gilbert 1983; Free 1993; Wratten et al. 1995; Irvin et al. 1999). Robber flies are known to predate upon other insects, but have also been recorded targeting other beneficial insects, including bees (Bromley 1930; Wei et al. 1995; Hayat 1997). In Turkey, the prey of robber flies was comprised of 57.4% Hymenoptera, followed to a lesser degree by members of Diptera, Coleoptera, Hemiptera, Homoptera, and Lepidoptera (Hayat 1997). Tachinid fly larvae will consume insect pests, but the adult flies generally visit flowers for nourishment (Stireman et al. 2006). Previous studies have demonstrated the beneficial impact of flowering strips on hover fly abundance and diversity (e.g. Jonsson et al. 2015; Meyer et al. 2017). Many of these biological control agents are also known to pollinate, including hover flies, tachinid flies, and wasps (Free 1993), although in my study, they were counted as natural enemies. Among the six groups of beneficial insects I studied, there was typically at least one life cycle stage that required flowering resources to provide food. I was interested in whether providing flowering resources near lowbush blueberry agroecosystems would impact the abundance and diversity of beneficial insects.

1.6 THE CONSERVATION CONUNDRUM

Although biodiversity is important, not all bees found within agroecosystems contribute to crop pollination (Senapathi et al. 2015). A relatively small number of wild pollinators dominate the majority of agricultural crop pollination (Biesmeijer et al. 2006; Kleijn et al. 2015), and many wild bees are active only after the lowbush blueberry bloom period (Sheffield et al. 2003; Cutler et al. 2015b). Consequently, some argue that focus should be on conserving and enhancing bee species contributing directly to crop pollination (Moisan-Deserres et al. 2014b). Although solitary bees emerge throughout the season and have an adult lifespan of only a few weeks (Michener 2007), bumble bee queens are important blueberry pollinators and require nearby floral resources after blueberry bloom has finished in order to support the growing colony. Despite the appeal of boosting the pollinators most involved in blueberry pollination, other pollinators cannot be ignored, especially with concerns of climate change (Senapathi et al. 2015). With uncertainty pertaining to the impact of climate change on plant flowering and pollinator phenology, a diversity of pollinators is key; as Tscharntke et al. (2005) said, “in dynamic, agricultural landscapes, only a diversity of insurance species may guarantee resilience”. Thus, conserving the overall bee fauna in blueberry-growing regions is important, for biodiversity’s sake, for increased ecosystem resilience, and as an ‘insurance policy’ for blueberry pollination (Senapathi et al. 2015).

1.7 OBJECTIVES

This dissertation examines the impacts of several habitat management techniques on beneficial insects in lowbush blueberry agroeocsystems. I defined ‘wild’ bees as unmanaged bees, and included native, non-native, and naturalized bees within the scope of this research. I defined lowbush blueberry as an ‘agroecosystem’ as it is an ecosystem that serves an agricultural function (the production of lowbush blueberries), is managed (e.g. the use of managed pollinators, application of fertilizers and crop protection agents), and consists of both biotic and abiotic factors.

I first used habitat management to explore nesting substrates for solitary bees. Bees within the Megachilidae, such as *Megachile* and *Osmia*, are effective pollinators, and many species show potential to be managed in cropping systems (Sheffield et al. 2014). Artificial nesting substrates including clay lids, milk carton nests, and wooden nests were evaluated for nesting occupancy by solitary Megachilidae bees (Chapter 2). The impacts of field type and distance from the field edge were also tested, and emergence and parasitism of bees from successful nesting blocks were evaluated (Chapter 2).

Buckwheat (*Fagopyrum esculentum* Moench) was planted in blueberry field margins, and the abundance and diversity of bees in these plantings were compared to unenhanced (‘control’) field margins (Chapter 3). I expected bee abundance and diversity to be higher in buckwheat margins compared to control margins due to the food resources (nectar and pollen) provided by buckwheat. In Chapter 3, I determined if the same bee taxa visiting buckwheat flowers were also present during blueberry bloom. The abundance and diversity of bees were monitored during blueberry bloom, and two collection methods (aerial netting and pan trapping) were evaluated for their effect on bee collection (Chapter 3).

I predicted that the buckwheat planted for wild bees in Chapter 3 would also benefit natural enemy communities, including beetles (particularly Carabidae and

Coccinellidae families), hover flies, robber flies, tachinid flies and wasps. The impact of buckwheat on natural enemy abundance was therefore simultaneously tested during wild bee sampling (Chapter 4).

Forage crops including legumes (Fabaceae) were established near blueberry fields, and floral density, bloom period, bee visitation, and plant-pollinator interactions were recorded (Chapter 5).

All habitat management techniques tested were practical and able to be implemented on-farm by blueberry growers, and no productive blueberry land was taken out of production in order to encourage producer adoption. Information on the ability and efficacy of various habitat management techniques in lowbush blueberry to enhance pollinator and natural enemy communities were generated in this study.

Identification of specimens within this thesis were based on a number of resources. Reputable keys including Laverty and Harder (1988), Packer et al. (2007), and Williams et al. (2014) were used to identify bees. Voucher specimens of both bees and natural enemies were submitted to the Canadian National Collection (CNC) of Insects in Ottawa for identification. Identification experts were consulted when necessary. I was fortunate to attend the American Museum of Natural History’s Bee Course in Arizona in 2014, where I had the opportunity to further my bee identification skills with some of the best bee researchers in the world.

CHAPTER 2: AN ASSESSMENT OF ARTIFICIAL NESTS FOR CAVITY-NESTING BEES IN LOWBUSH BLUEBERRY

2.1 ABSTRACT

Declining bee (Hymenoptera: Apoidea) populations jeopardize pollination services. Nesting habitat for solitary bees is limited in many agroecosystems (Westrich 1996), but the provision of artificial nests could augment bee communities and the pollination services they provide in these habitats. I investigated whether various cavity-nesting bees (Hymenoptera: Megachilidae) in lowbush blueberry (*Vaccinium angustifolium* Aiton) fields would nest in artificial trap nests. Different nest designs were compared, as was nesting occupancy between fruit-bearing and vegetative fields. Parasitism and bee emergence were recorded. Milk carton nests had significantly more uptake by and emergence of *Osmia* and *Megachile* than wooden nests. Only 3% of the wooden nests had at least one occupied nesting tube versus 73% of milk carton nests, with a total of 176 out of 512 nesting tubes (34%) occupied. Bee emergence was significantly higher in nesting tubes from fruit-bearing fields than vegetative fields. Overall emergence of *Osmia* and *Megachile* was low from milk carton nests, with bees emerging from less than 10% of occupied nesting tubes, in large part due to parasitism from wasps and flies. Overturned clay lids were also tested as potential nesting sites for *Osmia inermis* Zetterstedt, but only 3% of deployed lids had evidence of nesting. My results suggest that certain artificial nests used in this study have potential for conserving and boosting natural communities of cavity-nesting bees around lowbush blueberry fields, but further study is needed on trap nest designs and handling protocols.

2.2 INTRODUCTION

Lowbush blueberry (*Vaccinium angustifolium* Aiton), an important crop in Eastern Canada and the state of Maine in the U.S., relies heavily on bees (Hymenoptera: Apoidea) for cross-pollination (Aras et al. 1996; Eaton and Nams 2012). The crop is typically managed on a two-year cycle of an initial year of vegetative growth ("sprout year") followed by a second year of fruit development and harvest ("crop year"). Managed honey bees (*Apis mellifera* L.) are often used for blueberry pollination (Yarborough 1997; Eaton and Nams 2012), but blueberry growers are interested in using and promoting non-*Apis* bees to pollinate their crop. Numerous species of wild bees are effective pollinators of blueberry (Javorek et al. 2002) but their abundance can vary, and blueberry growers are usually unable to rely entirely on wild populations for adequate pollination (Eaton and Murray 1997). Various tactics to boost wild bee populations have been shown to improve pollination of several crops (Vaughan and Black 2008; Wratten et al. 2012; Blaauw and Isaacs 2014a), and such techniques could be adapted to lowbush blueberry.

Osmia and *Megachile* bees (Hymenoptera: Megachilidae) collect lowbush blueberry pollen (Drummond and Stubbs 1997; Hicks 2009) but may not be as abundant in lowbush blueberry agroecosystems as other wild bees (Bushmann and Drummond 2015; Cutler et al. 2015b). Different *Osmia* and *Megachile* species nest in a variety of natural habitats including plant stems and abandoned tunnels in wood from previous insect inhabitants, as well as under rocks, but will also nest in artificial structures made of wood or other materials that mimic their natural nesting substrates (Torchio 1987; Cane et al. 2007; Packer et al. 2007; Hicks 2009; Guisse and Miller 2011; Sheffield et al. 2013, 2014). In Nova Scotia, Canada, wax-cardboard milk cartons containing paper tubes were used as artificial nests for solitary bees in apple (*Malus* spp.) pollination, and provided suitable and effective nesting habitat for *Osmia tersula* Cockerell and other species (Sheffield et al. 2008). Certain *Osmia* species prefer to nest under rocks, and although these populations can be difficult to manage (Cane et al. 2007), 10% of overturned clay lids placed in lowbush blueberry fields in Newfoundland, Canada, were used by *O. inermis* Zetterstedt as an artificial nesting substrate (Sheffield et al. 2014). Despite the potential of artificial nests to support *Osmia* and *Megachile* populations in lowbush blueberry (Stubbs et al. 1997), little research has been published testing nest design and dispersal in lowbush blueberry fields. Artificial nests were placed in lowbush blueberry fields in Nova Scotia to examine if Megachilidae would nest in these substrates. Nesting occupancy in three different nest designs (milk carton, wooden, and clay lid) was tested. Nesting occupancy was compared between fruit-bearing and vegetative fields for milk cartons and clay lids, and was also compared between field edges and within fields for clay lids. Although *Osmia* and *Megachile* bees may not be abundant in certain lowbush blueberry fields (Bushmann and Drummond 2015; Cutler et al. 2015b), I predicted there would be moderate occupancy of nests in this experiment. Nesting occurrence, emergence, and parasitism were also evaluated. Nesting occupancy was expected to be higher along the field edges near natural habitat compared to within fields, and I predicted that nesting occupancy would be higher in fruit-bearing fields than vegetative fields due to the pollen provided by blueberry flowers.

2.3 MATERIALS AND METHODS

2.3.1 ARTIFICIAL NEST DESIGNS

The study was conducted over two years, with n=4 fields in 2014, and n=12 fields in 2015. In 2014, one milk carton nest design was tested along with eight different wooden nest designs (Table S1). Wooden nests (9.5 cm deep x 5 cm wide x 18.5 cm tall) were constructed from spruce wood (*Picea* sp.) and each contained twelve 8-cm long drilled holes, either all 0.7 cm or 0.9 cm in diameter, and approximately 1.5 cm apart (Figure 2.1). Two different nesting tube diameters were used as this can be an important factor in nesting occupancy (Westerfelt et al. 2015) and preference varies among bees (Fye 1965; MacIvor 2016). The two diameters selected were previously used in trap-nest studies in lowbush blueberry (Drummond & Stubbs 1997; Stubbs et al. 1997). Some wooden nests had exteriors and roofs that were charred by lightly burning the wood with a propane torch until the wood exterior turned black. Roofs consisted of a 14.5 cm long x 5 cm wide x 2.5 cm thick piece of wood nailed to the top of the nest, providing an overhang at the front of the nest. These two features were tested as roofs may provide beneficial protection from rain and sun (Taki et al. 2004), and because some blueberry growers have anecdotally suggested that darker or charred surfaced are attractive to trap-nesting bees.

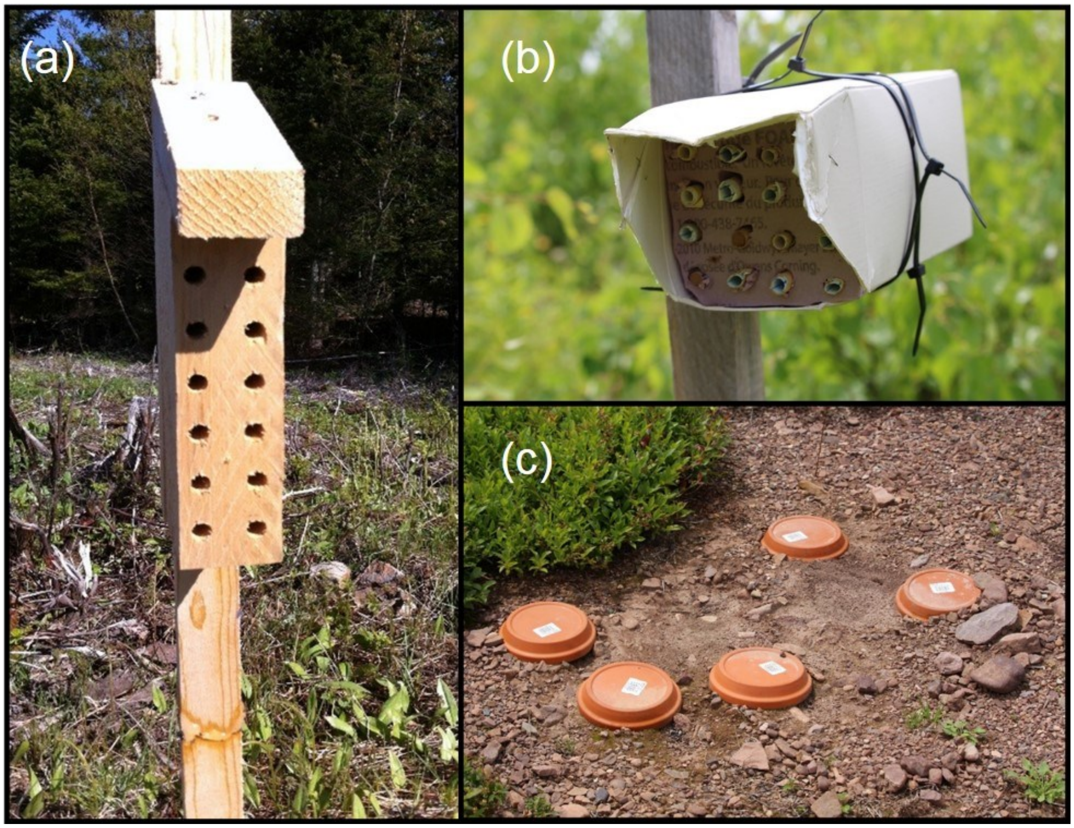

Figure 2.1. Artificial nests for Megachilidae bees in Nova Scotia lowbush blueberry fields: (a) a wooden nest with a roof; (b) milk carton nest (notice capped nesting tubes); (c) clay lids in a blueberry field. (Photos by N. L. McLean and R. S. McCallum.)

Milk carton nests in 2014 were made by inserting paper nesting tubes into washed 2 L milk cartons that were painted white (Beauti-Tone ® interior/exterior latex paint, Home Hardware, St. Jacobs, Ontario) (Figure 2.1). Nesting tubes were made by rolling together a sheet of newsprint over a sheet of white multiuse paper (21 cm x 10 cm) (Staples, Richmond Hill, Ontario). A wooden dowel (0.7 or 0.9 cm diameter) was used to roll the paper into tubes, with the newsprint on the outer surface of the nesting tube. There were six 0.7 cm and six 0.9 cm diameter nesting tubes per milk carton. All nesting tubes were trimmed to 15 cm long and placed through a square (9.5 cm x 9.5 cm) piece of pink polystyrene. Spray foam insulation (Great Stuff™, Home Hardware, St. Jacobs, Ontario) was applied around the nesting tubes and the polystyrene, and the nesting tube structure was then inserted into the milk carton such that it was held in place when the spray foam dried, with the polystyrene block containing the nesting tube openings fitted snuggly into the front opening of the milk carton (Taki et al. 2004; Sheffield et al. 2008). The milk carton design was modified slightly in 2015 to include sixteen nesting tubes instead of twelve, all of which were 0.7 cm in diameter. In 2014 and 2015, both milk carton and wooden nests were secured to wooden stakes using nylon cable ties, at a height of 1 m. Tanglefoot® was applied around each stake at the base to deter ants and other arthropods (Sheffield et al. 2008). Clay lids (syn. “nesting saucers” or “terra cotta lids”) (14 cm diameter) (Canadian Tire Corporation, Toronto, Ontario) were tested as potential nesting substrates for *O. inermis* (Sheffield et al. 2014). Overturned clay lids were placed directly on the soil surface of blueberry fields with a small opening made in the soil underneath to facilitate bee access (Sheffield et al. 2014) (Figure 2.1).

2.3.2 2014 NEST STUDY

Wooden and milk carton nests were installed at four fruit-bearing lowbush blueberry fields in Nova Scotia in 2014 (Tables S1, S2). A randomized complete block design (RCBD) was used with each site (field) serving as a block. Sites were separated by at least 2 km and were considered to be independent, given the limited foraging distances of solitary bees (Gathmann and Tscharntke 2002). Four milk carton nests and two wooden nests of each of the eight unique designs were installed at each field (Table S1). Nests were installed on 22 April 2014, before *Osmia* nesting occurred. Nests were randomly placed 5 m apart along the south-facing edge of each field, and were retrieved on 9 October 2014. The nests were monitored bi-weekly for the presence of capped nesting tubes. An *Osmia* or *Megachile* female caps the end of a nesting tube when she has completed provisioning her offspring in that nest (Bosch and Kemp 2000; Guisse and Miller 2011) and nesting tubes were therefore classified as occupied if a cap was observed (Figure 2.1). Retrieved nests were placed in an unheated outdoor shed at the Dalhousie Agricultural Campus in Truro, Nova Scotia, and capped nesting tubes were brought to the laboratory for dissection the following spring (2015). Bees in tubes were counted and identified. The effect of nest design on nesting occupancy was measured by the total number of capped nesting tubes per field per nest design. Model assumptions of normal distribution and constant variance of the residuals could not be met for the original data or through transformation, and a non-parametric Kruskal-Wallis test using Proc npar1way was therefore conducted in SAS v. 9.4 (SAS Institute Inc. 2014) for this analysis.

2.3.3 2015 MILK CARTON STUDY

Based on results in 2014, only milk carton nests were studied in 2015. Nesting occupancy was compared between fruit-bearing and vegetative blueberry fields. The progression of capped nests was monitored throughout the season to determine when nesting occurred and if nesting overlapped with blueberry bloom. Bee emergence after overwintering was examined, as well as emergence of parasitoids. A completely randomized design (CRD) was used with one factor (field type: fruit-bearing or vegetative) and six replicates (fields) per factor level, for a total of twelve fields (Table S2). There were three milk carton nests per field, placed 5 m apart along the south-facing field edge, for a total of 36 nests in the experiment. Nests were placed in fields on 5 and 6 May 2015, and monitored bi-weekly as in 2014. All nests were collected from fields on 20 October 2015 and placed in an unheated shed (as in 2014) until 4 March 2016. The nests were then placed in an environmental chamber to observe emergence of bees and parasitoids. Each capped nesting tube was removed, labelled, and placed in its own inflated plastic bag in the environmental chamber (J. H. Cane, United States Department of Agriculture, personal communication). The temperature was initially set at 8 °C and then slowly warmed with daily increments of 4 °C up to 25 °C. After ten days at 25 °C, the environmental chamber temperature was increased to 30 °C for an additional three days. Relative humidity was maintained at 60% throughout the experiment (MacIvor and Packer 2015). Bee and parasitoid emergence were recorded daily. Nesting occupancy, measured as number of capped nests from all possible nesting tubes per nest (16), was compared between fruit-bearing and vegetative fields using one-way analysis of variance (ANOVA) using the Mixed Procedure (SAS Institute Inc. 2014). A Kruskal-Wallis test using Proc npar1way (SAS Institute Inc. 2014) was used to test the effect of field type on bee and parasitoid emergence, as the assumptions of normal distribution and constant variance of the residuals could not be met.

2.3.4 2015 CLAY LID STUDY

Overturned clay lids were evaluated as potential nesting substrates for *O. inermis* (Sheffield et al. 2014), at different distances from field edge and between fruit-bearing and vegetative fields. Parasitism of bees was also recorded. A completely randomized design (CRD) was used for a 2 x 2 factorial experiment with field type (fruit-bearing or vegetative) and distance from the field edge (0 m or 25 m) as the two factors of interest. There were three replicate fields per factor level for a total of twelve fields. These twelve fields were also used for the 2015 milk carton nest experiment (Table S2). Within each field, ten lids were placed either along the field edge (0 m) or 25 m from the field edge, into the blueberry field. The lids were placed in the fields on 5 and 6 May 2015 and collected on 20 October 2015. Each lid was placed overturned onto bare ground and pushed firmly into the soil, with a ~2 cm-wide entrance formed in the soil under the lid for bees to gain access (Sheffield et al. 2014). The lids were stored in a freezer upon retrieval until they could be dissected.

2.3.5 INSECT IDENTIFICATION

Bees were identified using characters described in Mitchell (1962), and parasitoids were identified using descriptions from Bohart and Kimsey (1980) and McAlpine et al. (1987). Voucher specimens were sent to the Canadian National Collection (CNC) of Insects

(Ottawa, Ontario, Canada) for identification based on morphology to the lowest possible taxonomic level (family, genus, or species). Voucher specimens were pinned and deposited at the A. D. Pickett Entomology Museum, Dalhousie University Agricultural Campus.

2.4 RESULTS

2.4.1 2014 NEST STUDY

Nest design affected bee nesting, with significantly more capped nesting tubes in milk carton nests than wooden nests ($X^2 = 39.9$; df = 8; $P < 0.0001$) (Table 2.1). Only 3% of wooden nests - two nesting blocks in total - contained at least one capped nest compared to 71% of milk carton nests that had at least one capped nesting tube (Table 2.1). The two wooden nests that had capped nesting tubes were of different designs: one was burned with 0.7 cm diameter holes and a roof, and the other was not burned with 0.9 cm diameter holes and no roof. These two wooden nests had two and five capped nesting tubes, respectively, out of twelve possible nesting tubes per nesting block. Although more than 70% of milk carton nests had at least one capped nesting tube, none had more than two capped tubes, and 50% of successful nests contained only one capped nesting tube (Table 2.1). Two milk carton nests, one each from Masstown and Portapique field sites, were discarded due to damage by animals (possibly black bears). After overwintering in an unheated shed, 13 nesting tubes were dissected. Sixty-one *Osmia tersula* bees were identified, as well as 34 *Megachile* spp., 10 fully developed sapygid wasps (*Sapyga martinii* Smith) (Hymenoptera: Sapygidae) and one tachinid fly (Diptera: Tachinidae).

Table 2.1. Median, interquartile range, and percentage of nests and nesting tubes containing bees when placed in commercial fruit-bearing lowbush blueberry fields in Nova Scotia, Canada, 2014. A Kruskal-Wallis test was used to compare the number of capped nesting tubes in milk carton vs. wooden trap nests.

Nest block type[1]	No. nest blocks	Median no. capped tubes/nest block	Interquartile range (IQR) (Q_3-Q_1)	No. nest blocks with 0 capped tubes (% total)	No. nest blocks with 1 capped tube (% total)	No. nest blocks with 2 or more capped tubes (% total)
Milk carton	14	1.0	1.0	4 (29)	7 (50)	3 (21)
Wooden[2]	64	0	0	62 (97)	0	2 (3)

[1] Each of four fields had 4 milk carton trap nests and 16 wooden trap nests. Due to damage, a total of 14 milk cartons and 64 wooden nests were tested. Each nest had 12 possible nesting tubes.

[2] Multiple wooden trap nest designs were used but because occupancy by bees was low, data from all wooden nests were combined. The two trap nests containing capped nesting tubes were from two designs: roof, burned, small holes and no roof, not burned and large holes.

2.4.2 2015 MILK CARTON STUDY

Of the 36 milk carton nests placed in twelve different blueberry fields, three nests were damaged (possibly by black bears) at one site and removed from the study. Of the remaining 33 nests, 24 (73%) contained at least one capped nesting tube. A total of 176 out of 512 nesting tubes (34%) were capped and considered occupied. The first capped nesting tube was observed in a field on 25 June 2015, during late blueberry bloom, and the last capped nesting tube was observed on 30 July 2015, after blueberry bloom had finished. The majority of nest capping was completed by mid-July (Figure 2.2).

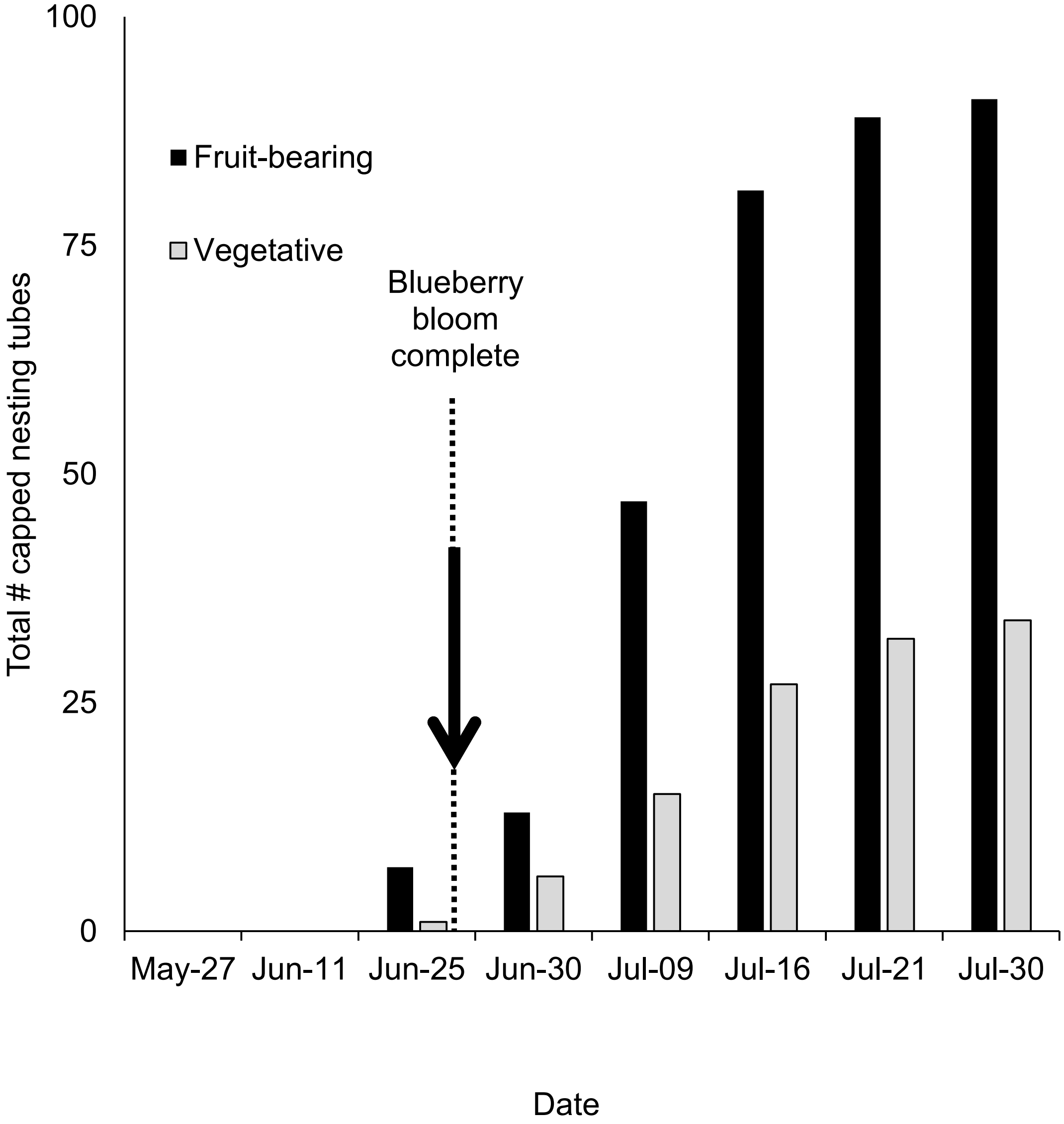

Figure 2.2. Occurrence of capped nesting tubes in milk carton nests by bees (Hymenoptera: Megachilidae) in lowbush blueberry fields (fruit-bearing and vegetative) in Nova Scotia, Canada, 2015.

Although nesting occupancy was not significantly different between the two field types, there were almost twice as many capped nesting tubes in fruit-bearing fields than vegetative fields (Table 2.2). In the environmental chamber, 40 *O. tersula*, 2 Sapygidae wasps, 1 Chrysidid wasp (Hymenoptera: Chrysididae), and 6 tachinid flies emerged from 17 of 176 capped nesting tubes. Significantly more bees emerged from capped nesting tubes from fruit-bearing fields than from vegetative fields (Table 2.2). Most bees emerged over a period of approximately one week, starting five days after placement in the environmental chamber and peaking at day nine (Figure 2.3).

Table 2.2. Bee nesting, emergence, and parasitism in milk carton trap nests in Nova Scotia lowbush blueberry fields in 2015. A mixed model was used to compare the mean number of capped nesting tubes per carton in different field types, and a Kruskal-Wallis test was used to compare bee, wasp, and fly emergence in different field types. Medians are presented with the interquartile range (IQR) of capped nesting tubes per field in parentheses for non-parametric analyses. Only milk cartons with at least one capped nesting tube were compared.

Field Type	Median # capped tubes/carton (IQR)	Median # bees emerged/carton (IQR)	Mean # wasps emerged/carton (IQR)	Mean # flies emerged/carton (IQR)
Fruit-bearing	6.4 (2.3- 15.7)	3.5 (15)	0	0
Vegetative	3.5 (2.3- 6.3)	0	0	0
Statistics	F = 1.25 *P* = 0.29	X^2 = 46.03 *P* = 0.0030	X^2 = 23.29 *P* = 0.44	X^2 = 18.22 *P* = 0.76

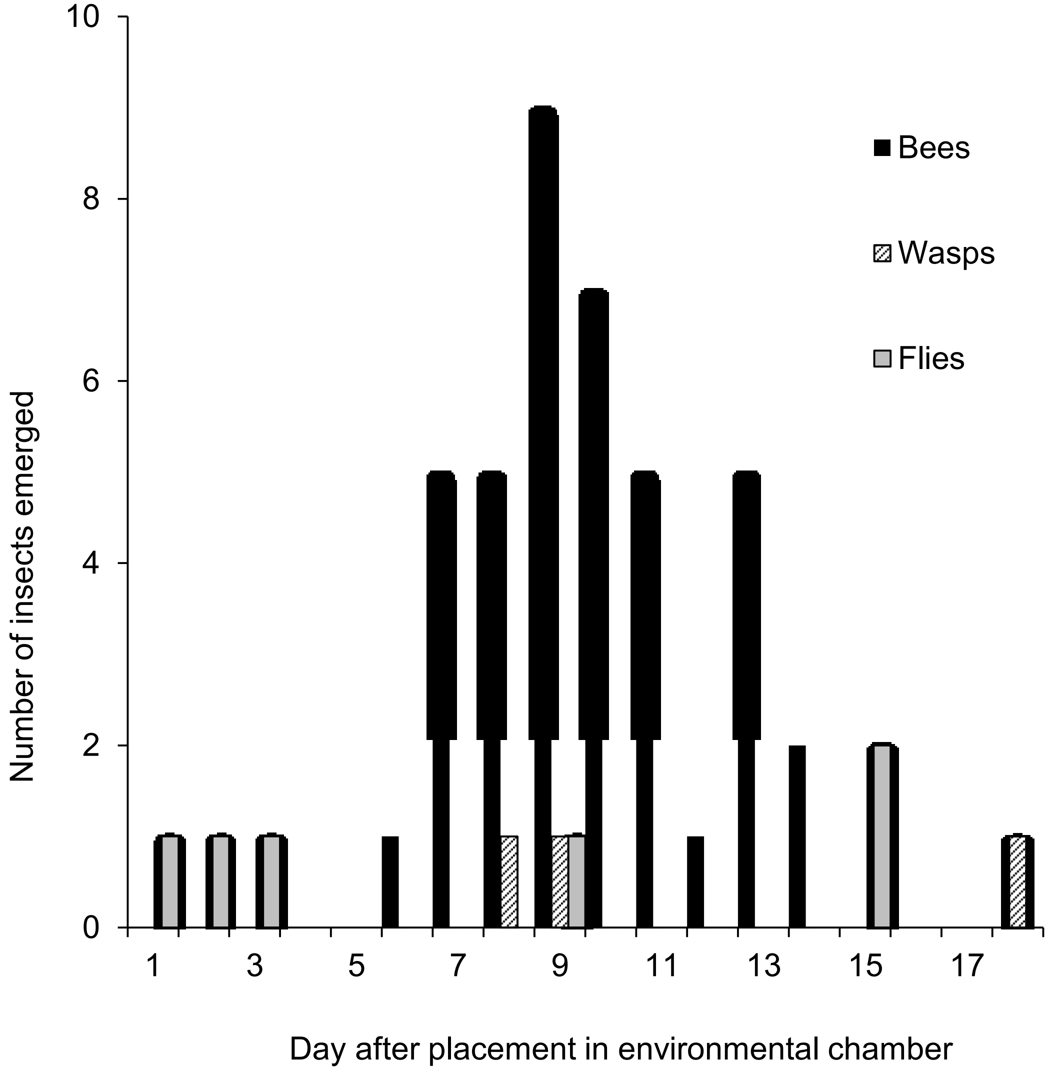

Figure 2.3. Bee and parasitoid emergence from milk carton nests within an environmental chamber after removal from a lowbush blueberry field in Nova Scotia, Canada, 2015. The temperature was initially set at 8° C and then warmed with daily increments of 4° C up to 25° C. After ten days at 25° C, the temperature was increased to 30° C for an additional three days.

Field type did not have a significant effect on emergence of wasps or flies (Table 2.2), although insects only emerged from one capped nesting tube from a vegetative field. After removal of nesting tubes from the environmental chamber and placement in the laboratory at room temperature, sixteen leafcutter bees (*Megachile* spp.) emerged. No *Osmia* emerged from tubes that contained *Megachile*. Dissection of the 176 nesting tubes after emergence found 266 failed or incomplete cells that could be recognized as well as fully developed dead bees that were mouldy. It is possible more cells were present but many of the tubes were damp and mouldy, and nesting evidence was not recognizable. The number of failed cells per tube ranged from one to sixteen and included *Osmia* and *Megachile* bees, and chrysid and sapygid wasps. Additionally, 6 Phoridae puparia (Diptera), 2 satellite fly adults and 10 fly puparia (Diptera: Sarcophagidae, subfamily Multigramminae), and 7 Tachinidae (Diptera) in various stages of development were dissected from the nesting tubes.

2.4.3 2015 CLAY LID STUDY

Only 3.3% (4/120) of overturned clay lids had *Osmia inermis* nesting evidence. All successful lids were found in fruit-bearing fields and three of four lids were found at the field edge. The successful lids had nesting aggregations of five to seventeen *O. inermis*, as determined by separating and identifying each bee the following spring. The bees ranged from pupae to adults and were moldy, but identification was still possible. Only one of the lids showed evidence of parasitism upon dissection, with three *Chrysaora pacifica* (Say) wasps (Hymenoptera: Chrysididae) detected next to fully developed *O. inermis*.

2.5 DISCUSSION

Female cavity-nesting bees and wasps carefully search their habitat and seem to prefer conspicuous, high-quality holes (Westerfelt et al. 2015). In my study, nest occupancy was significantly affected by nest design in 2014, with more bees nesting in tubes of milk cartons than wooden nests. The rate of occupancy in the wooden nesting blocks – a total of only 2 and 5 capped nesting tubes in two wooden nests – was lower than in other studies. For example, in Maine (U.S.) lowbush blueberry fields, 20% of wooden nesting blocks and 6% of available holes (120 nests made in 2086 holes) were occupied by *Osmia*, and the rate of uptake did not change in two subsequent years (Stubbs et al. 1997). In a Swedish boreal forest, more than 30% of artificial wooden nests, consisting of pine poles with predrilled holes, were occupied by bees or wasps, with *Megachile* utilizing mostly holes that were 7 or 10 mm in diameter (Westerfelt et al. 2015). In my study, it is possible that the deeper nesting tubes of milk carton nests (15-cm) were more attractive to Megachilidae than shallower tubes of wooden nests (8-cm) (Stubbs et al. 1997; Bosch & Kemp 2002; MacIvor 2016), although *Megachile* may also readily occupy artificial holes in wood that are 8-cm or less (Westerfelt et al. 2015). The smoothness of the hole may be important for cavity-nesting bees. Whereas the drilled holes of my wooden nests were not modified and had a relatively coarse inner surface, the milk carton tubes had smooth paper inner surfaces and had higher occupancy. Stubbs et al. (1997) inserted cellophane-coated straws into drilled holes and had greater occupancy than I did in wooden trap nests. It is also possible that the white milk carton nests were visually more attractive than the wooden nests; further research is required regarding the importance of visual cues in nest recognition or preference of wild cavity-nesting bees (MacIvor 2016). Temperature and humidity can also influence nest uptake and emergence success by cavity-nesters (Bosch & Kemp 2002; Westerfelt et al. 2015), although these factors were not measured in my study. Relatively poor nesting occupancy overall in the 2014 experiment may have partially been due to lack of established *Osmia* populations in the fields sampled. In a study examining the wild bee community in lowbush blueberry fields in Nova Scotia, only five *Osmia* were collected from ten commercial fields over nine collection events throughout the summer (Cutler et al. 2015b). Similarly, low captures of *Osmia* were reported from lowbush blueberry fields in Maine (Bushmann & Drummond 2015).

The experiment was modified in 2015 to focus on nesting in milk carton nests and potential differences in nesting between fruit-bearing and vegetative fields, as well as parasitism. I predicted nesting occupancy would be higher in fruit-bearing fields due to the food source offered by blueberry flowers for the provisioning females, and that early season emergence of *Osmia* would overlap with blueberry bloom (Drummond & Stubbs 1997; Sheffield et al. 2003). Although I found no significant difference in nest occupancy between fruit-bearing and vegetative fields, significantly more bees emerged from occupied nesting tubes collected from fruit-bearing fields. The study sites were in close proximity (within 500 m) of other blueberry fields. The industry practice of maintaining both fruit-bearing and vegetative fields in close proximity in any given year ensures that there are harvestable berries every year (Yarborough 1997). If vegetative and fruit-bearing fields are in close proximity to one another, bees that emerge near vegetative fields may be able to fly to nearby fruit-bearing fields to forage during blueberry bloom. On the other hand, I found that provisioning and capping of most nesting tubes occurred after blueberry bloom was completed, suggesting that bees also collected pollen and nectar from non-crop flowering plants. Whereas the foraging period of *Osmia* is from mid-April to late June, *Megachile* have been recorded in lowbush blueberry in Nova Scotia from early June to late September (Sheffield et al. 2003), suggesting nesting tube capping observed in July was from *Megachile* bees rather than *Osmia*. Thus, activity of *Osmia* and *Megachile* bees may coincide with blueberry bloom (Drummond & Stubbs 1997; Sheffield et al. 2003), but the availability of alternative floral resources in and around fields after blueberry bloom is also important for nesting success of Megachilidae. I recovered both *Megachile* spp. and *O. tersula* bees from milk carton trap nests, which contained 7-mm and 9-mm tubes. In contrast, in Nova Scotia apple orchards, 97% of collected *O. tersula* were recovered from nesting tubes that were 3-mm and 5-mm diameter, while most *Megachile* occupied tube diameters ranging from 5-mm to 9-mm, depending on the species (Sheffield et al. 2008). If milk carton nests containing nesting tubes of variable diameters can simultaneously attract multiple *Osmia* and *Megachile* species, a more diverse pollinating force could be supported.

I detected parasitism by kleptoparasites (e.g. Sapygidae wasps, tachinid flies), as in previous studies (Drummond & Stubbs 1997; Stubbs et al. 1997; Sheffield et al. 2008; MacIvor & Packer 2015). Of the 65 insects that emerged from tubes, nine were parasitoids. Upon dissection of the nesting tubes, more than 200 failed cells were observed, as well as additional wasps and flies that may have caused parasitism and prevented development of bees. Field conditions may have further reduced nest occupancy and development of bees and parasitoids. Many cells with undeveloped bees were in damp nesting tubes. Nesting success of Megachilidae can be reduced by cool, damp weather conditions (Pitts-Singer & James 2008) and associated bacterial or fungal activity (Frankie et al. 1998). In 2015, 404.6 mm of precipitation were recorded for the study region from May to August, but this was only slightly higher than the thirty-year average (1981-2010) of 397.1 mm from May to August (Government of Canada 2016).

Nesting by *O. inermis* in clay lids was lower than previously reported; in my study only 3.3% of lids were occupied, as compared to 10% lid occupancy reported by Sheffield et al. (2014), despite more extensive sampling effort. I detected parasitism by chrysid wasps in one clay lid, whereas Hicks (2009) and Sheffield et al. (2014) did not report any parasitism of *O. inermis*. I predicted nest occupancy would be greater in fruit-bearing fields and along the field edge due to proximity of food sources (Cutler et al. 2015b). Although more nesting in clay lids along field edge and in fruit-bearing fields was observed, the overall low number of lids occupied (four) prohibits any conclusion on the importance of these factors in *O. inermis* nesting. Blueberry bloom would provide a mass-provision of flowers for bees and could make nesting in fruit-bearing fields more efficient for female *O. inermis*. As offspring would then emerge the following year in vegetative fields, ensuring fields are split into nearby fruit-bearing and vegetative rotations could be important to optimize pollination from wild bees. The low nesting occupancy in clay lids could have been due to poor ventilation or high humidity under lids (some mold was observed), or simply low incidence of *O. inermis* in the blueberry fields sampled. In Maine and Nova Scotia blueberry fields, relatively few *O. inermis* were collected (Cutler et al. 2015b; Bushmann & Drummond 2015), and this was also the case for other agricultural habitats sampled in Nova Scotia (Sheffield et al. 2013). My clay lid experiment suggests prospects for managing *O. inermis* in Nova Scotia blueberry fields may be limited, but further investigation into nesting already occurring in fields, for instance, in rock piles, may be of value.

2.6 SUMMARY OF CHAPTER 2 AND TRANSITION TO CHAPTER 3

Given the efficacy of wild bees for lowbush blueberry pollination (Javorek et al. 2002), enhancement efforts to promote wild bees will continue to be an important complement to pollination by managed bees. Nesting occupancy in certain nest block designs was promising and could be implemented to conserve cavity-nesting bees in and around lowbush blueberry fields. The wooden and clay lid nests were not well utilized in my experiments, but success in previous studies (Stubbs and Drummond 1997; Sheffield et al. 2014; Westerfelt et al. 2015) suggests that further examination is warranted into the role of nest design in determining nest occupancy and emergence success of Megachilidae.

Effective enhancement measures for beneficial insects must not only examine nesting resources, but also the availability of floral resources. The next three chapters focus on the provision of floral resources along blueberry field edges for bees and natural enemies.

2.7 SUPPLEMENTARY INFORMATION

Table S1. Trap nest designs tested for bees (Hymenoptera: Megachilidae) in Nova Scotia fruit-bearing lowbush blueberry fields in 2014.

Nesting design	Number of nests tested per site	Total number of nests tested
Milk carton	4	16
Wooden (roof, burned, 0.7 cm holes)	2	8
Wooden (roof, burned, 0.9 cm holes)	2	8
Wooden (roof, not burned, 0.7 cm holes)	2	8
Wooden (roof, not burned, 0.9 cm holes)	2	8
Wooden (no roof, burned, 0.7 cm holes)	2	8
Wooden (no roof, burned, 0.9 cm holes)	2	8
Wooden (no roof, not burned, 0.7 cm holes)	2	8
Wooden (no roof, not burned, 0.9 cm holes)	2	8
Total	20	80

Table S2. Lowbush blueberry field sites used in bee trap-nesting study (Nova Scotia, 2014-2015).

Year	Location	Field Type	Coordinates	Field size (ha)
2014	Londonderry	fruit-bearing	45°26'31.23"N, 63°34'22.32"W	2.5
	Debert	fruit-bearing	45°25'11.62"N, 63°30'51.11"W	5
	Earltown	fruit-bearing	45°35'8.27"N, 63°11'1.62"W	6.75
	Portapique	fruit-bearing	45°24'16.29"N, 63°40'21.12"W	3.25
2015	Debert	vegetative	45°25'11.62"N, 63°30'51.11"W	5
	Portapique	vegetative	45°24'16.29"N, 63°40'21.12"W	3.25
	Carrobie Road	vegetative	45°26'31.23"N, 63°34'22.32"W	2.5
	Parrsboro	vegetative	45°31'3.74"N, 64°19'47.03"W	3
	Parrsboro	fruit-bearing	45°30'40.88"N, 64°19'53.64"W	3.5
	Parrsboro	fruit-bearing	45°30'44.29"N, 64°19'36.91"W	7
	Parrsboro	fruit-bearing	45°30'58.03"N, 64°19'35.17"W	6
	Parrsboro	fruit-bearing	45°25'24.34"N, 64°20'42.64"W	3.6
	Great Village	fruit-bearing	45°24'36.55"N, 63°36'36.65"W	2.2
	Great Village	fruit-bearing	45°24'24.08"N, 63°36'24.08"W	3.2
	Great Village	vegetative	45°26'50.30"N, 63°38'27.69"W	5
	Great Village	vegetative	45°25'50.95"N, 63°35'27.67"W	2.8

CHAPTER 3: ENHANCING LOWBUSH BLUEBERRY FIELD MARGINS FOR WILD BEES

3.1 ABSTRACT

Wild bees provide important pollination services to agricultural crops, but a lack of season-long floral resources, particularly before and after crop bloom, can limit the persistence and growth of wild bee communities in agricultural ecosystems (‘agroecosystems’). Planting floral resources along crop field margins has been suggested as a tactic to support or enhance communities of wild bees in agricultural landscapes. Given the dependence of commercial lowbush blueberry (*Vaccinium angustifolium* Aiton) production on bees for pollination, I examined the effect of planting buckwheat (*Fagopyrum esculentum* Moench) along blueberry field margins on wild bee abundance and diversity. The bee community was also surveyed during blueberry bloom to determine if the same bee genera that visited buckwheat were present during blueberry pollination, and if sampling method (aerial netting or pan trapping) affected bee collection. I found that bee abundance and diversity were higher in buckwheat transects than in control transects only in mid-August, but high variability occurred across years and collection periods. After three years of augmenting floral resources around blueberry fields, no significant differences in bee abundance or diversity were detected between buckwheat and control sites. All bee genera recorded during blueberry bloom were also collected in buckwheat transects. Bee diversity was significantly greater during late blueberry bloom, and abundance was also highest during late blueberry bloom, although not significantly so. Complementary sampling techniques are recommended for future research on bee communities. Field edges in certain lowbush blueberry fields may

already support wild bees and so not all habitat management efforts may boost bee communities. Habitat management decisions should therefore be site-specific.

3.2 INTRODUCTION

Insect pollinators contribute substantially to agricultural crop productivity (Klein et al. 2007; Gallai et al. 2009), but declining wild bee populations and an insufficient number of managed honey bee colonies may threaten pollination services (Aizen and Harder 2009; Garibaldi et al. 2011). Numerous factors can contribute to bee declines, including climate change, pests and diseases, pesticide use, and decreasing food and habitat resources (Goulson et al. 2008; Brown and Paxton 2009; Winfree et al. 2009; Potts et al. 2010). To conserve and enhance wild bees in agricultural ecosystems (‘agroecosystems’), season-long floral resources must be available to bees within their foraging range (Carreck and Williams 2002; Goulson et al. 2008; Brown and Paxton 2009). This can be achieved through habitat management, which involves manipulating agricultural landscapes to provide food and habitat resources for beneficial insects (Landis et al. 2000).

Lowbush blueberry is an economically important crop in eastern Canada and in Maine, U.S., that relies on insect pollination for fruit set (Aras et al. 1996; Eaton and Nams 2012). As wild bee communities fluctuate annually, and are often assumed to be insufficient to fulfill pollination requirements for commercial lowbush blueberry fields, honey bees (*Apis mellifera* L.), commercial bumble bees (*Bombus impatiens* Cresson), and/or alfalfa leafcutter bees (*Megachile rotundata* Fabricius) are brought into fields during crop bloom to supplement wild bee pollination (Stubbs and Drummond 1997; Drummond 2012; Eaton and Nams 2012). Shortages or increasing costs of managed bees can make using managed pollinators challenging at times. As such, the focus of many growers is shifting to wild bees and how best to increase their communities in lowbush blueberry agroecosystems. In order to remain in the vicinity as potential pollinators, wild bees may require food and habitat resources before and after blueberry bloom (Carreck & Williams 2002). Unlike solitary *Andrena*, *Halictus*, and *Lasioglossum* bees that typically forage only a few weeks (Michener 2007), colonial bumble bees (*Bombus*) require food resources throughout the season, in order to sustain a growing colony. By providing floral resources for bees within the vicinity of lowbush blueberry fields, a rich community of bees may be supported that could enhance crop pollination. Furthermore, as a wild, perennial crop system with minimal soil disturbance due to the absence of tillage, lowbush blueberry is an attractive agroecosystem in which to test habitat management techniques. Perennial agricultural systems may be more responsive to conservation biology measures due to decreased disturbance (Landis et al. 2000).

Habitat management has been successfully implemented for pollinators in apples (*Malus domestica)* (Blitzer et al. 2016) and highbush blueberries (*Vaccinium corymbosum* Linnaeus) (Blaauw & Isaacs 2014a), but has not been widely tested in lowbush blueberries. To the best of my knowledge, only one published study has examined the effect of floral plantings along lowbush blueberry field edges for pollinators, and it was conducted in Maine, U.S. (Venturini et al. 2017). Bumble bees were collected more frequently in clover plantings, while solitary bees were more abundant in wildflower plantings (Venturini et al. 2017). Visitation to nearby blueberry flowers increased in fields with floral resource plantings, and positive effects were also demonstrated on fruit set after four years (Venturini et al. 2017).

Few studies in lowbush blueberry have implemented multiple sampling techniques including pan trapping, hand collection, and observational data (e.g.

Bushmann and Drummond 2015). Many previous studies have used only a single sampling method to survey bee communities (Hicks 2011; Moisan-DeSerres et al. 2014a; Cutler et al. 2015b; Melathopoulos 2015). Each sampling method contains its own inherent bias, and the bee community structure is potentially misrepresented if only a single method is used. Bee abundance has varied in previous lowbush blueberry surveys according to sampling method. For example, *Bombus frigidus* was determined to be the most abundant pollinator in Quebec, followed by *Andrena* species, when aerial netting was used (Moisan-Deserres et al. 2014a). *Lasioglossum* was the most abundant genus recorded in Nova Scotia, followed to a much lesser degree by *Andrena*, when pan trapping was used (Cutler et al. 2015). Utilization of multiple collection methods may, therefore, allow for a more representative survey of bees during blueberry bloom.

The objectives of this study were to 1) compare wild bee diversity and abundance between enhanced field edges (buckwheat transects) and unenhanced field edges (control transects) after blueberry bloom, 2) evaluate bee abundance and diversity during blueberry bloom at sites planted with buckwheat the previous year, 3) compare two different sampling methods for bee collection, and 4) determine how bee abundance and diversity change throughout blueberry bloom. Buckwheat was chosen due to its previous use in habitat management studies, adaptability to poor soil conditions typical of lowbush blueberry fields, known ease of establishment, lengthy flowering period, and attractiveness to pollinators (Stephens et al. 1998; Carreck & Williams 2002; Racys and Montviliene 2005; Pontin et al. 2006). I hypothesized that by providing buckwheat to bees after blueberry bloom, bee abundance and diversity would be higher in buckwheat sites than control sites, and would increase over subsequent years in buckwheat transects due to greater availability of food resources. I also predicted that sampling method would influence which bee genera were captured due to bee size and behaviour, and that bee abundance and diversity would vary throughout blueberry bloom, corresponding to bee emergence (Sheffield et al. 2003; Hicks 2011; Bushmann and Drummond 2015; Cutler et al. 2015b).

3.3 MATERIALS AND METHODS

3.3.1 BUCKWHEAT AND CONTROL TRANSECT SAMPLING

3.3.2 STUDY SITES

Common buckwheat (Mancan variety, Co-Op Atlantic, Moncton, New Brunswick) was planted during three field seasons (2014-2016) along the edges of commercial lowbush blueberry fields in Colchester and Cumberland Counties, Nova Scotia, Canada. In 2014, five buckwheat sites were planted but only two successfully established and flowered and were used in data collection (Table S3). In 2015, four buckwheat and three control sites were sampled, and in 2016, three buckwheat and three control sites were sampled (Table S3). Buckwheat was seeded on 12 June 2014, 17 June 2015, and 21 June 2016, using a Tye no-till seeder (Dulath, Georgia, U.S.) at a rate of 67.2 kg ha^{-1}. Blueberry fields were on average 5.0 ± 0.75 ha (range 2.2- 9.8 ha), and sites were separated by at least 1 km.

3.3.3 SAMPLING

Bee diversity and abundance in buckwheat transects were compared to field edges in other blueberry fields that had no buckwheat planted. In each field, a sampling transect was established along a south-facing adjacent forest edge, within 2 m of the blueberry field. Transects were 2 m by 40 m. Bees were sampled three times during buckwheat bloom: in late July (25 July - 31 July), mid-August (10 August - 16 August), and late August (17 August - 25 August). Aerial netting and pan trapping were used at each site for sampling bees and other insects, and sampling of sites was alternated to ensure that morning and afternoon collecting occurred at each site. Any bee observed visiting a buckwheat flower during aerial netting sampling was collected, and the pan traps were set up directly along the buckwheat planting, adjacent to the blueberry field. In the control sites, a variety of flowers were documented including wild rose (*Rosa acicularis*), goldenrod (*Solidago* spp.), vetch (*Vicia* spp.), clovers (*Trifolium* spp.), sweet clovers (*Melilotus* spp.), and St John’s Wort (*Hypericum perforatum*).

Transects were aerial netted by two trained people, consistent among the three years of study, for a combined total of 30 minutes per collection period when weather conditions were optimal for pollinator activity: between 10 a.m. and 4 p.m., above 15 °C, and with sunny conditions and low wind (Morandin et al. 2007; Melathopoulos 2015; Blitzer et al. 2016). Aerial netted bees were placed in jars with ethyl acetate to kill the specimens, placed on ice after collection, and returned to the lab for identification.

Pan traps were activated for 24-48 hours when favourable weather conditions were forecasted to ensure sampling occurred during optimal bee foraging activity. Abundances were standardized to a per-day measure for each site and day (Cutler et al. 2015b). Thirty pan traps were set out in each transect, approximately 1 m apart. White, yellow, and blue coloured pan traps were alternated for a total of ten traps per color (Morandin et al. 2007). Each pan trap consisted of a 355 mL bowl (SOLO Cup Company, Urbana, IL) filled with approximately 200 mL of tap water and three drops of Dawn Ultra dish detergent (Procter and Gamble, Toronto, ON) as a surfactant (Cutler et al. 2015b). Pan trap specimens were filtered from the soapy water solution using a wire sieve, transferred to plastic bags filled with water, and placed on ice for transport to the laboratory. In the lab, insects were transferred to jars and stored in 70% ethanol until identification and pinning.

3.3.4 IDENTIFICATION

Bees were identified to genus according to Packer et al. (2007). Specimens were deposited at the A. D. Pickett Entomological Museum at Dalhousie University Agricultural Campus in Truro, Nova Scotia.

3.3.5 STATISTICAL ANALYSIS

Wild bees were the focus of my study and thus any data collected on honey bees were excluded from analysis. Abundance was measured in treatment (buckwheat) and control plots as the total number of bees, while diversity was calculated as number of bee genera. As fields were sampled multiple times, samples from each field were not independent, and a repeated measures analysis was conducted on the abundance and diversity of bees during three collection periods, using the Mixed Procedure (SAS Institute Inc. 2014). A compound symmetry covariance structure was used as this best described the type of dependence among values measured at various time points, based on the lowest resulting Akaike’s Information Criterion (AIC) value. The assumptions of normal distribution and constant variance of the error terms were verified using Proc univariate and Proc plot (SAS Institute Inc. 2014). Multiple means comparisons were conducted using Tukey's test to compare the least squares means for significant effects. Letter groupings (pdmix macro) were produced to show significant differences among means using α = 0.05 for main effects and α = 0.01 for interaction effects, in order to protect Type I experiment-wise error rate from over inflation. All analyses were completed using SAS v. 9.4 (SAS Institute Inc. 2014).

3.3.6 BLUEBERRY BLOOM SAMPLING

3.3.7 STUDY SITES

Bee abundance and diversity were monitored on blueberry plants throughout blueberry bloom. Three collections occurred in 2016 during early (26 May), mid (01 June), and late (07 June) blueberry bloom in two lowbush blueberry fields in Colchester County, Nova Scotia: Earltown (45°35'04.0"N, 63°11'01.1"W) and Kemptown (45°32'45.0"N, 63°06'53.2"W). The fields were conventionally managed, and were 3 ha and 3.5 ha, respectively. Buckwheat transects were planted at both of these sites in 2015 and again in 2016.

3.3.8 SAMPLING

Two blueberry fields were sampled during blueberry bloom to determine if the same bee genera visiting buckwheat also visited lowbush blueberry flowers, and also to examine how abundance and diversity changed during early, mid, and late blueberry bloom. I additionally examined whether sampling method (aerial netting or pan trapping) affected the taxa of bees collected. Aerial net collections were conducted by two collectors walking through the blueberry field slowly in a zigzag pattern for a combined total of 30 minutes per sampling event. Collectors sampled evenly along the field edge and in the field interior, following the same general sampling sequence during each sampling event. Netting was conducted when weather conditions were optimal for pollinator activity: between 10 a.m. and 2 p.m., above 13° C, and during sunny conditions with low wind.

After aerial net collections were completed, 30 pan traps of alternating colors (white, yellow, and blue) were placed along blueberry field edges on the soil surface, 1 m apart. Each pan trap consisted of a 355 mL bowl (SOLO Cup Company, Urbana, Illinois, U.S.) filled with approximately 200 mL of a tap water and three drops of Dawn Ultra dish detergent (Procter and Gamble, Toronto, Ontario) as a surfactant (Cutler et al. 2015b). The pan traps remained in the fields for 24 hours and were then retrieved (Bushmann and Drummond 2015). Sampling only took place when no precipitation was forecast so that pan traps were activated during favourable weather conditions (Hicks 2011). Sampling was conducted as described in the previous section for buckwheat and control transect monitoring. Bees were identified to genus according to Packer et al. (2007) and bumble bees were identified to species according to Laverty and Harder (1988) and Williams et al. (2014). Abundance was measured as the total number of bees, while diversity was calculated as number of genera.

3.3.9 STATISTICAL ANALYSIS

Honey bees were excluded from analysis as wild bees were the focus of this study. No other managed bees were present in the sampled fields. All analyses were completed using SAS v. 9.4 (SAS Institute Inc. 2014) and the same analysis was used as for the buckwheat and control transect experiment (described above).

3.4 RESULTS

3.4.1 BUCKWHEAT AND CONTROL TRANSECTS EXPERIMENT

A total of 4,340 wild bees from 5 families and 23 genera were collected from both treatments in nets and pan traps from 2014 to 2016 (Table 3.1). 1,043 bees were collected in 2014 (24%), 2,788 bees in 2015 (64.2%) and 509 bees in 2016 (11.8%) (Table 3.1). *Bombus*, *Calliopsis*, and *Lasioglossum* comprised 85% of total specimens collected. Although these three genera were most abundant, they displayed large yearly variation. Abundance of *Bombus*, *Calliopsis*, and *Lasioglossum* was highest during 2015, but there were inconsistent population increases and decreases among the genera. *Augochlora* was the only genus where a single specimen was found in a control site only, while *Anthidium*, *Coelioxys*, *Holcopasites*, and *Nomada* were only collected in buckwheat sites. The remaining genera were collected in both buckwheat and control sites. Bee collections from buckwheat or control plots varied with sampling method. Of the 4340 bees collected, 666 (15.3%) were captured using aerial netting while 3674 (84.7%) were collected using pan trapping (Table 3.2).

Table 3.1. Wild bees collected from buckwheat and control transects along Nova Scotia blueberry field edges, 2014-2016. The genera with the top three total number of specimens are bolded.

Family	Genus	Yearly specimens collected (% relative abundance)			Total number of specimens (%)
		2014	2015	2016	
Andrenidae	*Andrena*	19 (1.8)	32 (1.1)	23 (4.5)	74 (1.7)
	Calliopsis	**297 (28.5)**	**1337 (48.0)**	22 (4.3)	**1656 (38.3)**
	Perdita	1 (0.1)	0 (0)	7 (1.4)	8 (0.2)
	Protandrena	11 (1.1)	1 (0)	0 (0)	12 (0.3)
Apidae	*Bombus*	**170 (16.3)**	**710 (25.5)**	**245 (48.1)**	**1125 (26.0)**
	Ceratina	2 (0.2)	7 (0.3)	6 (1.2)	15 (0.3)
	Holcopasites	3 (0.3)	147 (5.3)	0 (0)	150 (3.5)
	Melissodes	17 (1.6)	1 (0)	7 (1.4)	25 (0.6)
	Nomada	0 (0)	1 (0)	0 (0)	1 (0)
	Triepeolus	21 (2.0)	3 (0.1)	17 (3.3)	41 (0.9)
Colletidae	*Colletes*	0 (0)	0 (0)	2 (0.4)	2 (0)
	Hylaeus	7 (0.7)	28 (1.0)	1 (0.2)	36 (0.8)
Halictidae	*Agapostemon*	1 (0.1)	0 (0)	1 (0.2)	2 (0)
	Augochlora	0 (0)	0 (0)	1 (0.2)	1 (0)
	Augochlorella	2 (0.2)	17 (0.6)	4 (0.8)	23 (0.5)
	Halictus	16 (1.5)	30 (1.1)	**77 (15.1)**	123 (2.8)
	Lasioglossum	**404 (38.7)**	**418 (15.0)**	**88 (17.3)**	**910 (21.0)**
	Sphecodes	62 (5.9)	37 (1.3)	4 (0.8)	103 (2.4)
Megachilidae	*Anthidium*	1 (0.1)	0 (0)	0 (0)	1 (0)

Family	Genus	Yearly specimens collected (% relative abundance)			Total number of specimens (%)
		2014	2015	2016	
	Coelioxys	1 (0.1)	1 (0)	0 (0)	2 (0)
	Hoplitis	1 (0.1)	3 (0.1)	0 (0)	4 (0.1)
	Megachile	2 (0.2)	10 (0.4)	2 (0.4)	14 (0.3)
	Osmia	5 (0.5)	5 (0.2)	2 (0.4)	12 (0.3)
Total		1043 (24.0)	2788 (64.2)	509 (11.8)	4340 (100)

Table 3.2. Collection of bees in buckwheat and control transects along Nova Scotia lowbush blueberry fields post blueberry bloom (July-August) using two sampling techniques (aerial netting and pan trapping), 2014-2016.

Genus	No. bees collected in aerial nets			No. bees collected in pan traps			Total net (%)	Total pan (%)
	2014	2015	2016	2014	2015	2016		
Agapostemon	0	0	0	1	0	1	0	2 (100)
Andrena	3	13	7	16	19	16	23 (31.0)	51 (69.0)
Anthidium	0	0	0	1	0	0	0	1 (100)
Augochlora	0	0	1	0	0	0	1 (100)	0
Augochlorella	0	0	1	2	17	3	1 (4.3)	22 (95.7)
Bombus	50	351	186	120	359	59	587 (52.2)	538 (47.8)
Calliopsis	0	4	4	297	1333	18	8 (0.5)	1648 (99.5)
Ceratina	0	1	1	2	6	5	2 (13.3)	13 (86.7)
Coelioxys	0	0	0	1	1	0	0	2 (100)
Colletes	0	0	0	0	0	2	0	2 (100)
Halictus	1	7	4	15	23	73	12 (9.8)	111 (90.2)
Holcopasites	0	0	0	3	147	0	0	150 (100)
Hoplitis	0	0	0	1	3	0	0	4 (100)
Hylaeus	0	4	0	7	24	1	4 (11.1)	32 (88.9)
Lasioglossum	0	11	3	404	407	85	14 (1.5)	896 (98.5)
Megachile	0	1	1	2	9	1	2 (14.3)	12 (85.7)
Melissodes	2	0	2	15	1	5	4 (16)	21 (84)
Nomada	0	0	0	0	1	0	0	1 (100)
Osmia	0	0	0	5	5	2	0	12 (100)
Perdita	0	0	1	1	0	6	1 (12.5)	7 (87.5)
Protandrena	0	1	0	11	0	0	1 (8.3)	11 (91.7)
Sphecodes	1	4	0	61	33	4	5 (4.9)	98 (95.1)
Triepeolus	1	0	0	20	3	17	1 (2.4)	40 (97.6)
Total	58	397	211	985	2388	296	666 (15.3)	3674 (84.7)

Bee abundance and diversity from buckwheat sites were compared to those from control sites (no buckwheat). Mean bee abundance (mean abundance per collection period per site) significantly varied among years (Table 3.3). Mean bee abundance trended highest during the first year of study in 2014, but was not significantly higher than in 2015 (Figure 3.1). Mean bee abundance in 2014 was nearly 3-fold greater than in 2016, despite a consistent sampling effort throughout the three study years. Examining the effect of treatment alone, significantly more bees were collected in buckwheat transects (mean bee abundance = 78.3, SE ± 8.5) than in control transects (mean bee abundance = 44.9, SE ± 8.4). However, mean bee abundance was also significantly affected by the interaction of treatment and collection period (Table 3.3). Although mean abundance of bees did not differ between buckwheat and control sites in late July or late August, in mid-August approximately 3-fold more bees were collected in buckwheat sites than control sites (Figure 3.2). Since different field types were used within the experiment (vegetative and fruit-bearing), I also examined the impact of field type on pollinator abundance. I found slightly higher pollinator abundance in fruit-bearing fields of the buckwheat treatment (1810/3152 bees = 57.4%) compared to vegetative fields (1342/3152 bees = 42.6%), but the opposite was true for the control sites; 34.6% of bees were found in fruit-bearing fields (411/1188 bees), while 65.4% (777/1188 bees) were found in vegetative fields.

The effect of treatment (buckwheat or control) did not influence bee diversity between buckwheat and control sites, but collection period significantly impacted diversity (Table 3.3). Significantly greater bee diversity was recorded during the mid-August collection period while the lowest number of genera were recorded in late August (Figure 3.3).

Table 3.3. Comparison of bee abundance and diversity between flowering buckwheat transects and control field margins in commercial lowbush blueberry fields in Nova Scotia, 2014-16. A significance level of α = 0.05 was used for main effects and a significance level of α = 0.01 was used for interaction effects, in order to protect Type I experiment-wise error rate from over inflation.

Factor	Abundance	Diversity
Year	$F_{2,29}$ = 7.96, ***P* = 0.0071**	$F_{2,29}$ = 0.64, *P* = 0.55
Treatment (buckwheat or control)	$F_{1,4}$ = 7.81, ***P* = 0.017**	$F_{1,5}$ = 1.46, *P* = 0.25
Collection period (CP)	$F_{2,26}$ = 9.61, ***P* = 0.0011**	$F_{2,27}$ = 4.30, ***P* = 0.027**
Year * treatment	$F_{2,29}$ = 4.38, *P* = 0.040	$F_{2,29}$ = 0.72, *P* = 0.51
Year * CP	$F_{4,26}$ = 2.88, *P* = 0.049	$F_{4,27}$ = 2.20, *P* = 0.10
Treatment * CP	$F_{2,26}$ = 13.17, ***P* = 0.0002**	$F_{2,27}$ = 3.83, *P* = 0.039
Year * treatment * CP	$F_{4,26}$ = 3.19, *P* = 0.035	$F_{4,27}$ = 1.39, *P* = 0.27

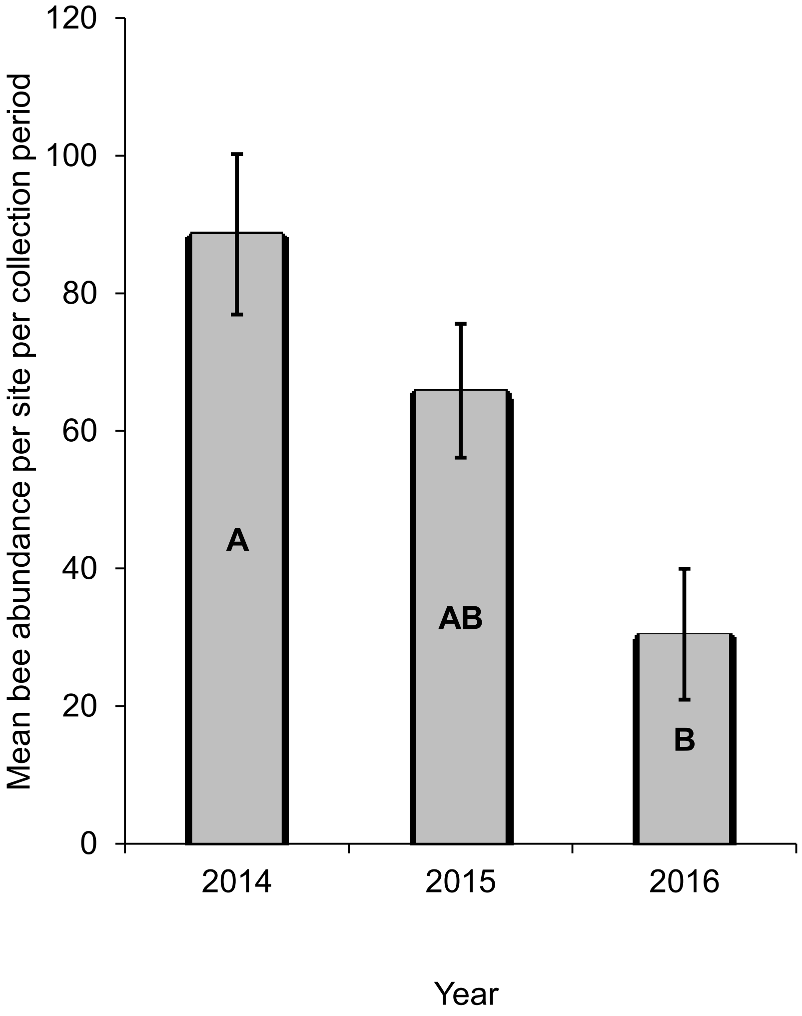

Figure 3.1. The effect of year on mean bee abundance (± SE) in buckwheat and control transects along lowbush blueberry field margins in Nova Scotia over 3 years (2014-2016). Years sharing the same letter are not significantly different (Tukey's test, α = 0.05).

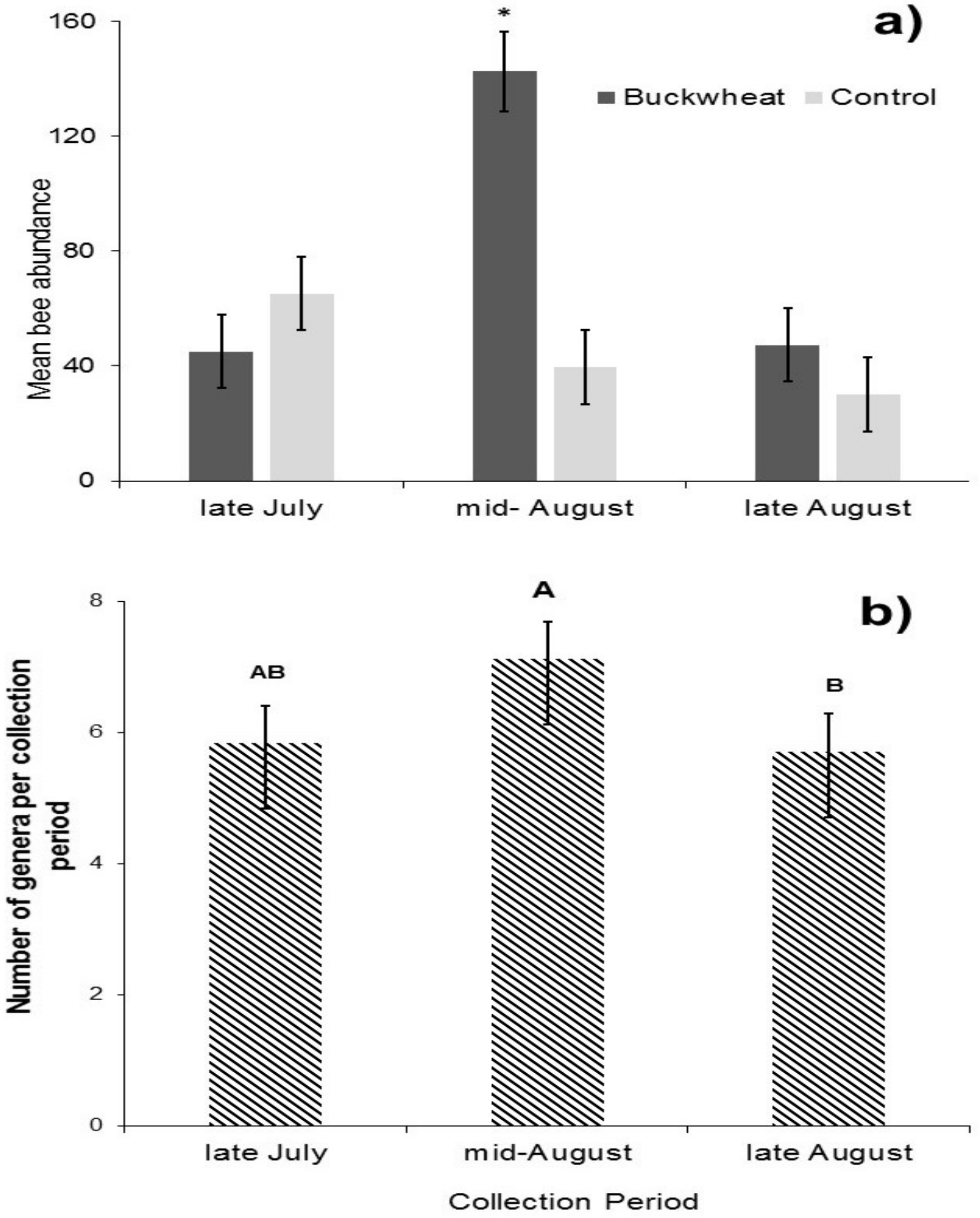

Figure 3.2. a) The interacting effects of treatment and collection period on mean bee abundance (± SE) in buckwheat and control transects along lowbush blueberry field margins in Nova Scotia, 2014-2016. The asterisk indicates a significant difference between treatments within a given collection period (Tukey's test, α = 0.05) b) The effect of collection period on number of bee genera (SE ± 0.57) collected in buckwheat and control transects along lowbush blueberry field margins in Nova Scotia, 2014-2016. Collection periods sharing the same letter are not significantly different (Tukey's test, α = 0.05).

3.4.2 BLUEBERRY BLOOM EXPERIMENT

Two hundred and fifty-two individual bees representing five families and twelve genera were collected during blueberry bloom at experimental sites planted the previous year with buckwheat (Table 3.4). Most small solitary bees were captured in pan traps, whereas larger *Bombus* were captured in aerial nets (Table 3.4). All of the genera captured during blueberry bloom were also recorded visiting buckwheat.

Time of sampling (early, mid, or late bloom) did not significantly affect the abundance of bees captured in this study ($F_{2,6} = 1.44$, $P = 0.33$), nor did collection method ($F_{1,6} = 0.10$, $P = 0.81$). The interaction between collection method and time of sampling for bee diversity was significant ($F_{2,6} = 31.00$; $P = 0.0037$) (Figure 3.3). *Andrena*, *Bombus*, and *Lasioglossum* were the most abundant genera of the bees collected (Table 3.4). Each of these genera peaked during different periods of blueberry bloom; *Bombus* was most abundant during early bloom, followed by *Andrena* during mid-bloom, and *Lasioglossum* during late bloom (Table 3.5). *Bombus* was the most abundant genus collected (95 individuals, 37.7% of total specimens collected), and was represented by six species (Table 3.6). One specimen of the parasitic species *B. insularis* was collected during late blueberry bloom. The other five species were generally collected throughout blueberry bloom (Table 3.6). *B. perplexus* and *B. ternarius* comprised more than 76% of all bumble bees collected (Table 3.6). The *Bombus* collected were all queens. Sixteen bees from the cleptoparasitic genera *Nomada* and *Sphecodes* were also found (Table 3.4). Parasitic bees comprised 6.7% (17/252) of all bees collected.

Table 3.4. Bee fauna collected during blueberry bloom in two Nova Scotia lowbush blueberry fields in 2016 using two sampling techniques: pan trapping and aerial netting.

Family	Genera	No. of specimens	No. bees in pan trap (%)	No. bees in aerial net (%)
Andrenidae	*Andrena*	93	71 (76.3)	22 (23.7)
	Calliopsis	1	0 (0)	1 (100)
Apidae	*Bombus*	95	1 (1.1)	94 (98.9)
	Ceratina	2	2 (100)	0 (0)
	Nomada	4	4 (100)	0 (0)
Colletidae	*Colletes*	1	1 (100)	0 (0)
Halictidae	*Augochlorella*	6	6 (100)	0 (0)
	Halictus	1	1 (100)	0 (0)
	Lasioglossum	35	35 (100)	0 (0)
	Sphecodes	12	12 (100)	0 (0)
Megachilidae	*Megachile*	1	1 (100)	0 (0)
	Osmia	1	1 (100)	0 (0)
Total		252	135 (53.6)	117 (46.4)
			SE = ± 6.1	SE = ± 7.9

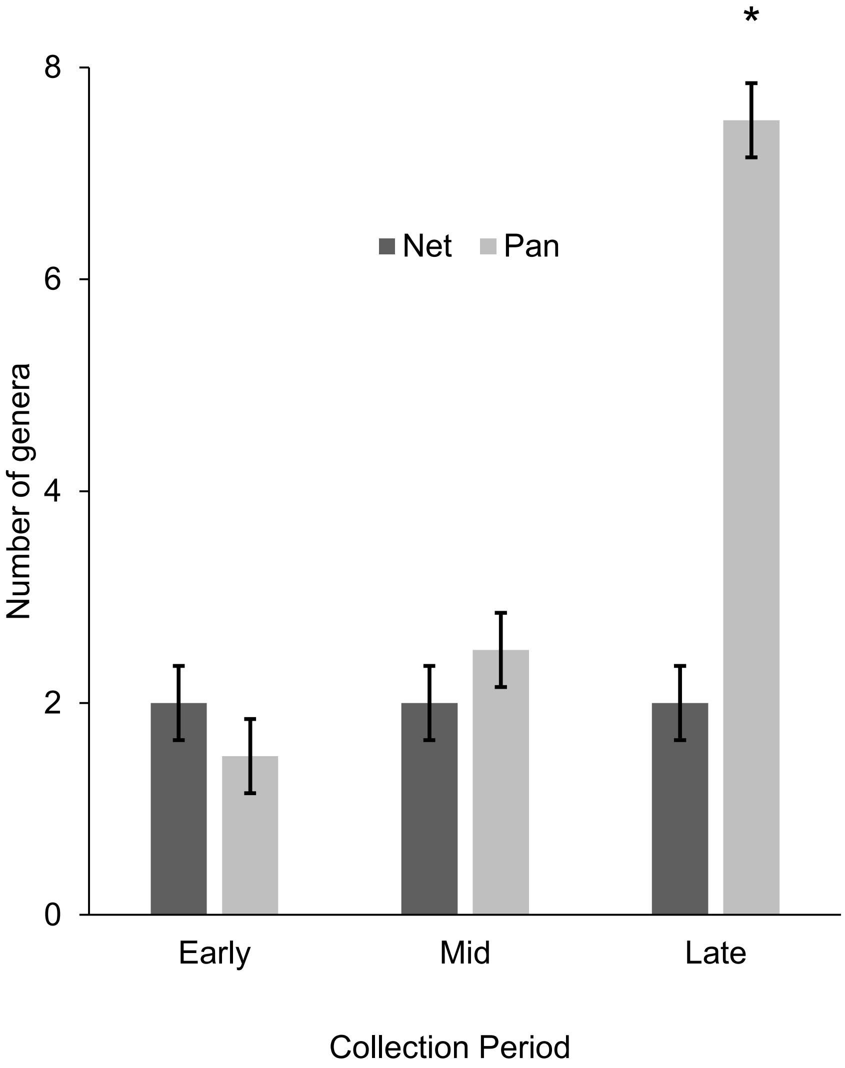

Figure 3.3. Mean number (± SE) of bee genera collected from lowbush blueberry fields (Nova Scotia, 2016) by aerial netting or pan trapping during early, mid, or late bloom of blueberry plants. Means were compared using the LSD test. The asterisk indicates a mean that is significantly different among treatments (least square means, $\alpha = 0.05$).

Table 3.5. Total number and percent relative abundance of bees collected by aerial netting and pan trapping (combined) in two lowbush blueberry fields in Nova Scotia, 2016.

Bee genera	Number of individuals (% relative abundance per bloom period)			Total number of individuals (% relative abundance throughout bloom)
	Early bloom	Mid-bloom	Late bloom	
Bombus	41 (59.4)	20 (37.0)	34 (26.3)	95 (37.7)
Andrena	25 (36.2)	31 (57.4)	37 (28.6)	93 (36.9)
Lasioglossum	2 (3.0)	0	33 (25.5)	35 (13.9)
Sphecodes	0 (0)	1 (1.9)	11 (8.5)	12 (4.8)
Augochlorella	0 (0)	0	6 (4.7)	6 (2.3)
Nomada	0 (0)	2 (3.7)	2 (1.6)	4 (1.6)
Ceratina	0 (0)	0	2 (1.6)	2 (0.8)
Calliopsis	1 (1.4)	0	0 (0)	1 (0.4)
Colletes	0 (0)	0	1 (0.8)	1 (0.4)
Halictus	0 (0)	0	1 (0.8)	1 (0.4)
Megachile	0 (0)	0	1 (0.8)	1 (0.4)
Osmia	0 (0)	0	1 (0.8)	1 (0.4)
Total	69 (27.4)	54 (21.4)	129 (51.2)	252 (100)
	SE = ± 3.8	SE = ± 2.9	SE = ± 4.3	

Table 3.6. Bumble bees (*Bombus* spp.) collected during bloom in Nova Scotia lowbush blueberry fields, 2016.

Bombus species	Number of individuals (relative % abundance)	Bloom period collected
B. impatiens	6 (6.3)	Early, mid, late
B. insularis	1 (1.1)	Late
B. perplexus	34 (35.8)	Early, mid, late
B. ternarius	39 (41.0)	Early, mid, late
B. terricola	2 (2.1)	Early, late
B. vagans	13 (13.7)	Early, mid, late
Total	95 (100)	
	SE = ± 6.8	

3.5 DISCUSSION

Bee abundance and diversity were documented in buckwheat and control transects along lowbush blueberry fields after crop bloom. I expected abundance to increase over the three study years but this was not demonstrated. Instead, abundance decreased over the three years, with significantly fewer bees collected in 2016 than 2014. As there was a slightly higher abundance of bees in buckwheat transects in fruit-bearing blueberry fields than in control transects in fruit-bearing fields, a ‘legacy’ effect may have occurred, whereby the blueberry bloom attracted pollinators and they were subsequently recorded in buckwheat transects. This trend may suggest buckwheat provided floral resources after blueberry bloom. By examining the effect of treatment alone, mean bee abundance was significantly higher in buckwheat transects than in control transects, supporting my hypothesis that more wild bees would be detected in buckwheat field edges than in control field edges. However, the significant interaction of treatment and collection period showed that higher bee abundance was only detected in buckwheat in mid-August, in comparison to other collection periods. Given the three-fold greater abundance of bees during mid-August in buckwheat, buckwheat may be an attractive floral resource under certain conditions, but it is not clear why this effect was not seen earlier (late July) or later (late August) in the season. There was no effect of treatment on bee diversity between buckwheat and control sites, contrary to my expectation. There was a significant effect of collection period, however, with the most bee genera detected in mid-August, although not significantly more than in late July. These findings correspond to increased abundance during mid-August, and may be related to bee emergence and foraging behaviour. Previous Nova Scotia surveys have found the majority of bee flight periods (Sheffield et al. 2003) and captures (Cutler et al. 2015b) to be during August in lowbush blueberry fields.

Calliopsis, *Bombus*, and *Lasioglossum* together comprised 85% of total specimens captured over the three-year study, but displayed wide variation in abundance among the three years of study. All three genera increased from 2014 to 2015 (*Calliopsis* and *Bombus* greatly so) and decreased from 2015 to 2016. The remaining twenty genera each had a relative abundance of 3.5% or less. Previous surveys of bee fauna in lowbush blueberry have reported similar results. In Nova Scotia, 12 different bee genera were recorded throughout the season (Cutler et al. 2015b), and in Maine, 19 different genera were documented (Bushmann and Drummond 2015). All genera collected by Cutler et al. (2015) were recorded in my study, but I did not find *Augochloropsis* and *Macropsis*, which were recently collected in Maine lowbush blueberry fields (Bushmann and Drummond 2015). *Augochloropsis* is found in Ontario but has not been recorded east to Nova Scotia, and *Macropis* is considered relatively rare in the study region (Packer et al. 2007). I anticipated high collections of *Bombus* and *Lasioglossum* based on previous surveys in lowbush blueberry (Bushmann and Drummond 2015; Cutler et al. 2015b), but the high abundance of *Calliopsis*, of which only one species is documented in eastern Canada (*C. andreniformis*) (Packer et al. 2007), was unexpected. *Calliopsis* was recorded in both buckwheat and control transects, and there are records for this bee foraging on buckwheat (Discover Life: http://www.discoverlife.org/20/q?search=Fagopyrum+esculentum).

Bee abundance and diversity varied throughout collection periods and years. I propose several possible reasons for this observation. First, wild bee populations are known to fluctuate naturally annually (Minckley et al. 1994; Cane and Tepedino 2001;

Williams et al. 2001). Weather conditions may have also impacted bee communities. During the three year study, significant snowfall was recorded during December 2014 to April 2015. The 1981-2010 climate normal for snowfall from December to April for my study region is 202.3 cm, but 362.9 cm of snowfall were recorded from December 2014 to April 2015 (Government of Canada 2016). This abundant snowfall may have provided exceptional insulation, potentially positively impacting overwintering and resulting in the high abundance of bees recorded in 2015. Weather may also have impacted floral resource availability and nectar provision. The twenty year precipitation average (1981-2010) for the study region is 352.1 mm between May and August, but 2014 received 223.2 mm, 2015 received 404.6 mm, and 2016 received 290.5 mm (Government of Canada 2016). The dry year of 2016 may have resulted in fewer floral resources or decreased nectar production, negatively affecting food provision to bees, although 2014 was even dryer than 2016 and bee abundance was highest during this time. In addition to 2016 being below the precipitation average, precipitation events tended to be limited to 2-4 events each month that produced the majority of the total precipitation (Government of Canada 2016). These inconsistent precipitation events and subsequent bee collections make determining how weather impacted bee abundance and diversity difficult.

It is possible that buckwheat's flowering biology impacted the results, as buckwheat is visited most frequently in the morning, before nectar production ceases shortly after mid-day (Goodman et al. 2001; Racys and Montviliene 2005). To minimize this potential impact, sampling was rotated among sites, and buckwheat transects were sampled during the morning and afternoon. It is therefore unlikely that floral biology impacted the results greatly. It is also unlikely that the seasonal collection caused population declines (Gezon et al. 2015). Declines have been noted for certain bee species, but this is not a clear trend across all bees (Colla and Packer 2008; Cameron et al. 2011; Colla et al. 2012a). I do not have sufficient data to draw any conclusions on the long-term community trends of wild bees in Nova Scotia.

Buckwheat was selected due to its ability to establish readily in poor soil fertility conditions and flower quickly to provide a concentrated food resource for bees. Despite these benefits, certain difficulties with using buckwheat were noted. The 2014 and 2016 field seasons were uncharacteristically dry for Nova Scotia, negatively impacting buckwheat establishment. Buckwheat did not tolerate drought, resulting in poor or failed establishment at multiple sites (3/5 in 2014, 1/5 in 2015, and 2/5 in 2016). Once established, buckwheat bloomed for four weeks beginning in late July. Had all three sample years been ‘typical’, with historical average precipitation events, it is possible buckwheat would have established readily and bloomed sooner, providing flower resources immediately after blueberry bloom had finished, rather than having to be re-planted and become delayed in flowering. The initial reasoning behind planting buckwheat in mid- to late- June was to avoid the busy season of blueberry bloom for farmers, thus encouraging future producer adoption. If buckwheat is used for future habitat management, however, planting should occur earlier in the season to ensure buckwheat blooms immediately following lowbush blueberry, and it may need to be planted a second time to extend the flowering window until late summer. Others have experienced success with buckwheat establishment and flowering around agricultural fields (Stephens et al. 1998; Carreck and Williams 2002), and my inspiration for this study came from a blueberry grower who had success in establishing buckwheat immediately following blueberry bloom, under adequate precipitation events. Although buckwheat is known to be attractive to bees, the challenges I observed in buckwheat establishment during dry conditions and its poor nutritional quality (11% crude protein in the pollen) (Somerville 2001), may suggest alternative floral resources could be better suited to habitat management for pollinators, especially as weather patterns change in our region. In Maine, U.S., numerous flowering resources surrounding lowbush blueberry fields were attractive to bees (Bushmann and Drummond 2015), and perhaps some of these ‘weeds’ could be further explored for habitat management.

Evaluating bee genera present during blueberry bloom in two of the buckwheat sites allowed me to determine whether the same genera visited buckwheat and lowbush blueberry. All of the genera recorded during blueberry bloom were also detected in buckwheat transects. This suggests that buckwheat is suitable for wild bees also involved in blueberry pollination. Although many of the solitary bees live only for a few weeks (Michener 2007) and would not be present for both blueberry bloom and buckwheat flowering, the second generation may be (e.g. *Andrena*). Longer-lived bees, such as bumble bees, seemed to benefit from buckwheat after blueberry bloom had finished. I predicted bee abundance would increase as bloom progressed, but there was no significant increase over the bloom period. The high relative abundance of *Andrena*, *Bombus*, and *Lasioglossum* bees noted in this study is likely due to their timely emergence with blueberry bloom and their adaptations to effectively pollinate blueberry flowers (Hicks 2011; Moisan-Deserres et al. 2014b).

The interaction of sampling method and period of blueberry bloom significantly impacted diversity. Aerial netting only ever captured two different genera during each sampling event throughout blueberry bloom, but pan trapping collected greater bee diversity. More genera were collected using pan trapping as blueberry bloom progressed, with an average of 7.5 genera captured per field during late blueberry bloom. This could be a reflection of greater bee emergence and foraging activity as the season progressed (Sheffield et al. 2003). Since collection only occurred in two fields, limited conclusions can be drawn about the population trends of bees during blueberry bloom.

I had anticipated *Lasioglossum* to be the most abundant genera during blueberry bloom based on a previous survey in Nova Scotia (Cutler et al. 2015b). Whereas Cutler et al. (2015b) found more than five times as many *Lasioglossum* as *Andrena* bees, I found *Andrena* to be almost three times as abundant as *Lasioglossum*. The *Lasioglossum* collected by Cutler et al. (2015b) peaked during July (post-bloom), whereas my survey focused on the bee fauna during blueberry bloom, potentially explaining the discrepancy in findings. Cutler et al. (2015b) reported *Andrena* to be six-fold more abundant than *Bombus*, but I collected approximately the same number of specimens for each genus. This discrepancy may be explained by the pan trapping conducted by Cutler et al. (2015b) versus the combined sampling method I used, as bumble bees were noted to crawl out of the pan traps.

Pan trapping captured the most bees in the buckwheat and blueberry bloom experiments and was more effective than aerial netting for capturing genera such as *Augochlorella*, *Andrena*, *Calliopsis*, *Ceratina*, *Halictus*, *Holcopasites*, *Hylaeus*, *Lasioglossum*, *Megachile*, *Melissodes*, *Sphecodes* and *Triepeolus*. Nearly three-fourths of all *Andrena* collected were captured using pan traps, while slightly more *Bombus* were collected by aerial nets (56%) than pan traps. The use of two sampling techniques in this study demonstrated the differences in bees captured between pan trapping and aerial netting. If surveying had implemented only one sampling method, one of these groups may have been misrepresented or not detected (e.g. *Andrena*), but this may not be the case across all genera (e.g. *Bombus*). The ‘best’ collection method for bees is still up for debate, with various studies reporting differing results (Cane et al. 2000; Popic et al. 2013; Meyer et al. 2017).

Although many short-lived solitary bees are involved in blueberry pollination, my results demonstrate that the pollinator fauna is dominated by longer-lived bumble bees. The five pollinating bumble bee species were documented from early to late bloom, supporting previous records of early spring emergence (Laverty and Harder 1988; Colla and Dumesh 2010) and visitation to lowbush blueberry (Sheffield et al. 2003). Bumble bees are the most dependent bees on season-long food resources, driving the need to provide abundant, high-quality sources of pollen and nectar near blueberry fields before and after crop bloom. Bumble bees emerge as solitary queens in the spring, establish a nest, forage for resources and build a colony to several hundred individuals (Heinrich 2004; Michener 2007). The colony will be active until mid- to late autumn (Laverty and Harder 1988). Bumble bee queens are more likely to contribute to blueberry pollination, as workers have not yet emerged when blueberries are in bloom. However, floral resources to support a growing bumble bee colony and subsequent production of new queens, who will contribute to blueberry pollination the following year, is important (Persson and Smith 2013). A conservation case for shorter-lived solitary bees can also be made; due to small foraging ranges (often under 600 m) (Gathmann and Tscharntke 2002), solitary bees depend on nearby floral resources for food. If bee foraging activity extends before or beyond blueberry bloom, alternative floral resources are needed to support bees nesting within the crop vicinity.

3.6 SUMMARY OF CHAPTER 3 AND TRANSITION TO CHAPTER 4

The success of habitat management techniques for bees depends on a number of factors, including available nesting sites, foraging ranges, and the floral resources needed to sustain a given population (Wratten et al. 2012). Bee abundance and diversity typically did not differ significantly between buckwheat and control sites, except for mid-August, when significantly more bees were present in buckwheat transects. Unmanaged control sites contained bee diversity equivalent to that in buckwheat sites, suggesting wildflowers along the edge of blueberry fields may be adequate to support the bee community. Buckwheat is an attractive flowering plant to bees, but challenges with establishment during dry conditions suggest alternative flowering plants may be better suited to habitat management in lowbush blueberry agroecosystems.

My findings indicate that habitat management decisions may need to be made on an individual field basis. Given the unique landscape of lowbush blueberry agroecosystems, general conclusions about the need for and benefits of habitat management are difficult. Fields containing adequate post-bloom floral resources may not require habitat management, but fields with limited post-bloom floral resources may be good candidates for habitat management, either by planting floral resources or managing the field edges to encourage wildflower growth. Further study is required to determine the threshold of surrounding resources needed to support wild bees.

While I studied the wild bee visitation to buckwheat and control transects, I also evaluated various natural enemy groups at the same experimental sites (Chapter 4). I was interested in whether floral enhancements within lowbush blueberry agroecosystems affected natural enemy communities similarly to wild bees, or if certain natural enemy communities clearly benefited from buckwheat plantings adjacent to blueberry fields.

3.7 SUPPLEMENTARY INFORMATION

Table S3. Established buckwheat and control sites and sampling information in lowbush blueberry agroecosystems in Nova Scotia, Canada, 2014-2016.

Year	Location	Coordinates	Field Type	Size (ha)	Treatment
2014	Great Village	45°24'36.55"N 63°36'36.65"W	Vegetative	2.2	Buckwheat
	Parrsboro	45°25'24.34"N 64°20'42.64"W	Vegetative	3.6	Buckwheat
	Great Village	45°24'24.08"N 63°36'24.08"W	Vegetative	3.2	Control
	Parrsboro	45°41'95.47"N 64°35'42.25"W	Vegetative	9.8	Control
2015	Great Village	45°24'36.55"N 63°36'36.65"W	Fruit-bearing	2.2	Buckwheat
	Parrsboro	45°25'24.34"N 64°20'42.64"W	Fruit-bearing	3.6	Buckwheat
	Earltown	45°58'43.63"N 63°18'35.19"W	Vegetative	3.0	Buckwheat
	Kemptown	45°54'63.64"N 63°11'49.30"W	Vegetative	4.0	Buckwheat
	Great Village	45°24'24.08"N 63°36'24.08"W	Fruit-bearing	3.2	Control
	Parrsboro	45°41'95.47"N 64°35'42.25"W	Fruit-bearing	9.8	Control
	Newville Lake	45°30'25.4"N 64°19’59.7”W	Fruit-bearing	9.2	Control
2016	Great Village	45°24'36.55"N 63°36'36.65"W	Vegetative	2.2	Buckwheat
	Earltown	45°58'43.63"N 63°18'35.19"W	Fruit-bearing	3.0	Buckwheat
	Kemptown	45°54'63.64"N 63°11'49.30"W	Fruit-bearing	4.0	Buckwheat
	Great Village	45°24'24.08"N 63°36'24.08"W	Vegetative	3.2	Control
	Parrsboro	45°41'95.47"N 64°35'42.25"W	Vegetative	9.8	Control
	Newville Lake	45°30'25.4"N 64°19’59.7”W	Vegetative	9.2	Control

CHAPTER 4: ENHANCING LOWBUSH BLUEBERRY FIELD MARGINS FOR NATURAL ENEMIES

4.1 ABSTRACT

Natural enemies are beneficial insects that provide important biological pest control services in agroecosystems. With increasing demand to produce more food for a growing human population, and desire to reduce insecticide use, natural enemies may represent an effective means of pest management moving forward. Lowbush blueberry (*Vaccinium angustifolium* Aiton) is targeted by a number of insect pests, many of which are naturally managed by various natural enemies, including ground beetles (Coleoptera) and parasitic wasps (Hymenoptera). Buckwheat (*Fagopyrum esculentum* Moench) was established in lowbush blueberry field margins to provide food and habitat resources to natural enemies, in order to enhance their communities and promote greater biological pest control. Natural enemy abundance was compared between buckwheat margins and typical, unenhanced field margins ('control'). More hover flies and robber flies were detected in buckwheat transects than in control transects, while ground beetle and ladybird beetle abundance were generally higher in control sites than buckwheat sites, although not significantly so. Tachinid flies were more abundant in buckwheat sites in the first two years of study, but became more abundant in control sites in 2016. An opposing trend was observed for wasps, whereby wasps were more abundant in control sites in 2014, but became more abundant in buckwheat sites in 2015 and 2016. My results demonstrate that typical blueberry field margins may already support a diverse and abundant natural enemy fauna, and planting buckwheat along field

edges may not impact natural enemy groups evenly. The need for habitat management techniques should be made on an individual field basis.

4.2 INTRODUCTION

Insect pests cause significant damage to agricultural crops and are commonly managed using insecticides. With growing interest in minimizing pesticide use there is increasing focus on biological control (Losey and Vaughan 2006; Bommarco et al. 2013). Natural enemies provide biological pest control, and include beneficial insects such as predatory beetles (e.g. Carabidae and Coccinellidae families), parasitic wasps (Hymenoptera), and certain flies (e.g. Asilidae, Syrphidae, and Tachinidae families). Natural enemies that inhabit agroecosystems require access to food and shelter throughout much of the growing season, and habitat management is a conservation strategy that aims to enhance the quality of food and shelter resources for natural enemies in an agroecosystem (Landis et al. 2000).

Habitat management has been implemented in highbush blueberry (*Vaccinium corymbosum* L.) in an attempt to conserve and boost communities of natural enemies (Walton and Isaacs 2011; Blaauw and Isaacs 2012, 2015; Renkema et al. 2016), but this strategy has not been well-studied in lowbush blueberry (*Vaccinium angustifolium* Aiton). Lowbush blueberry is a wild ericaceous plant that is native to eastern Canada and Maine, U.S. Fields are established through natural growth and establishment of the plant by removal of competing vegetation. Lowbush blueberry was chosen as the model crop in this study as it is a significant crop in northeastern North America, has many insect pests (Wood et al. 1983; Kinsman 1993), and there is interest within the industry to increase use of non-chemical control methods, including biological control.

Since lowbush blueberry is grown in its native range, native natural enemies that have co-evolved with the crop can be found in this agroecosystem. Several ground beetle (Coleoptera: Carabidae) species were found to consume blueberry spanworm and blueberry fruit fly pupae in the laboratory (Renkema et al. 2013) and field (Renkema et al. 2014), and the enhancement of ground beetles communities could therefore provide valuable biological control services to lowbush blueberry (Renkema et al. 2014). Parasitism of blueberry spanworm have been recorded by parasitic wasps (Hymenoptera: Ichneumonidae) and flies (Diptera: Tachinidae) in lowbush blueberry fields in Nova Scotia (Renkema et al. 2013; Loureiro and Cutler 2016). These studies indicate that biological pest control occurs naturally in this agroecosystem and support the research of enhancement techniques to further enhance these beneficial insects.

I used a habitat management technique to determine if natural enemy communities could be enhanced through the provision of buckwheat (*Fagopyrum esculentum*) as a flowering resource along lowbush blueberry field margins. Buckwheat was selected due to its food provision (pollen and nectar) and reported agronomic characteristics, including ease of establishment and tolerance for poor, acidic soils typical of lowbush blueberry land, as well as attractiveness to a variety of beneficial insects (Platt et al. 1999; Goodman et al. 2001; Racys and Montviliene 2005; Taki et al. 2009). Additionally, buckwheat flowers quickly (within three to four weeks of planting), is an annual, will smother alternative weed growth, and is not invasive. In this study, blueberry field margins with buckwheat were compared to ‘control’ margins. I hypothesized that more natural enemies would be collected from buckwheat plots than control plots over the three year study. I also expected natural enemy abundance to increase in buckwheat transects after the three year study period.

4.3 MATERIALS AND METHODS

4.3.1 STUDY SITES

The impact of buckwheat on natural enemy abundance was studied over three field seasons (2014-2016) in Colchester County and Cumberland County, Nova Scotia, Canada. All field margins were adjacent to commercial lowbush blueberry fields. The same field sites (Table S3), experimental design, and collection methods were used as for Chapter 3. Buckwheat plantings along blueberry field edges were compared to control field margins that received no floral enhancement. All sites were separated by at least 1 km. Study transects were established within 2 m of the lowbush blueberry fields along the south-facing field margin of each study site and were 2 m by 40 m. The blueberry fields were 5.0 ± 0.75 ha on average. Each site was sampled three times per year, from late July to late August. Buckwheat was seeded using a Tye no-till seeder (Dulath, Georgia, U.S.) at a rate of 67.2 kg ha^{-1} on 12 June 2014, 17 June 2015, and 21 June 2016.

4.3.2 SAMPLING

The natural enemies evaluated were ground beetles (Coleoptera: Carabidae), hover flies (Diptera: Syrphidae), ladybird beetles (Coleoptera: Coccinellidae), robber flies (Diptera: Asilidae), tachinid flies (Diptera: Tachinidae), and wasps (Hymenoptera). These insects were sampled in buckwheat and control transects during each of the three field seasons, concurrently with wild bee sampling (Chapter 3). This occurred 25-31 July, 10-16 August, and 17-25 August. Aerial netting and pan trapping were used at each site, and sampling of sites was alternated to ensure that morning and afternoon collections occurred at each site. Any natural enemy (ground beetle, hover fly, ladybird beetle, robber fly, tachinid fly, or wasp) observed visiting a buckwheat flower during aerial netting sampling was collected, and the pan traps were set up directly along the buckwheat planting, adjacent to the blueberry field. In the control sites, a variety of flowers were documented including wild rose (*Rosa acicularis*), goldenrod (*Solidago* spp.), vetch (*Vicia* spp.), clovers (*Trifolium* spp.), sweet clovers (*Melilotus* spp.), and St John's Wort (*Hypericum perforatum*). Any natural enemy observed visiting flowering plants in the control transect were collected with a net during aerial netting sampling, and pan traps were placed directly along the control transect adjacent to the blueberry field.

Transects were aerial netted for a total of 30 minutes per sampling event between 10 a.m. and 4 p.m., when the temperature was above 15 °C, and conditions were sunny with low wind. Thirty pan traps were set out in each transect, approximately 1 m apart, and were activated for 24-48 hours when favourable weather conditions were forecasted (i.e. no precipitation). Abundances were standardized to a per-day measure for each site and day (Cutler et al. 2015b). White, yellow, and blue pan traps were alternated along the transects for a total of ten traps per color (Morandin et al. 2007). Each pan trap consisted of a 355 mL bowl (SOLO Cup Company, Urbana, IL) filled with approximately 200 mL of tap water and three drops of Dawn Ultra dish detergent (Procter and Gamble, Toronto, ON) as a surfactant (Cutler et al. 2015b). Pan trap specimens were filtered from the soapy water solution using a wire sieve, transferred to plastic bags filled with water, and placed on ice for transport to the laboratory. Aerial netted insects were placed in jars with ethyl acetate to kill the specimens, and placed on ice after sampling and returned to the lab for identification. In the lab, insects were transferred to jars and stored in 70% ethanol until identification and pinning.

4.3.3 IDENTIFICATION

Natural enemies were identified to family according to Marshall (2007). Specimens were deposited at the A. D. Pickett Entomological Museum at Dalhousie University Agricultural Campus in Truro, Nova Scotia.

4.3.4 STATISTICAL ANALYSIS

Natural enemies were captured using both pan trapping and aerial netting, but total abundances were combined from each method for analysis. Statistical models were used to test whether the planting of buckwheat transects influenced the abundance of different natural enemy groups (e.g. carabid beetles) along lowbush blueberry field edges. Due to high variability among years and field sites, the model assumptions of normal distribution and constant variance of the residuals could not be met for the original data or through transformation. A non-parametric Kruskal-Wallis test was used to detect differences in natural enemy abundance in buckwheat and control sites using Proc npar1way in SAS v. 9.4 (SAS Institute Inc. 2014). The Kruskal-Wallis test ranks observations to test for the equality of treatment means. The abundance of each natural enemy group was modeled as a function of sampling year (2014, 2015, 2016) and floral treatment (buckwheat and control).

4.4 RESULTS

A total of 1358 natural enemies were collected from 2014 to 2016: 133 ground beetles, 281 hover flies, 48 ladybird beetles, 163 robber flies, 36 tachinid flies, and 697 wasps.

729 (53.7%) natural enemies were captured in buckwheat transects compared to 629 natural enemies (46.3%) captured in control transects. The statistical models indicated significant differences in abundance between buckwheat and control sites for ground beetles and hover flies, while abundance was significantly or marginally significantly different among years for hover flies, ladybird beetles, robber flies, tachinid flies, and wasps (Table 4.1).

Table 4.1 Summary of statistical tests for six natural enemy groups (ground beetles, hover flies, ladybird beetles, robber flies, tachinid flies, and wasps) in buckwheat and control sites in Nova Scotia, Canada, 2014-2016. A significance level of α = 0.05 was used, and significant (< 0.05) and marginally significant (≥0.05 *P* ≤ 0.09) *P*-values are indicated in bold.

Natural enemy and factors tested	df	X^2	*P*-value
Ground beetles			
Treatment	1	6.83	**0.0089**
Year	2	3.32	0.19
Collection Period (CP)	2	0.27	0.87
CP * treatment	5	8.30	0.14
Treatment * year	5	10.48	**0.06**
Hover flies			
Treatment	1	5.89	**0.015**
Year	2	5.05	**0.08**
Collection period	2	2.16	0.34
CP * treatment	5	8.82	0.12
Treatment * year	5	10.5	**0.06**
Ladybird beetles			
Treatment	1	1.12	0.29
Year	2	9.57	**0.0084**
Collection period	2	0.28	0.87
CP * treatment	5	5.32	0.38
Treatment * year	5	9.57	**0.0084**
Robber flies			
Treatment	1	0.52	0.47
Year	2	9.12	**0.0104**
Collection period	2	2.19	0.33
CP * treatment	5	3.88	0.57
Treatment * year	5	10.20	**0.07**

Natural enemy and factors tested	df	X^2	*P*-value
Tachinid flies			
Treatment	1	1.06	0.30
Year	2	7.06	**0.029**
Collection period	2	2.54	0.28
CP* treatment	5	4.15	0.53
Treatment * year	5	15.63	**0.0080**
Wasps			
Treatment	1	2.42	0.12
Year	2	11.58	**0.0031**
Collection period	2	0.55	0.76
CP * treatment	5	6.67	0.25
Treatment * year	5	14.72	**0.012**

Interactions between year (2014, 2015, and 2016) and treatment (buckwheat or control) significantly or marginally significantly impacted all six natural enemy groups (Table 4.1), although the effects varied (Figure 4.1). For instance, ground beetle abundance trended higher in control transects than buckwheat transects, but significantly fewer ground beetles were detected in the buckwheat transects only in 2016 (Figure 4.1). In contrast, hover fly abundance trended higher in buckwheat transects than control transects, although only control transects in 2014 contained significantly fewer hover flies (Figure 4.1). Ladybird beetle abundance trended higher in control sites than in buckwheat sites, but not significantly so. The only significant difference in robber fly abundance was between buckwheat transects in 2014 and control transects in 2016, although abundance trended higher in buckwheat sites than in control sites across all years (Figure 4.1). Robber fly abundance trended higher in buckwheat, but there were no clear statistical differences. Tachinid fly abundance was significantly lower in control transects than in buckwheat transects in 2014 and 2015, but increased in 2016. Tachinid fly abundance did not significantly change over the three year period in buckwheat transects (Figure 4.1). Wasp abundance was lowest in control transects in 2015. In 2014, more wasps were collected from control sites, but in 2015 and 2016, more wasps were collected in buckwheat sites (Figure 4.1).

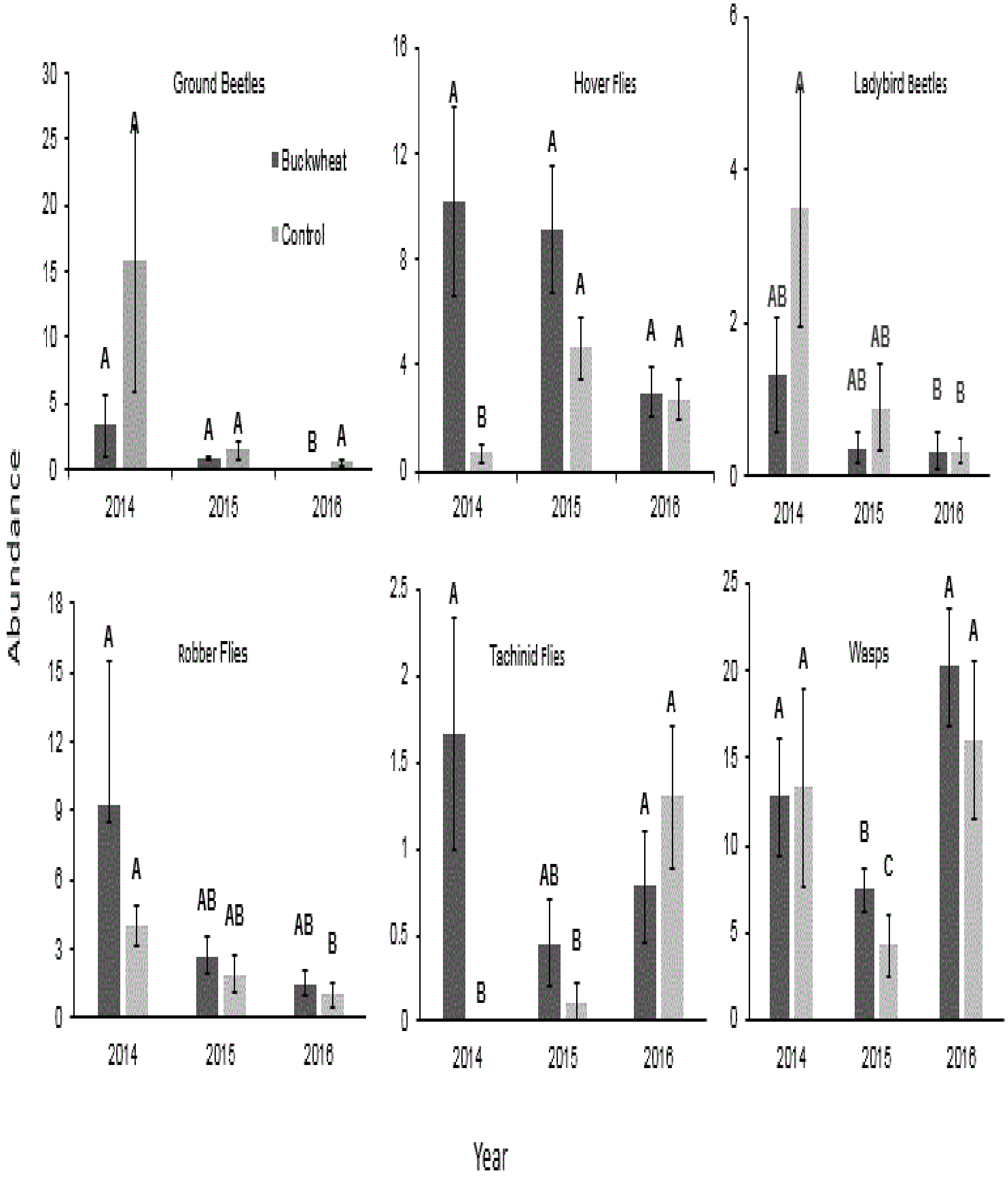

Figure 4.1. The impact of treatment (buckwheat or control) and year (2014, 2015, or 2016) combinations on natural enemy abundance (± SE) in buckwheat and control transects adjacent to lowbush blueberry fields in Nova Scotia, 2014-2016. Means sharing the same letter are not significantly different (α = 0.05).

4.5 DISCUSSION

Natural enemies are important pest control agents in agroecosystems. I tested whether the abundance of natural enemies was affected by the presence of buckwheat along blueberry field edges in comparison to control edges. The interaction effect of treatment (buckwheat or control) and collection year (2014, 2015, or 2016) significantly affected all natural enemies studied, indicating the strong influence of year on the benefit of floral enhancement for natural enemies. Ground beetle and ladybird beetle abundances were higher in control sites than buckwheat sites, but hover flies and robber flies trended higher in buckwheat sites. Wasp abundance was initially higher in control sites, but this natural enemy group became more abundant in buckwheat sites during the last two years of study. In contrast, tachinid flies were more abundant in buckwheat sites in 2014 and 2015 than control sites, but shifted to be more plentiful in control sites in 2016. My results suggest that buckwheat may benefit certain natural enemies after blueberry bloom, but there was high variability, particularly among years.

I expected natural enemy abundance to increase in buckwheat transects over the three years of study but the exact opposite trend was observed for all groups, except wasps. Similar findings were found in Chapter 3, where wild bee abundance decreased over the three-year study period. As with wild bees, it is possible that natural enemy communities were affected by the weather conditions during the study period, although the data indicate weather conditions, if a factor, impacted natural enemy groups differently. Higher than average snowfall was recorded for the winter of 2014/2015 (362.9 cm from December 2014 to April 2015, compared to the 1981-2010 climate normal of 202.3 cm for this same time period) (Government of Canada 2016). In 2015, 404.6 mm of precipitation were recorded for the study region from May to August, but this was only slightly higher than the thirty-year average (1981-2010) of 397.1 mm from May to August (Government of Canada 2016). It is not understood if and how climate affected natural enemy abundances, as there were no clear trends in natural enemy abundance among the three years.

Although consistent benefits were not demonstrated from buckwheat plantings for various natural enemies, I did not measure pest control and thus cannot draw conclusions on this ecosystem service. It is possible that although higher natural enemy abundance was not recorded in buckwheat transects for most groups studied, there may have been effects on pest numbers or parasitism in the adjacent blueberry field. In a recent study of parasitism in lowbush blueberry parasitism in Nova Scotia, mean parasitism by tachinid flies and ichneumonid wasps was 21.4%, but these levels ranged from 0 to 36.8% depending on the field (Loureiro and Cutler 2016). Furthermore, parasitism levels varied according to date, with increased parasitism observed in early July compared to early June (Loureiro and Cutler 2016). In a previous study in Nova Scotia blueberry fields, higher parasitism levels were reported, with 50-60% of field-collected blueberry spanworm larvae being parasitized and killed by tachinid flies and ichneumonid wasps (Cutler et al. 2015a).

Variable success of habitat management has also been noted in other studies. In Michigan, U.S., a flowering mixture established along highbush blueberry field margins did not clearly increase natural enemy abundance in comparison to control margins (Blaauw and Isaacs 2015), demonstrating similar variability among field margins and natural enemy groups. In Virginia, U.S., buckwheat strips planted adjacent to vegetable crop fields were attractive to both insect pests and natural enemies, including hymenopterans, tachinids and hover flies (Platt et al. 1999). Strips of buckwheat planted in soybean (*Glycine max*) field margins contained greater Coccinellidae abundance than in control margins (Woltz et al. 2012), and conservation strips of wildflowers established in highbush blueberry field margins increased hover fly abundance in comparison to control margins (Walton and Isaacs 2011). Similarly, higher hover fly abundance was detected in my study in buckwheat transects than in control transects, but overall abundance did not significantly increase over the three year period.

Pesticide use may have impacted natural enemies (Desneux et al. 2007). All of the fields in the study received pesticides, including insecticides, fungicides, and herbicides. Although insecticides can provide effective control for insect pests, natural enemies are also negatively impacted (Desneux et al. 2007). It is also possible that the sampling methods affected the natural enemies collected. Since natural enemies were studied concurrently with wild bees, the same collection methods were used (pan trapping and aerial netting). However, alternative collection methods, including pitfall traps, may have collected certain natural enemies more effectively (O’Neal et al. 2005a; Cutler et al. 2012b; Mullins 2014; Renkema et al. 2016). Vacuum sampling, sticky traps, and sweep netting are often used to collect Dipteran and Hymenopteran natural enemies (Renkema et al. 2013; Blaauw and Isaacs 2015). Although effective, vacuum sampling and sweep netting would have destroyed many of the buckwheat plants in the study transects and impacted future sampling events. Aerial netting effectively captured wasps and hover flies, the two most abundant groups recorded. In future studies, I would recommend installing sticky traps in the sample transects to better monitor tachinid flies, as this group was collected the least in comparison to all other natural enemies studied. Studying natural enemies and wild bees in the same study sites provided complementary data for beneficial insects, but adapting collection methods to specifically target key groups would be advantageous in future studies.

The relatively small plot sizes (2 m by 40 m) may have been too small to have a significant influence on the natural enemy fauna of lowbush blueberry agroecosystems. In Michigan, U.S., (Blaauw and Isaacs 2015) were able to increase natural enemy abundance with wildflower patches ranging in size from 0.06-1.01 ha, while my study transects were only 0.008 ha in size. Should farmers wish to implement floral resources along blueberry field edges to benefit natural enemies, larger patches than what I tested may be required. My study was conducted in relatively small blueberry fields (typically ≤ 5 ha), so ample field margins were accessible to natural enemies, likely providing suitable habitat (Bianchi et al. 2006; Karem et al. 2006, 2010). Had the effects of planting buckwheat for natural enemies been tested in larger fields with intensive field edge management, including weed removal, the results may have differed. Although field size was not correlated to wasp abundance in Maine, U.S. (Karem et al. 2010), pollinator communities have been positively associated with small lowbush (Eaton and Nams 2012) and highbush (Isaacs and Kirk 2010) blueberry fields. On the other hand, a Nova Scotia study documented a rich ground beetle fauna throughout unenhanced lowbush blueberry fields that averaged from 10-15 ha (Cutler et al. 2012b), two to three times the average size of my study sites. The authors suggested that due to the low disturbance involved in lowbush blueberry compared to other agroecosystems, the establishment of this crop in its native range, and blueberry fields remaining fairly similar to the surrounding landscape, this agroecosystem may be better suited to natural enemy enhancement than other, more intensive, farming systems. This may explain the higher levels of ground beetles detected in control transects compared to buckwheat transects.

The control margins in this study contained floral resources, or ‘weeds’, after blueberry bloom, including wild rose (*Rosa acicularis*), goldenrod (*Solidago* spp.), vetch (*Vicia* spp.), clovers (*Trifolium* spp.), sweet clovers (*Melilotus* spp.), and St John’s Wort (*Hypericum perforatum*). It is possible that natural enemy abundance in control margins did not differ significantly from buckwheat margins due to these alternative floral resources that may also provide shelter (Karem et al. 2006, 2010; Martin et al. 2015). Although floral resources (nectar and pollen) are important for certain insects at particular life stages (e.g. adult hover flies), floral resources are also important for habitat (e.g. shelter, nesting). In a Maine, U.S. survey, wasp abundance was positively associated with a number of flowering weeds (Karem et al. 2010). By providing floral resources throughout the season, the habitat needs of natural enemies during critical times may be met.

Multiple natural enemy groups were examined in the buckwheat and control plots. In South Korea, Martin et al. (2013) noted complementary pest control services for aphids with multiple natural enemies in the agroecosystem, including ground-dwelling beetles and flying insects. Managing and enhancing the habitat for multiple natural enemy groups simultaneously is challenging, however, as these groups respond differently to landscape features (Caballero-López et al. 2012). In Michigan, U.S., different species of ground beetles responded differently to effects of flower type (perennial or annual), tillage, pesticide use, and cropping system (perennial or annual), revealing the diversity of responses based on life cycles and habitat needs (Clark et al. 1997). In the U.K., wasps were not significantly higher in enhanced field margins in comparison to control margins, due to adequate access to alternative nectar resources (Wood et al. 2015a). Similar to pollinators, landscape greatly impacts natural enemy success. Natural enemies benefit from increasingly complex landscapes that provide alternative food and habitat resources (Kromp 1999; Bianchi et al. 2006; Woltz et al. 2012), and these beneficial insects may subsequently contribute to pest control (Martin et al. 2015). It is possible that many lowbush blueberry agroecosystems are already so complex that their threshold of supporting natural enemies has been reached and no additional benefits of habitat management could be detected. Habitat management is often most effective in simplified landscapes with large fields (Tscharntke et al. 2005; Bianchi et al. 2006; Woltz et al. 2012). One meta-analysis revealed that natural pest control of aphids declined by 46% when the proportion of arable land increased from 2% to 100%, demonstrating the negative effects of landscape simplification (Rusch et al. 2016). It is possible that control margins better served the diverse group of natural enemies I examined, rather than the monoculture provision of buckwheat. Maintaining these undisturbed field margins could have substantial impacts on natural enemy communities and potentially reduce the reliance on insecticides. Despite trends for higher natural enemy abundance in buckwheat transects (except for ground beetles and ladybird beetles), no significant differences were clear between the two treatments.

4.6 SUMMARY OF CHAPTER 4 AND TRANSITION TO CHAPTER 5

Natural enemies are important biological pest control agents in lowbush blueberry agroecosystems, and there is interest in conserving these valuable insects. Floral resources were established in blueberry field margins to support various natural enemy groups after blueberry crop bloom. After three years, overall natural enemy abundance did not significantly increase. More hover flies and robber flies were detected in buckwheat transects than in control transects, although not significantly so. Ground beetle and ladybird beetle abundance generally trended higher in control sites than buckwheat sites, although not significantly so. Tachinid flies were more abundant in buckwheat sites in the first two years of study, but became more abundant in control sites in 2016. An opposing trend was observed for wasps, whereby wasps were more abundant in control sites in 2014, but became more abundant in buckwheat sites in 2015 and 2016. Buckwheat may benefit certain natural enemies, but the high variation among years requires further study. Additionally, optimizing floral enhancement size is needed. Due to the relatively undisturbed habitat of smaller lowbush blueberry fields, and the retention of alternative floral resources and habitat (weeds), certain blueberry agroecosystems appear to already support natural enemies in their current form. Management to preserve these important landscapes could preserve natural enemy communities and their pest control services.

To further explore floral resources that could benefit beneficial insects after blueberry bloom, various forage plants were established near lowbush blueberry agroecosystems. Bee visitation to these plants was evaluated (Chapter 5).

CHAPTER 5: DETERMINING THE INFLUENCE OF FORAGE CROP TYPE ON PLANT-POLLINATOR INTERACTIONS

5.1 ABSTRACT

Wild bees are effective pollinators of flowering plants, including agricultural crops. Despite their importance, wild bees face threats from habitat modification and insufficient floral resources outside of agricultural crop bloom. Providing floral resources after principal crop bloom could support these important beneficial insects. Habitat management studies have been conducted in a variety of agroecosystems with the aim of nourishing beneficial insects at critical times in the season, but little evaluation has been carried out on forage crops, particularly legumes, for bees. Legumes are potentially advantageous for habitat management for bees as they provide high quality pollen, their seed is relatively inexpensive, the plants are well suited to our Atlantic Canada region, and many legumes are perennial in nature, persisting for multiple years.

Forage crops were established to determine their attractiveness to pollinators. Parameters including bloom period, floral density, bee visitation, and plant-pollinator interactions were evaluated. Based on floral density, red clover, birdsfoot trefoil, and alsike clover provided the most inflorescences per site for bees, but when florets per inflorescence were considered, phacelia, red clover and alsike clover provided the greatest floret density. Red clover, birdsfoot trefoil, and sweet clover bloomed for the longest period, while sweet clover was visited most frequently by bees, followed by red clover, alsike clover and birdsfoot trefoil. Differences in plant-pollinator interactions were noted among sites, depending upon floral density, bloom period, and floral specialization. Based on these findings, red clover, sweet clover, alsike clover, and to a lesser degree,

birdsfoot trefoil, are attractive forages to bees. This study provides information on flowering duration and bee visitation to six forage crops, guiding future habitat management establishment in agroecosystems.

5.2 INTRODUCTION

Many agroecosystems depend upon insect pollinators for crop pollination, but the surrounding landscape may not provide ideal pollinator habitat. Although crop bloom may provide a concentrated food resource for a limited period of time, floral resources before and after crop bloom are needed to sustain the wild bee fauna (Hymenoptera: Apoidea). Habitat management, a component of conservation biology, involves implementing resources within agroecosystems to support and enhance beneficial insects (Landis et al. 2000). Examples of habitat management techniques include planting floral resources, and providing nesting substrates (Landis et al. 2000).

Floral resources have been planted along crop field edges in various agroecosystems to support bees after crop bloom, with variable success. When a diverse floral mixture was planted near highbush blueberries (*Vaccinium corymbosum*), wild bee and syrphid fly abundance increased over the four-year study period, with positive results on pollination (Blaauw and Isaacs 2014a). In strawberries (*Fragaria*), wildflower plantings along the field edge resulted in higher crop visitation by pollinators (Feltham et al. 2015). Declines in available forage, including red clover (*Trifolium pratense*), have been associated with bumble bee declines in Britain (Carvell et al. 2006), reiterating the important relationship between forage crops and bees. Not all habitat management studies have demonstrated clear success, however (Wood et al. 2015a). In the U.K., floral mixtures including attractive and nutritious forages enhanced wild bee abundance but not pollination in adjacent apple orchards (Campbell et al. 2017). Given the inconsistency of habitat management outcomes in agroecosystems, and the need to provide nutritious, accessible floral resources to pollinators, I examined forages as potential food sources for bees.

Forages, particularly perennials, could positively impact pollinators in a number of ways. Perennial plants do not require annual tillage, avoiding disturbance to soil-nesting bees beyond initial establishment. Since perennials do not need to be planted each year, producer adoption may increase for floral enhancement on-farm. Legumes flower for a lengthy duration (Delaplane and Mayer 2000), providing floral resources throughout the summer. Forages, including legumes, provide good nutrition for bees through high-protein pollen (Somerville 2001).

In this study, six forage crops were individually planted to determine which flowering plants attract particular bees (bumble bees, honey bees, and solitary bees). I studied the floral density, bloom period, bee visitation, and plant-pollinator interactions of the forage crop plots at five different sites in Nova Scotia, Canada. Sites were planted in 2015 and sampled in 2016. I hypothesized that floral density and bloom period would vary among the plant species based on agronomic characteristics. Pollinator visitation was expected to vary among the forage crops based on floral specialization, overlap of foraging period and bloom period, and physiological adaptions (e.g. tongue length) (Delaplane and Mayer 2000; Heinrich 2004; Michener 2007). Legumes (alsike clover, birdsfoot trefoil, crimson clover, red clover, and sweet clover) were expected to be most attractive to bumble bees, as they require large bees to trip the flower (release of staminal column that includes stamens and pistil) (Free 1993). Honey bees and solitary bees were expected to be most abundant on sweet clover and phacelia due to shorter corolla tubes and ease of accessibility (Free 1993). Red clover was anticipated to be more attractive to bees later in the summer as flower heads are smaller, becoming more accessible (Vickery 1991; Free 1993). Red clover and sweet clover were expected to bloom for the longest duration.

5.3 MATERIALS AND METHODS

Six forage crops were established to determine their attractiveness to pollinators. Most of the forages selected were legumes (Fabaceae) due to their nutritional quality and non-invasive nature (Pernal and Currie 2000, 2001; Somerville 2001) (Table 5.1). Phacelia (Boraginaceae) was also tested due to its previous use in bee foraging studies (Carreck and Williams 1997; Gradish et al. 2016; Sprague et al. 2016) and high pollen quality (Pernal and Currie 2000). Seeding rates for each forage crop are given in Table 5.1. In addition to the listed forage crops, all plots were seeded with 5 kg ha^{-1} Itasca timothy. Timothy, a bunchgrass, was included in each treatment to reduce soil erosion. All seed was purchased from Scotian Gold Co-op Ltd., Coldbrook, Nova Scotia.

Table 5.1 Species, growth habits, cultivars, and seeding rates of forage crops established for pollinator sampling in Nova Scotia, Canada, 2015.

Species	Growth habit	Cultivar	Seeding rate (kg ha^{-1})
Alsike clover *(Trifolium hybridum* L.)	Perennial	Canada No. 1 common seed	7.35
Birdsfoot trefoil (*Lotus corniculatus* L.)	Perennial	Bruce	14.75
Crimson clover (*Trifolium incarnatum* L.)	Annual/ winter annual	Canada No. 1 common seed	12.3
Phacelia *(Phacelia tanacetifolia* Benth*)*	Annual	Forage phacelia	18.5
Red clover (*Trifolium pratense* L.)	Perennial	Juliet	12.3
Sweet clover (*Melilotus officinalis* (L.) Pall.)	Biennial	Yellow Blossom	14.75

5.3.1 SITE ESTABLISHMENT

Each forage crop was established separately in 2 x 10 m plots in a randomized complete block design (RCBD) (Figure 5.1). Five blocks were seeded on 17-18 June and 05-06 August, 2015 in Cumberland and Guysborough counties in Nova Scotia: Archibald, Davison 1, Davison 2, Smith, and Wessie (Figure 5.1). Each block contained six plots, one plot for each forage crop studied (alsike clover, birdsfoot trefoil, crimson clover, phacelia, red clover, and sweet clover), resulting in a block 2 x 60 m (Figure 5.1, 5.2). A Tye no-till drill seeder (Dulath, Georgia, U.S.) was used to seed all plots. All plots were seeded into cultivated soil except for the Archibald site, which was seeded into mowed sod, and the Wessie site, which was seeded into a non-cultivated field border. Successfully established plots were fertilized with 1000 kg ha^{-1} Acti-sol 4-10-2 and 1.5 kg ha^{-1} Borax.

Site (block)	Plot					
Archibald Guysborough Co. 45°21'38.4"N 62°07'44.1"W	Red clover	Birdsfoot trefoil	Sweet clover	Crimson clover	Phacelia	Alsike clover
Davison 1 Cumberland Co. 45°30'25.3"N 64°20'00.6"W	Sweet clover	Birdsfoot trefoil	Crimson clover	Alsike clover	Phacelia	Red clover
Davison 2 Cumberland Co. 45°30'23.3"N 64°20'00.4"W	Alsike clover	Phacelia	Red clover	Sweet clover	Crimson clover	Birdsfoot trefoil
Smith Cumberland Co. 45°31'32.7"N 64°20'57.9"W	Crimson clover	Alsike clover	Phacelia	Red clover	Birdsfoot trefoil	Sweet clover
Wessie Guysborough Co. 45°21'47.6"N 62°08'26.2"W	Birdsfoot trefoil	Alsike clover	Phacelia	Sweet clover	Red clover	Crimson clover

Figure 5.1. Randomization chart for the forage crop blocks established at five sites in 2015 in Nova Scotia. Each block contained six forage crops and was monitored for floral density, bloom period, and bee visitation in 2016. Sites are indicated in bold.

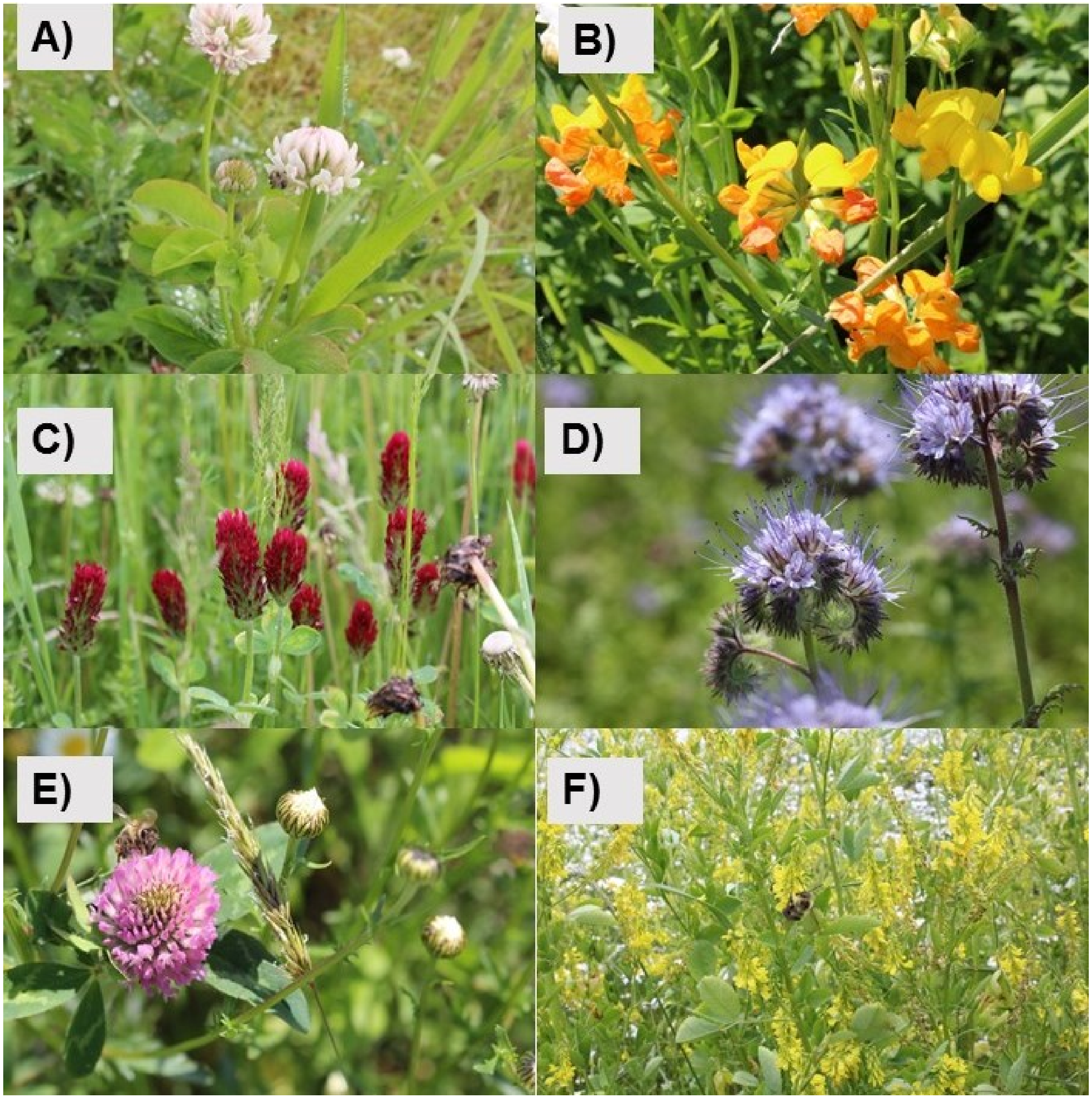

Figure 5.2. The six forage crops established in 2015 and sampled in 2016 in Nova Scotia, Canada: A) alsike clover, B) birdsfoot trefoil, C) crimson clover, D) phacelia, E) red clover, and F) sweet clover. Photos by N. McLean.

5.3.2 POLLINATOR AND FLORAL SAMPLING

Bee sampling and floral assessments were conducted every second week from 06 June to 28 September 2016. Sampling was conducted when weather conditions were considered suitable for pollinator activity: between 10 a.m. and 4 p.m., above 15° C, and during sunny conditions with low wind. Sampling at sites was alternated to ensure each site was sampled both in the morning and afternoon. Pollinator activity was recorded by slowly walking along each plot for 10 minutes and identifying to genus bees that landed on flowers of the forage species dedicated to each plot. Flower densities were based on a minimum of 3 samples per plot using a randomly thrown 0.25 m^2 quadrat. The number of florets per inflorescence was later determined to further compare the number of florets among forage crops. Both seeded and non-seeded species were recorded, but only flowers from the seeded species were included in the analyses.

5.3.3 IDENTIFICATION

Bees were identified to genus on flowers in the field, although honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.) were identified to species. Voucher specimens were collected using aerial netting to confirm identifications using Laverty and Harder (1988) and Packer et al. (2007). *B. borealis* and *B. fervidus* are similar and may have been confused on occasion.

5.3.4 STATISTICAL ANALYSIS

Due to the high variability among sites, the model assumptions of normal distribution and constant variance of the residuals could not be met for the original data or through transformation. A non-parametric Kruskal-Wallis test was used to detect differences in bee abundance among forage crops using Proc npar1way in SAS v. 9.4 (SAS Institute Inc. 2014).

To evaluate pollinator-plant interactions, a data matrix was constructed using each site as a replicate, and contained the total number of interactions observed between each pollinator-plant pair pooled across all observation periods during 2016. All network visualizations and calculations were performed using the bipartite package (Dormann et al. 2009) in R version 3.3.2 (R Development Core Team 2016). This analysis has been used in pollinator-plant interaction studies previously (e.g. Russo et al. 2013; Carman and Jenkins 2016). For each matrix (plant-pollinator interaction values), a quantitative interaction web was constructed, in which the thickness of the connecting line between two nodes (plants and pollinators) represents the frequency with which that interacting pair was observed. Additionally, several qualitative and quantitative network- and species-level parameters were calculated using the 'networklevel' and 'specieslevel' function, respectfully (Dormann et al. 2009). By using this package, interactions were weighted by their frequency, thereby reducing the sensitivity of quantitative parameters to network size and the intensity of sampling across sites. The network parameters of pollinator generality, pollinator vulnerability, connectance, specialization asymmetry (d_i'), level of specialization within the network (H_2'), and niche overlap within both the pollinator and plant communities were evaluated. Pollinator generality represents the weighted mean number of forage crops visited per pollinator group (species for *Apis* and

Bombus, genus for other bees), while pollinator vulnerability represents the weighted mean number of pollinator visitors per forage crop, with calculations for both parameters weighting values by the marginal or row totals. Connectance refers to the realized proportion of all possible interactions weighted by the visitation rate of each pollinator group. Specialization asymmetry (d_i') refers to the asymmetry of interaction strengths of a species pair in the absence of single interaction pairs, with networks with more forage crop specialization having negative values and networks with more pollinator specialization having positive values. This parameter is, however, sensitive to rare events, including the visitation of rare pollinators to rare plants (resulting in values of 1) or common plants (resulting in values of 0) (Dormann et al. 2009). Pollinator specialization (H_2') represents the degree of complementary specialisation for an entire network, describing the extent to which observed interactions deviate from the expected values based on marginal totals. Values closer to zero indicate no specialisation and values closer to 1 indicate full specialisation. The niche overlap of pollinators and plants both indicate the mean similarity in interaction pattern between species within its respective trophic level. The number of forage crops and pollinators within each network and the degree (total links for each plant and each pollinator) (Dormann et al. 2009) were calculated.

Solitary bees (*Andrena*, *Halictus*, and *Lasioglossum*) and bumble bees (all seven species recorded) were grouped into one category each for the Kruskal-Wallis analysis of treatment effect of forages on bee abundance (Venturini et al. 2017). Honey bees remained as their own category. All three categories were also grouped into a 'total' category to gauge overall effects of forage crops on bee fauna recorded. For the bipartite analysis, individual genera, in addition to bumble bees species and the honey bee, were analyzed.

5.4 RESULTS

5.4.1 FLORAL DENSITY AND BLOOM PERIOD

Floral density and bloom period varied among the forage crops, as expected (Figure 5.3). Sweet clover bloomed at high densities from 06 June to 20 July, peaking at approximately 100 flowers per m^2 (Figure 5.3). Sweet clover floral density was low for the remainder of the season, with slight bloom peaks in later July and late September. Red clover bloomed consistently from 06 June to 16 August, reaching approximately 60 flowers per m^2 (Figure 5.3). Red clover was still recorded at lower floral densities from 24 August to 28 September. Birdsfoot trefoil peaked for the first time on 27 June at nearly 40 flowers per m^2, peaked again on 14 July at approximately 20 flowers per m^2, bloomed at the highest density on 28 July at more than 105 flowers per m^2, and then decreased for the remainder of the season (Figure 5.3). Bloom was not recorded for birdsfoot trefoil after late August. Alsike clover flowering peaked at nearly 50 flowers per m^2 on 27 June and held steady until 14 July (Figure 5.3). It then peaked again on 28 July, followed by a declining floral density until the end of August. Crimson clover was only recorded flowering from 06 June to 04 July, at approximately 5 flowers per m^2 (Figure 5.3). Phacelia was recorded at low levels (<5 flowers per m) after 06 June until 27 June (Figure 5.3). Both crimson clover and phacelia are annuals and bloomed in the establishment year (2015). The average number of florets per inflorescence was calculated in a separate greenhouse experiment (N. McLean, unpublished data). Alsike clover had 73.1 florets per inflorescence, birdsfoot trefoil had 4, crimson clover had 46.7, phacelia had 151.3, red clover had 88.7, and sweet clover had 43.9.

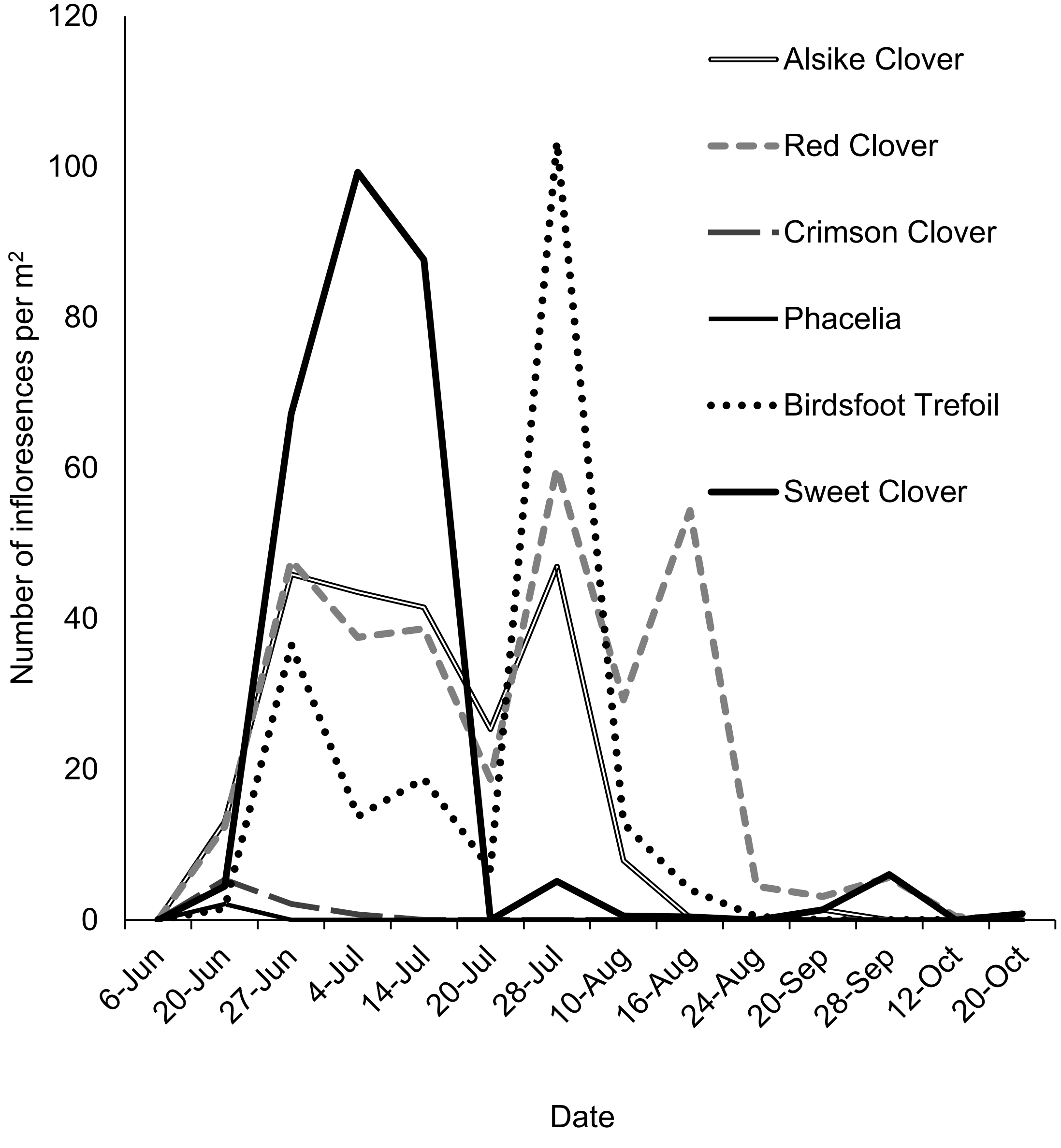

Figure 5.3. Average floral density (per m^2) and bloom period of six forage crops established in 2015 and sampled in 2016 across five sites in Nova Scotia, Canada.

5.4.2 BEE ABUNDANCE

A total of 440 bees were observed visiting forages across five plots in 2016. Sweet clover had the most bee visitors (186), followed by red clover (138) and alsike clover (90). Bee visitation to birdsfoot trefoil and phacelia was much lower, at 19 and 7 bees, respectively (Table 5.2). Bumble bees comprised the most abundant pollinator group, accounting for 65% (287/440) of total bees recorded (Table 5.2). *Bombus impatiens* was the bumble bee species recorded most frequently, followed by *Bombus vagans*, although *B. impatiens* was nearly twice as abundant as *B. vagans* during certain sampling events (Figure 5.4). Honey bees were more abundant than solitary bees, but their presence in forage plots likely depended on the proximity of honey bee yards. For example, honey bees may have been recorded frequently in forage plots in June due to their proximity for blueberry pollination, but once moved to summer yards elsewhere, were no longer recorded in our forage plots. Solitary bees generally peaked in early to mid-July.

Forage crop significantly impacted bumble bee and honey bee abundance, but not solitary bees (Figure 5.5). Bumble bee and honey bee visitation was highest on sweet clover, red clover, alsike clover, and birdsfoot trefoil. A similar trend was noted for solitary bees, although not significantly so, and phacelia was also attractive to solitary bees (Figure 5.5).

Table 5.2 Total number of bee visits (genus or species) to six different forage crops established across five sites in Nova Scotia, Canada, 2016.

Bee	Total Visits						Total
	Alsike clover	Birdsfoot trefoil	Crimson clover	Phacelia	Red clover	Sweet clover	
Andrena	2	1	0	0	1	2	6
Apis mellifera	42	2	0	1	22	57	124
Augochlorella	0	0	0	0	2	0	2
Bombus bimaculatus	0	0	0	0	9	0	9
Bombus borealis	1	0	0	2	15	2	20
Bombus citrinus	0	0	0	0	2	3	5
Bombus fervidus	0	0	0	0	2	0	2
Bombus impatiens	12	4	0	1	49	96	162
Bombus ternarius	23	11	0	2	11	17	64
Bombus vagans	2	0	0	0	22	1	25
Halictus	1	0	0	0	1	1	3
Lasioglossum	7	1	0	1	2	7	18
Total	90	19	0	7	138	186	440

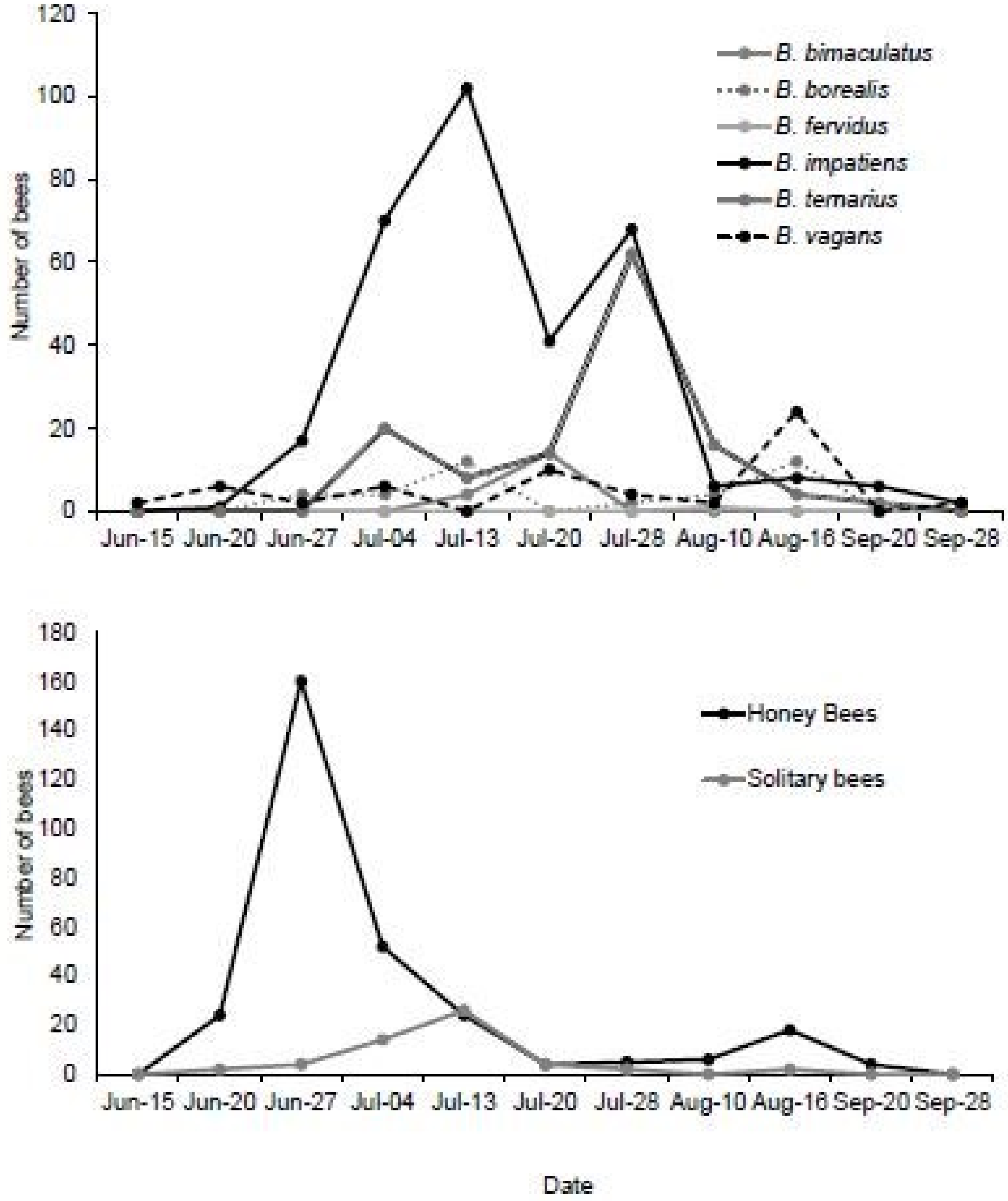

Figure 5.4. Abundance and flight periods of six bumble bee species, honey bees, and solitary bees across five forage sites in 2016 in Nova Scotia, Canada. Bees were monitored for ten minutes per forage crop per site per sampling event, for a combined total of sixty minutes per site for each sampling event. Scales vary among panels.

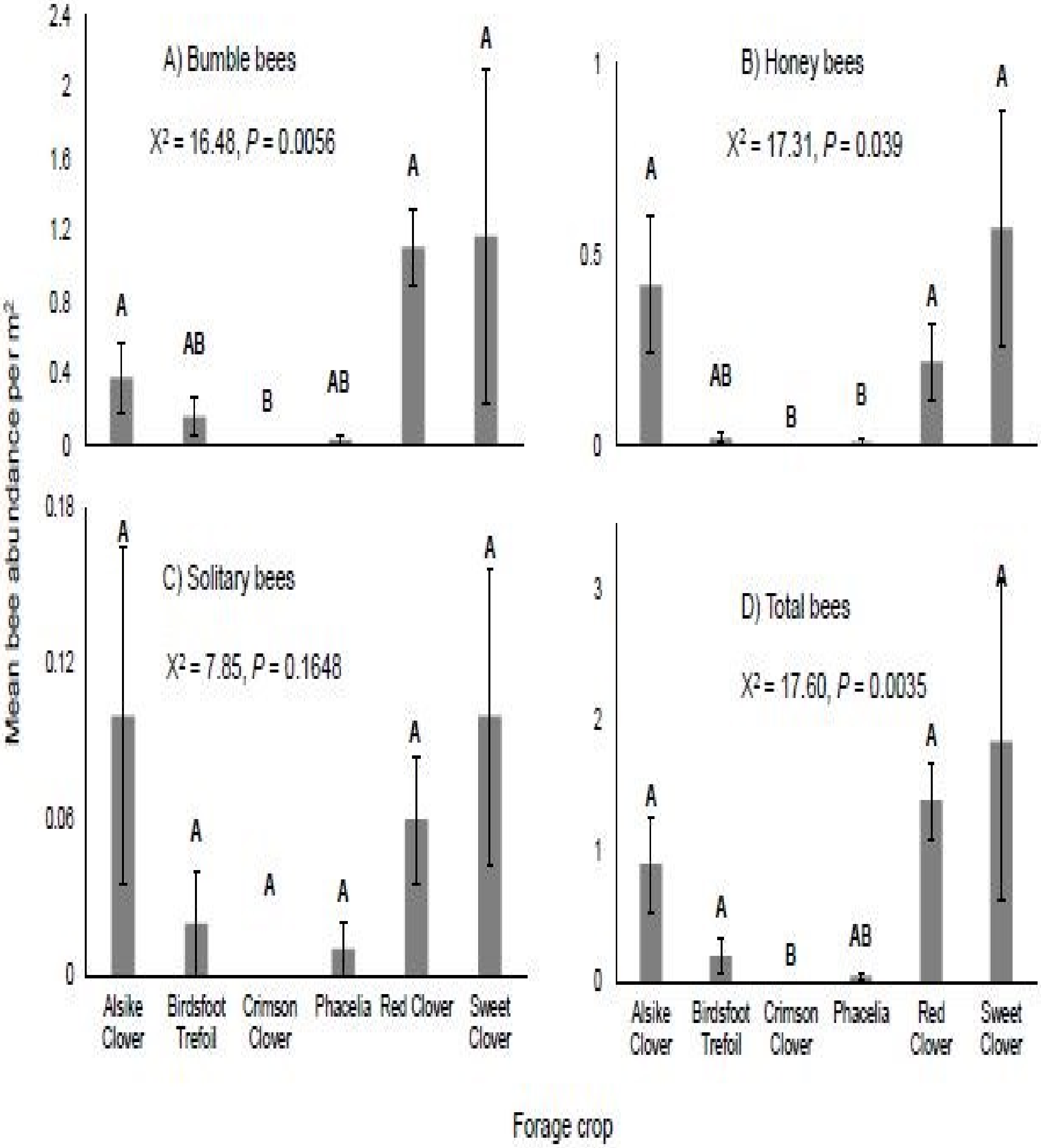

Figure 5.5. Mean bee abundance for A) bumble bees, B) honey bees, C) solitary bees, and D) total bees in the six forage crops evaluated at five sites in Nova Scotia, Canada in 2016. Means that do not share the same letter are significantly different (α = 0.05). Note: scales vary among panels.

5.4.3 PLANT-POLLINATOR INTERACTIONS

Augochlorella, *Bombus citrinus*, and *Bombus fervidus* were excluded from the plant-pollinator web due to low visitation rates. The most frequent interaction observed was *Bombus impatiens* visiting sweet clover, followed by *Apis mellifera* visiting sweet clover, and *B. impatiens* visiting red clover (Figure 5.6). *Bombus bimaculatus* was only recorded foraging on red clover, while *B. vagans* was observed on all three clovers (red, sweet, and alsike). *Bombus borealis* was recorded on red clover, phacelia, sweet clover, and alsike clover. *Bombus impatiens*, *B. ternarius* and *A. mellifera* visited red clover, phacelia, sweet clover, alsike clover, and birdsfoot trefoil. *Halictus* was documented on alsike, red, and sweet clovers. *Lasioglossum* was documented on red, sweet, and alsike clovers, as well as phacelia and birdsfoot trefoil, but the strongest interaction was with sweet and alsike clovers. *Andrena* was recorded on birdsfoot trefoil, alsike, sweet and red clovers, but the strongest interaction was with alsike clover. Sweet clover had the most bee visits, followed by red clover and alsike clover. Birdsfoot trefoil and phacelia had low floral densities and low visitation rates.

5.4.4 BIPARTITE ANALYSIS

A bipartite analysis was conducted to examine the plant-pollinator interactions at the five forage crop sites and the results are summarized in Table 5.3. Based on pollinator generality and vulnerability calculations, each unique pollinator group visited three different forage crops, while each forage crop was visited by five different pollinator groups, on average (Table 5.3). Connectance, the realized proportion of all possible plant-pollinator interactions, was recorded at 0.525, and the level of specialization was calculated to be 0.162 (Table 5.3). Specialization asymmetry was a negative value (-0.203) (Table 5.3). The niche overlap for forage crops was found to be 0.625, and slightly lower for pollinators, at 0.514 (Table 5.3). The total links, or total number of pollinator group visitors to each forage crop, were calculated, and ranged from 0 (crimson clover) to 14 (red clover) (Table 5.3). The total number of bees recorded visiting each forage crop was also recorded, and ranged from 0 bees (crimson clover) to 184 bees (sweet clover).

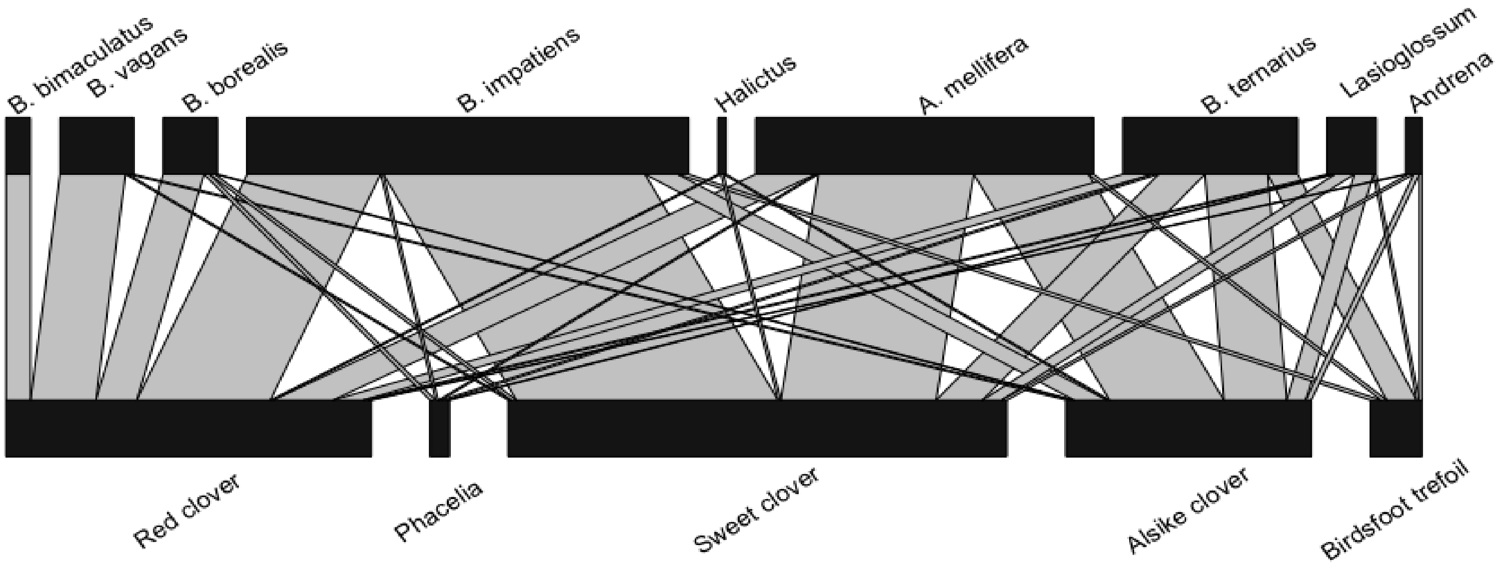

Figure 5.6. Pollinator-plant web displaying bee visitation to forage crops in 2016 across five sites in Nova Scotia, Canada. Forage crops are on the bottom while pollinator groups are on the top of the network illustration. The lines connecting forage crops to pollinators groups represent visitation events, and the thickness of each connecting line represents the frequency of interactions, with thicker lines indicative of more frequent interactions.

Table 5.3. Summary of bipartite analysis for plant-pollinator interactions at five forage crop sites established in Nova Scotia, Canada.

Parameter	Value	Forage Crop	Number total links/ plant	Number of bees recorded visiting
Pollinator generality	2.936	Alsike clover	8	90
Pollinator vulnerability	4.673	Birdsfoot trefoil	6	19
Connectance	0.525	Crimson clover	0	0
Specialization asymmetry (d_i')	-0.203	Phacelia	5	7
Level of specialization (H_2')	0.162	Red clover	14	138
Niche overlap (forage crop)	0.625	Sweet clover	9	184
Niche overlap (pollinator)	0.514	Total number of bees recorded		440

5.5 DISCUSSION

5.5.1 FLORAL DENSITY AND BLOOM PERIOD

Floral density was recorded throughout the season in 2016. Sweet clover, red clover, birdsfoot trefoil, and alsike clover bloomed at high densities throughout the season, and often peaked at different times, providing a constant supply of flowers to bees. Crimson clover was sparse at most sites, and only bloomed for a short period. This was not unexpected, however, as it is an annual or winter annual, and thus often blooms in the first year of seeding (2015). This explains the low frequency of pollinator foraging due to the lack of flowering. Similarly, the consistently low floral density was to be expected for phacelia as it is an annual and was seeded in 2015, thus flowering in 2015 and not during the sampling year of 2016. It would be worthwhile to evaluate phacelia as a food source for bees in Atlantic Canada as a U.K. study found phacelia to outperform other flowers in terms of establishment, floral density, and attractiveness to pollinators (Carreck and Williams 1997). I also considered the number of florets per inflorescence to further understand the floral resources provided per forage crop. I found that per inflorescence, phacelia, red clover, and alsike clover provide the most floral resources per plant, followed by crimson clover and sweet clover, while birdsfoot trefoil had the lowest recorded number of florets. Based on floral densities and bloom periods, sweet clover, red clover, birdsfoot trefoil, and alsike clover were attractive forages for floral enhancements, but when florets per inflorescence are considered, phacelia, red clover and alsike clover become most attractive, followed by sweet clover. The size of florets were not taken into consideration, although birdsfoot trefoil florets are larger than the other florets tested, and birdsfoot trefoil might therefore provide more nourishment than other inflorescences.

5.5.2 BEE ABUNDANCE

Bumble bees were the most abundant pollinator group recorded, followed by honey bees and solitary bees. Solitary bees were recorded throughout the sampling period (June to September), and were most abundant during early July. It is possible that fewer solitary bees were recorded than other bee groups due to the observation method used. Rather than capture bees using aerial nets or pan traps as in previous chapters, observational data was collected when a bee visited the flower of the forage crop being studied. In a Nova Scotia survey of lowbush blueberry agroecosystems, solitary bees were much more abundant than bumble bees, but pan trapping was used (Cutler et al. 2015b). There are limited studies exploring the proportion of bumble bees, honey bees, and solitary bees near blueberry agroecosystems. In Maine, U.S., only solitary bees were monitored during blueberry bloom, followed by only bumble bees post blueberry bloom (Bushmann and Drummond 2015), so comparisons cannot be made with my study.

It is also possible that by planting the forage crops, I disturbed soil-nesting bees. Since soil-nesters comprise the majority of all bees (Michener et al. 2007), this could have significantly impacted my results. Floral accessibility may explain the observed pollinator abundance; the long corolla tubes of the legumes planted may have prohibited the short-tongued solitary bees from visiting and garnering food resources (i.e. pollen and nectar) from these plants (Inouye 1980; Free 1993).

5.5.3 PLANT-POLLINATOR INTERACTIONS AND BIPARTITE ANALYSIS

Sweet clover, red clover, alsike clover, and birdsfoot trefoil were visited most frequently by bees, suggesting these flowers were most attractive to the pollinators recorded. Each pollinator group (genus) visited three different forage crops, and each forage crop was visited by five different pollinator groups, on average, revealing that the pollinators sampled across these five sites visited a diversity of flowers. Bees are known to prefer a diversity of pollen and nectar sources (Blaauw and Isaacs 2014b; Hendriksma et al. 2016). Connectance, or the realized proportion of all possible plant-pollinator interactions, varied greatly among sites depending on site establishment. For example, connectance was highest at the Archibald site, but this may be due to the low number of plants observed flowering and pollinators observed foraging, thus increasing the opportunity to realize the proportion of all possible interactions. Using this same reasoning, connectance at the Davison sites was low, potentially due to higher numbers of available flowers and pollinators. No strong trends were evident for niche overlap of plants and pollinators, perhaps due to the varying plant visits depending on bee species. The total number of links found in the bipartite analysis also supported the testing of treatment effects, i.e., sweet clover, red clover, and alsike clover resulted in the most pollinator visits. Considering floral density, bloom period, and plant-pollinator interaction, sweet clover, red clover, and alsike clover appear to be the best forage crops to implement in floral enhancement measures for bees.

Bees have a long-standing relationship with clover (e.g. Belt 1875), and have been documented as useful plants for floral enhancement (e.g. Hanley et al. 2008; Rundlof et al. 2014; Venturini et al. 2017). In apple orchards with added floral enhancements, alsike clover, red clover, and white clover were the three most frequently visited plant species (Campbell et al. 2017). Forages, particularly certain legumes, are considered inaccessible to short-tongued bees due to their long corolla tubes (Delaplane and Mayer 2000; Michener 2007), potentially explaining my low recording of *Andrena*, despite their known abundance in lowbush blueberry agroecosystems (Cutler et al. 2015b). A diversity of bees, including several short-tongued bees (other than *Andrena*) were, however, observed foraging on these legumes, suggesting floral accessibility was not an issue for all short-tongued bees. Red clover flower heads are usually shorter in the late summer compared to the first flowering (Delaplane and Mayer 2000), potentially explaining the high visitation to this crop by a number of pollinators. In Sweden, late season flowering red clover contained tenfold more *Bombus* workers than nearby field borders (that also contained flowers) (Rundlof et al. 2014). By providing late season forage, red clover could potentially positively impact bumble bee colonies as development switches to reproduction of new queens (Rundlof et al. 2014).

If these floral enhancement sites are left in perennial food sources, bees that nest in the soil may begin selecting these sites for nest establishment, further encouraging native bee abundance (Sarver 2007; Blaauw and Isaacs 2014b). Since roughly 70% of native bees select soil sites for nesting (Sarver 2007; Black et al. 2011) the potential benefit is considerable. Although perennial floral resources will persist beyond the first year, including annual floral resources is advantageous to provide flowers the first year, until perennials become established. The forages implemented in this study were well-suited to agroecosystems as they are non-invasive, are naturalized to the region, and will not spread to become weeds in nearby agricultural fields. Furthermore, legumes are able to fix nitrogen and may contribute to improved soil fertility, soil erosion prevention, and shelter for additional beneficial insects. Determining the pollen collection by bees from these nutritious forage crops would provide valuable insight into whether pollen is actually collected, or if nectar is more readily accessed (e.g. Sprague et al. 2016).

5.6 SUMMARY OF CHAPTER 5 AND TRANSITION TO CONCLUSION

Multiple forage crops were evaluated for their value in habitat management for bees. Based on floral density, red clover, alsike clover, and sweet clover provided the most flowers per site for bees. Red clover, birdsfoot trefoil, and sweet clover bloomed for the longest period. Sweet clover was visited most frequently, but not significantly more than red clover, alsike clover, and birdsfoot trefoil. Considering all of these factors together, I would recommend red clover, sweet clover, and alsike clover as the best forage crops for floral enhancement for bees, although birdsfoot trefoil is still an attractive floral resource that may provide bloom between clover flowering. This study provides information on flowering duration and bee visitation for six forage crops, guiding future habitat management in agroecosystems. Future research should examine the natural enemies present in forage plantings to better understand the additional benefits forage plantings may provide to agroecosystems. Due to the relatively low number of observations in this preliminary study, this research should be repeated at more sites as well as continued for multiple years to evaluate pollinator activity on the perennial forages. Given the known nutritional value of crimson clover and phacelia, measuring pollinator activity during the establishment year for these forages would also be valuable.

5.7 SUPPLEMENTARY INFORMATION

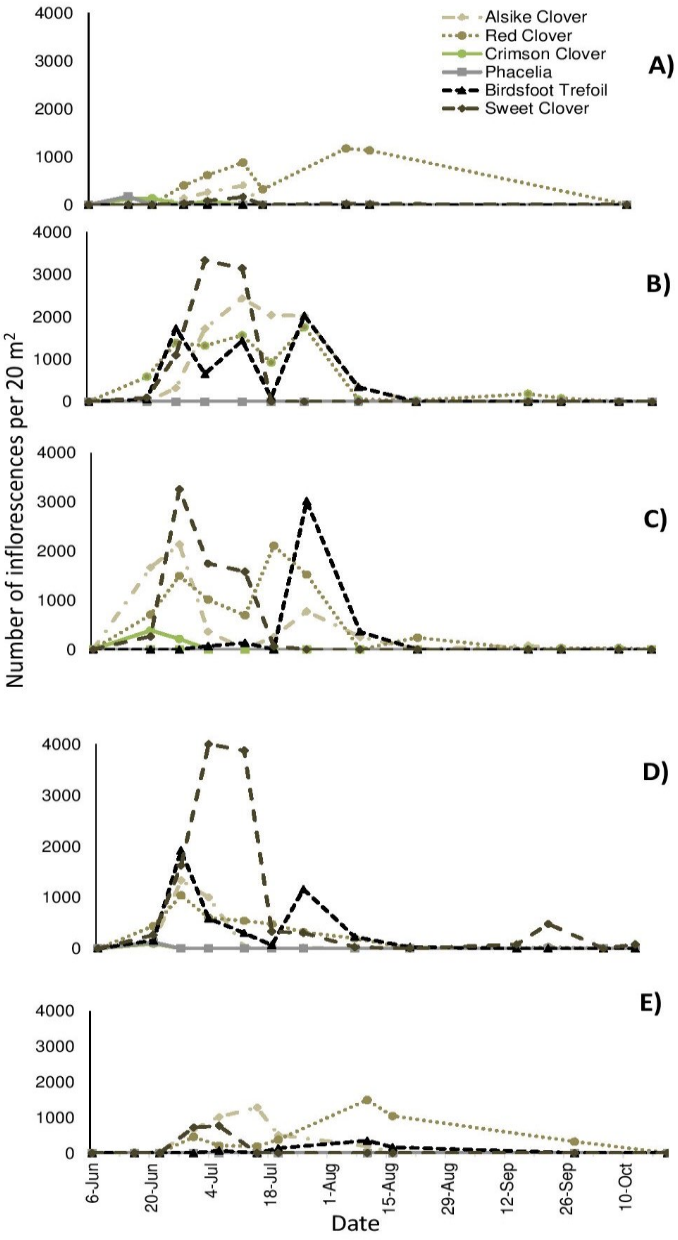

Figure S1. Floral density and bloom period of forage crops established in 2015 and sampled in 2016 at five sites in Nova Scotia, Canada: A) Archibald, B) Davison 1, C) Davison 2, D) Smith, and E) Wessie.

CHAPTER 6: CONCLUSION

6.1 INTRODUCTION

Agroecosystems are frequently touted as barren wastelands inhospitable to wild bees and natural enemies. While it is true that monoculture plantings, large fields, and intensive chemical management of insects, diseases, and weeds can negatively impact the opportunities for bees and natural enemies to survive and thrive in agroecosystems, there is much variability among farming systems, and numerous agricultural landscapes can facilitate healthy beneficial insect communities.

Wild bees and natural enemies provide important pollination and pest control services in agroecosystems, yet population declines have been documented in various cropping systems around the world. With concerns regarding producing enough food to feed a growing global population, habitat management research in agroecosystems to enhance beneficial insects has increased in the past decade, with variable results. Limited techniques were available for lowbush blueberry, so I endeavoured to examine the efficacy of habitat management techniques related to nesting and floral resource provision for both wild pollinators and natural enemies. I conducted tests in lowbush blueberry, a pollinator-dependent crop that is challenged by a number of insect pests. Nesting habitat was provided for solitary bees while various floral resources were provided for bees and natural enemies. The study was conducted over three years in commercial lowbush blueberry fields in Nova Scotia, Canada.

6.2 SUMMARY

In Chapter 2, I examined the impact of different nesting block designs for solitary Megachilidae bees, as well as the impact of field type and distance from field edge. Milk carton nests had significantly higher uptake by and emergence of *Osmia* and *Megachile* than wooden nests. Only 3% of the wooden nests had at least one occupied nesting tube versus 73% of milk carton nests, with a total of 176 out of 512 nesting tubes (34%) occupied. Bee emergence was significantly higher in nesting tubes from fruit-bearing fields than vegetative fields. Overall emergence of *Osmia* and *Megachile* was low from milk carton nests, with bees emerging from less than 10% of occupied nesting tubes, in large part due to parasitism from wasps and flies. Overturned clay lids were also tested as potential nesting sites for *Osmia inermis* Zetterstedt, but only 3% (4/120) of deployed lids had evidence of nesting. Due to the variable nesting occupancy, low emergence, and the challenges of parasitism, enhancing cavity-nesting wild bee communities through artificial nests is difficult, and more work is required to improve these techniques.

In Chapter 3, I tested the impact of planting buckwheat along lowbush blueberry field edges on wild bee abundance and diversity, in comparison to control (unplanted) edges. I expected bee abundance and diversity to increase over the three-year study in buckwheat transects, but these results were not clearly demonstrated. Instead, I found that bee abundance and diversity were higher in fields with buckwheat plantings than in control sites only in mid-August, but high variability occurred across years and collection periods. After three years of augmenting floral resources around blueberry fields, no significant differences in bee abundance or diversity were detected between buckwheat and control sites. My results suggest buckwheat may not be ideal for enhancing wild bee abundance and diversity along blueberry field edges, but it is unclear if this is due to buckwheat’s ineffectiveness as a floral resource, or the already supportive habitat found along certain lowbush blueberry field edges. Although it was discouraging to find that buckwheat did not clearly aid beneficial insect communities, it was interesting to determine that lowbush blueberry agroecosystems naturally support rich bee and natural enemy communities, countering the general thinking that agroecosystems are unsuitable and detrimental to beneficial insects. Caution should be exercised moving forward, however, as the need for habitat management should be decided on a per-field basis.

In Chapter 3 I also evaluated whether the same bee taxa visiting blueberry flowers during crop bloom were also visiting adjacent buckwheat strips outside of blueberry bloom. All of the bee taxa recorded during blueberry bloom were recorded in buckwheat transects. I also determined whether bee abundance and diversity changed throughout blueberry bloom, and evaluated the impact of collection method (aerial netting or pan trapping) on bee collection. Diversity was greater during late blueberry bloom than early or mid-bloom, but abundance did not significantly change throughout the bloom period. As expected, *Andrena*, *Bombus*, and *Lasioglossum* bees were most abundant during bloom, but each genus peaked at different times. Aerial netting and pan trapping tended to collect different and complementary bee genera. Complementary sampling techniques are recommended for future research on bee communities.

In Chapter 4, I tested the impact of buckwheat plantings near lowbush blueberry fields on the abundance of six natural enemies: ground beetles, hover flies, ladybird beetles, robber flies, tachinid flies, and wasps. Natural enemy abundance was compared between buckwheat margins and typical, unenhanced field margins (‘control’). There was much variability among the three years studied (2014-16), but hover flies, robber flies, tachinid flies, and wasps trended higher in buckwheat sites than control sites, although not significantly so. My findings suggest that certain blueberry field margins already support a diverse and abundant natural enemy fauna, and added floral enhancements may not be necessary for natural enemy enhancement. As in Chapter 3, decisions about the need for habitat management should be made on a per-field basis.

One disadvantage of using buckwheat was the poor establishment noted in lowbush blueberry field margins, potentially due to low precipitation in two study years, as well as poor soil conditions typical of lowbush blueberry landscapes. Buckwheat also provided poor nutritional quality for beneficial insects, with insufficient protein content in the pollen (Somerville 2001). The advantages of using buckwheat included relatively accessible and inexpensive seed, the annual growth pattern (allowing farmers the option to not commit to perennial species), the prevention of buckwheat spreading to become a weed in nearby blueberry fields, its quick flowering and lengthy flowering period, and accessibility to a variety of insects.

In Chapter 5, six forage crops were established and evaluated for their attractiveness to bees. Sweet clover attracted the most bees, but not significantly more than red clover, alsike clover, birdsfoot trefoil, or phacelia. Red clover, alsike clover, and sweet clover provided the most flowers per plot, while red clover, birdsfoot trefoil, and sweet clover bloomed for the longest duration. Based on these results, I would recommend sweet clover, red clover, and alsike clover for future bee management, followed to a lesser degree by birdsfoot trefoil. Additional management practices, including strategically mowing perennials and staggering plantings to ensure a season-long flowering, could allow the forage mixture to provide a succession of flowers throughout the season, post blueberry bloom. The advantages of using forages for bees included adequate nutrition, reliable establishment, a lengthy flowering period, a diversity of floral resources, and secondary benefits to the soil. Forage seed was accessible and though slightly more expensive than buckwheat seed, was still reasonable for habitat management on farms. As perennials persist for many years, they are likely more economical over the long term than annuals.

6.3 DISCUSSION

Based on my findings, I believe the unique agroecosystem of lowbush blueberry contributed to the variable results within the habitat management experiments. Lowbush blueberry in Nova Scotia is often grown in relatively small fields with abundant alternative flowering and nesting resources post crop bloom. This unique cropping system appears to contribute to the rich wild bee and natural enemy fauna found in this agroecosystem, and is key moving forward to conserving and enhancing these beneficial insects.

Throughout the experiments, I was mindful that nesting blocks and floral plantings must be adaptable on-farm to encourage producer adoption. Furthermore, no blueberry land was taken out of production to perform these experiments, demonstrating that habitat management can occur on marginal and unused land. Flowering resources for pollinators must have good agronomic (e.g. ease of establishment) and biological (e.g. nutritional value) properties to be of value for bees in agroecosystems (Carreck and Williams 2002), as well as being affordable. Buckwheat had notable agronomic and biological downfalls in my study, although others have had success with buckwheat establishment and flowering (Stephens et al. 1998; Carreck and Williams 2002; Gradish et al. 2016). While buckwheat is attractive to bees, alternative flowering resources that are more nutritious, easier to establish, and tolerate a variety of climatic conditions may be better suited to habitat management in lowbush blueberry.

In future experiments, I would place increased emphasis on timing. Ideally, any added floral resources would have begun blooming immediately after blueberry bloom had finished. Due to consideration for the busy time of blueberry bloom for farmers, I planted buckwheat immediately after blueberry bloom, but potentially missed an important floral dearth for bees and natural enemies. The forages tested are potentially more attractive to producers, as once established, many of these plants will persist for years, reducing the need to re-plant floral resources each year. The forages also began blooming toward the end of blueberry bloom, providing a continuous food source for bees in the vicinity.

6.4 CHALLENGES OF HABITAT MANAGEMENT IN LOWBUSH BLUEBERRY

One challenge within lowbush blueberry agroecosystems is that the crop is generally managed on a two-year cycle of vegetative (sprout) and fruit-bearing (crop) years. As such, blueberry fields only bloom every second year. The surrounding agroecosystem must provide alternative floral resources in order to retain and support pollinator communities, especially in this ‘feast or famine’ situation. If field margins are enhanced for pollinator habitat, care must also be taken to avoid pesticide drift and ensure these areas indeed provide refuge to pollinators.

Another concern is the potential to concentrate pollinators in an enhanced field margin, rather than into the adjacent crop field to provide pollination services (Woltz et al. 2012; Peters et al. 2013). When the flowering resource *Hamelia patens* Jacquin was planted near coffee agroecosystems, visits to coffee flowers increased by honey bees, but decreased by native bees, suggesting the *Hamelia patens* drew native bees away from the principle crop to be pollinated (Peters et al. 2013). In California, U.S., however, flowering hedgerows created in agricultural landscapes resulted in movement of bees into adjacent crop fields (Morandin and Kremen 2013), and habitat management in highbush blueberry field margins also resulted in natural enemy exportation to crop fields (Walton and Isaacs 2011). Similarly, wildflower plantings near strawberry fields resulted in increased pollinator visits to the crop compared to fields with no wildflower plantings (Feltham et al. 2015). I addressed this concern by targeting the enhanced field margins (buckwheat) to flower after blueberry had finished blooming, thereby not competing with the crop bloom and providing important food and habitat resources after this period.

6.5 CONCLUSION

My study provides records for the abundant and diverse bee community found in lowbush blueberry agroecosystems, and identifies key challenges and opportunities of habitat management within this cropping system. It is possible that artificial nests such as milk cartons could support certain cavity-nesting solitary bees, but drawbacks such as low emergence after overwintering and parasitism suggest this method requires further troubleshooting. The extremely low nesting occupancy of *Osmia inermis* in overturned clay lids was discouraging, but echoes warnings within the bee research community of the difficulty in providing artificial nesting substrates to certain solitary bees (e.g. Cane et al. 2007). Despite previously recorded success of *Osmia* nesting in wooden nests, low levels of nesting occupancy were documented in my study.

Planting buckwheat along blueberry fields benefited certain natural enemies and wild bees during certain times in the summer, but the benefits were not consistently demonstrated in comparison to unenhanced, control edges. The testing of forage crops revealed information about floral density, bloom period, and plant-pollinator interactions, shedding light on perhaps more effective flowers for habitat management. The wild bee fauna during blueberry bloom was also documented, and a difference in bee collection was demonstrated between two different collection methods: pan trapping and aerial netting. By incorporating both sampling methods, complementary captures could be made. Overall, my study documents the unique pollinator and natural enemy communities found within blueberry agroecosystems, and the need to direct efforts toward their enhancement. However, given the unique landscape of wild blueberry agroecosystems, habitat management decisions should be made on a per-field basis, based on presence of alternative floral resources before and after crop bloom, and the availability of diverse nesting habitats (e.g. sandy soil, old tree branches). My work serves as a starting point for designing and implementing habitat management techniques in lowbush blueberry agroecosystems.

6.6 IMPACT TO SCIENCE AND INDUSTRY

I believe my study provides new and practical information on which plants can benefit certain pollinator and natural enemy groups and which trap nest designs work best for cavity-nesting bees. This allows for applicable research techniques to be implemented on-farm. Additionally, my data indicate that small (< 5 ha) lowbush blueberry fields have the potential to support a rich beneficial insect fauna, which supports the ‘wild’ marketing campaign for lowbush blueberries (i.e. a ‘wild’ crop produced by ‘wild’ insects).

6.7 FUTURE DIRECTION

Nesting occupancy of Megachilidae bees was promising in certain nesting block designs in Chapter 2, but further investigation is required to minimize parasitism and improving emergence after overwintering. Additionally, optimizing nesting block design to be more attractive to cavity-nesting bees would be advantageous.

Based on results from Chapters 3 and 4, the implementation of buckwheat only appeared to benefit wild bees and certain natural enemies during certain periods in the summer. In general, unenhanced lowbush blueberry field edges (control transects) supported the same wild bee abundance and diversity as edges enhanced with buckwheat. My study was conducted in relatively small fields (mean < 5 ha), with abundant field edges and proximate nesting and floral resources for wild bees and natural enemies. This may indicate that typical lowbush blueberry fields already support rich wild bee and natural enemy communities. I do not have data to conclude whether this is also the case for larger, more intensively managed lowbush blueberry fields. Determining in which field types habitat management is beneficial is important moving forward.

Previous habitat management studies have examined the effect of floral plantings, including buckwheat, on concentrating insect pests from the adjacent crop fields, minimizing the need for pesticides. I did not monitor insect pest occurrence or abundance in the buckwheat transects, but these data would be valuable in order to evaluate the economic benefits of habitat management. Climate conditions, including snowfall and summer precipitation, helped explain some of the abundance noted in wild bees among the three study years, but did not clearly explain all trends, nor could natural enemy abundance trends be clearly linked to climate. As our climate continues to change, determining the impact of such factors on beneficial insects may be important. Given the abundance and diversity of wild bees and natural enemies in control edges, management to preserve attractive, non-invasive flowering plants ("weeds") and to leave soil undisturbed for nesting and shelter may support wild bee communities and natural enemies. Further research is needed to determine the threshold of weeds helpful to beneficial insects without compromising crop production. The plant-pollinator interaction data from Chapter 5 provide information on which flowers are most beneficial to various pollinator groups. Red clover, sweet clover, alsike clover, and birdsfoot trefoil established well, flowered for a lengthy period, and were all highly visited by pollinators. These flowers are therefore recommended for future floral enhancement for bees. As data were mainly collected in the second year for the forages trial, interactions between annual species (e.g. phacelia) and bees were not adequately captured, and require further study. There are also alternative flowering plants that could potentially benefit bees that were not tested in this study.

My research adds to the growing literature of habitat management for beneficial insects in agroecosystems. As the global human population continues to rise, practical techniques to conserve beneficial insects while also producing food effectively are important. I was able to demonstrate that lowbush blueberry agroecosystems host a diverse and abundant beneficial insect fauna, and that certain habitat management techniques may be beneficial at certain times, but techniques should be considered on an individual field basis.

REFERENCES

Agriculture and Agri-Food Canada. 2015. Canadian blueberries: A true taste of nature. [Online] Available: http://www.agr.gc.ca/eng/industry-markets-and-trade/exporting-and-buying-from-canada/buying-canadian-food-products/canadian-blueberries/?id=1426167712421 [2016 Aug. 30].

Aizen, M. A. and Harder, L. D. 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr. Biol. **19**: 915-918.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Feinsinger, P., Jones, C. E. and Kevan, P. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conserv. Biol. **12**: 8-17.

Aras, P., De Oliveira, D. and Savoie, L. 1996. Effect of a honey bee (Hymenoptera: Apidae) gradient on the pollination and yield of lowbush blueberry. J. Econ. Entomol. **89**: 1080-1083.

Barker, W. G., Hall, I. V., Aalders, L. E. and Wood, G. W. 1964. The lowbush blueberry industry in Eastern Canada. Econ. Bot. **18**: 357-365.

Bell, A., Zhang, W. and Nou, K. 2016. Pesticide use and cooperative management of natural enemy habitat in a framed field experiment. Agric. Syst. **143**: 1-13.

Belt, T., 1875. Bees and clover. Nature **13**: 26.

Bianchi, F. J. J. A., Booij, C. J. H. and Tscharntke, T. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B **273**: 1715-1727.

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., Settele, J. and Kunin, W. E. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science **313**: 351-354.

Blaauw, B. R. and Isaacs, R. 2012. Larger wildflower plantings increase natural enemy density, diversity, and biological control of sentinel prey, without increasing herbivore density. Ecol. Entomol. **37**: 386-394.

Blaauw, B. R. and Isaacs, R. 2014a. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. J. Appl. Ecol. **51**: 890-898.

Blaauw, B. R. and Isaacs, R. 2014b. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. Basic Appl. Ecol. **15**: 701-711.

Blaauw, B. R. and Isaacs, R. 2015. Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. Biol. Control **91**: 94-103.

Black, S. H., Sheperd, M. and Vaughan, M. 2011. Rangeland management for pollinators. Soc. Range Management **33**: 9-13.

Blitzer, E. J., Gibbs, J., Park, M. G. and Danforth, B. N. 2016. Pollination services for apple are dependent on diverse wild bee communities. Agric. Ecosyst. Environ. **221**: 1-7.

Bohart, R. M. and Kimsey, L. S. 1980. A generic synopsis of the Chrysididae of America north of Mexico (Hymenoptera). J. Kansas Entomol. Soc. **53**: 137-148.

Bommarco, R., Kleijn, D. and Potts, S. G. 2013. Ecological intensification: Harnessing ecosystem services for food security. Trends Ecol. Evol. **28**: 230-238.

Bosch, J. and Kemp, W. P. 2000. Development and emergence of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). Environ. Entomol. **29**: 8-13.

Bosch, J. and Kemp, W. P. 2002. Developing and establishing bee species as crop pollinators: the example of *Osmia* spp. (Hymenoptera: Megachilidae) and fruit trees. Bull. Entomol. Res. **92**: 3-16.

Boulanger, L. W., Wood, G. W., Osgood, E. A. and Dirks, C. O. 1967. Native bees associated with the lowbush blueberry in Maine and eastern Canada. [Online] Available: http://digitalcommons.library.umaine.edu/aes_techbulletin. [2017 Jan. 31].

Brittain, C., Kremen, C. and Klein, A. M. 2013. Biodiversity buffers pollination from changes in environmental conditions. Glob. Chang. Biol. **19**: 540-547.

Brittain, C. and Potts, S. G. 2011. The potential impacts of insecticides on the life-history traits of bees and the consequences for pollination. Basic Appl. Ecol. **12**: 321-331.

Bromley, S. W. 1930. Bee-killing robber flies. J. New York Entomol. Soc. **38**: 159-176.

Brown, M. J. F. and Paxton, R. J. 2009. The conservation of bees: a global perspective. Apidologie **40**: 410-416.

Bushmann, S. L. and Drummond, F. A. 2015. Abundance and diversity of wild bees (Hymenoptera: Apoidea) found in lowbush blueberry growing regions of Downeast Maine. Environ. Entomol. **44**: 975-989.

Caballero-López, B., Bommarco, R., Blanco-Moreno, J. M., Sans, F. X., Pujade-Villar, J., Rundlöf, M. and Smith, H. G. 2012. Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. Biol. Control **63**: 222-229.

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., Griswold, T. L. and Robinson, G. E. 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. U.S. A. **108**: 662-667.

Campbell, A. J., Wilby, A., Sutton, P. and Wackers, F. L. 2011. Do sown flower strips boost wild pollinator abudance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. Agr. Ecosyst. Environ. **239**: 20-29.

Cane, J. H., Griswold, T. and Parker, F. D. 2007. Substrates and materials used for nesting by North American *Osmia* bees (Hymenoptera: Apiformes: Megachilidae).

Ann. Entomol. Soc. Am. **100**: 350-358.

Cane, J. H., Minckley, R. L. and Kervin, L. J. 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. J. Kansas Entomol. Soc. **73**: 225-231.

Cane, J. H. and Tepedino, V. J. 2001. Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences. Ecol. Soc. **5**: 1.

Carman, K. and Jenkins, D. G. 2016. Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats. Biol. Conserv. **202**: 110-118.

Carreck, N. L. and Williams, I. H. 1997. Observations on two commercial flower mixtures as food sources for beneficial insects in the UK. J. Agric. Sci. **128**: 397-403.

Carreck, N. L. and Williams, I. H. 2002. Food for insect pollinators on farmland: Insect visits to flowers of annual seed mixtures. J. Insect Conserv. **6**: 13-23.

Carvalheiro, L. G., Seymour, C. L., Nicolson, S. W. and Veldtman, R. 2012. Creating patches of native flowers facilitates crop pollination in large agricultural fields: mango as a case study. J. Appl. Ecol. **49**: 1373-1383.

Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D. and Goulson, D. 2006. Declines in forage availability for bumblebees at a national scale. Biol. Conserv. **132**: 481-489.

Chaplin-Kramer, R., O'Rourke, M. E., Blitzer, E. J. and Kremen, C. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. **14**: 922-932.

Clark, M. S., Gage, S. H. and Spence, A. R. 1997. Habitats and management associated with common ground beetles (Coleoptera: Carabidae) in a Michigan agricultural landscape. Environ. Entomol. **26**: 519-527.

Colla, S. R., Ascher, J. S., Arduser, M., Cane, J. H., Deyrup, M., Droege, S., Gibbs, J., Griswold, T. L., Hall, H. G., Henne, C., Neff, J., Jean, R. P., Rightmyer, M. G., Sheffield, C., Veit, M. and Wolf, A. 2012a. Documenting persistence of most eastern North American bee species (Hymenoptera: Apoidae: Anthophila) to 1990-2009. J. Kansas Entomol. Soc. **85**: 14-22.

Colla, S. R. and Dumesh, A. S. 2010. The bumble bees of southern Ontario: notes on natural history and distribution. JESO **141**: 39-68.

Colla, S. R., Gadallah, F., Richardson, L., Wagner, D. and Gall, L. 2012b. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. Biodivers. Conserv. **21**: 3585-3595.

Colla, S. R., Otterstatter, M. C., Gegear, R. J. and Thomson, J. D. 2006. Plight of the bumble bee: Pathogen spillover from commercial to wild populations. Biol. Conserv. **129**: 461-467.

Colla, S. R. and Packer, L. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. Biodivers. Conserv. **17**: 1379-1391.

Cutler, G. C., Astatkie, T. and Chahil, G. S. 2016. Weed seed granivory by carabid beetles and crickets for biological control of weeds in commercial lowbush blueberry fields. Agric. For. Entomol. **18**: 390-397.

Cutler, G. C., Gariepy, T. D., De Silva, E. C. A. and Hillier, N. K. 2015a. High rates of parasitism of blueberry spanworm (Lepidoptera: Geometridae) by Ichneumonidae and Tachinidae in commercial lowbush blueberry fields. J. Pest Sci. **88**: 219-223.

Cutler, G. C., Nams, V. O., Craig, P., Sproule, J. M. and Sheffield, C. S. 2015b. Wild bee pollinator communities of lowbush blueberry fields: Spatial and temporal trends. Basic Appl. Ecol. **16**: 73-85.

Cutler, G. C., Reeh, K. W., Sproule, J. M. and Ramanaidu, K. 2012a. Berry unexpected: Nocturnal pollination of lowbush blueberry. Can. J. Plant Sci. **92**: 707-711.

Cutler, G. C., Renkema, J. M., Majka, C. G. and Sproule, J. M. 2012b. Carabidae (Coleoptera) in Nova Scotia, Canada wild blueberry fields: prospects for biological control. Can. Entomol. **144**: 808-820.

Delaplane, K. S. and Mayer, D. R. 2000. Crop pollination by bees. CABI Publishing, New York.

Desneux, N., Decourtye, A. and Delpuech, J.-M. 2007. The sublethel effects of pecticides on beneficial arthropods. Annu. Rev. Entomol. **52**: 81-106.

Dormann, C. F., Frund, J., Bluthgen, N. and Gruber, B. 2009. Indices, graphs and null models: Analyzing bipartite ecological networks. Open Ecol. J. **2**: 7-24.

Drummond, F. 2012. Commercial bumble bee pollination of lowbush blueberry. Int. J. Fruit Sci. **12**: 1-3.

Drummond, F. A. and Stubbs, C. S. 1997. Potential for management of the blueberry bee, *Osmia atriventris* Cresson. Acta Hortic. **446**: 77-85.

Eaton, L. J. and Murray, J. E. 1997. Relationships of pollinator numbers in blueberry fields to fruit development and yields. Acta Hortic. **446**: 181-188.

Eaton, L. J., and Nams, V. O. 2012. Honey bee stocking numbers and wild blueberry production in Nova Scotia. Can. J. Plant Sci. **92**: 1305-1310.

Eeraerts, M., Meeus, I., Van Den Berge, S. and Smagghe, G. 2017. Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. Agric. Ecosyst. Environ. **239**: 342-348.

European Commission. 2016. Agri-environment measures. [Online] Available: http://ec.europa.eu/agriculture/envir/measures/index_en.htm [2016 Aug. 30].

Feltham, H., Park, K., Minderman, J. and Goulson, D. 2015. Experimental evidence that wildflower strips increase pollinator visits to crops. Ecol. Evol. **16**: 3523-3530.

Frankie, G. W., Thorp, R. W., Newstrom-Lloyd, L. E., Rizzardi, M. A., Barthell, J. F., Griswold, T. L., Kim, J.-Y. and Kappagoda, S. 1998. Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. Environ. Entomol. **27**: 1137-1148.

Frazier, M. T., Mullin, C. A., Frazier, J. L., Ashcraft, S. A., Leslie, T. W., Mussen, E. C. and Drummond, F. A. 2015. Assessing honey bee (Hymenoptera: Apidae) foraging populations and the potential impact of pesticides on Eight U.S. Crops. J. Econ. Entomol. **108**: 2141-2152.

Free, J. B. 1993. Insect Pollination of Crops. Academic Press, San Diego.

Fye, R. E. 1965. The biology of Apoidea taken in trap nests in Northwestern Ontario (Hymenoptera). Can. Entomol. **97**: 863-877.

Gallai, N., Salles, J. M., Settele, J. and Vaissière, B. E. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecol. Econ. **68**: 810-821.

Garibaldi, L. A., Aizen, M. A., Klein, A. M., Cunningham, S. A. and Harder, L. D. 2011. Global growth and stability of agricultural yield decrease with pollinator dependence. Proc. Natl. Acad. Sci. **108**: 5909-5914.

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Kremen, C., Carvalheiro, L. G., Harder, L. D., Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S. K., Kennedy, C. M., Krewenka, K. M., Krishnan, S., Mandelik, Y., Mayfield, M. M., Munyuli, T., Nault, B. A., Potts, S. G., Rader, R., Ricketts, T. H., Seymour, C. L., Williams, N. and Klein, A. M. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science **339**: 160-1611.

Gathmann, A. and Tscharntke, T. 2002. Foraging ranges of solitary bees. J. Anim. Ecol. **71**: 757-764.

Gezon, Z. J., Wyman, E. S., Ascher, J. S., Inouye, D. W. and Irwin, R. E. 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. Methods Ecol. Evol. **6**: 1044-1054.

Gilbert, F. S. 1983. The foraging ecology of hoverflies (Diptera: Syrphidae): circular movements on composite flowers. Behav. Ecol. Sociobiol. **13**: 253-257.

Gill, R. J., Baldock, K. C., Brown, M. J., Cresswell, J. E., Fountain, M. T., Garratt, M. P., Gough, L. A., Heard, M. S., Holland, J. M., Ollerton, J., Stone, G. N., Tang, C. Q., Vogler, A. P., Woodward, G., Arce, A. N. and Boatman, N. D. 2016. Protecting an ecosystem service: approaches to understanding and mitigating. Adv. Ecol. Res. **54**: 13-206.

Goodman, R., Hepworth, G., Kaczynski, P., McKee, B., Clarke, S. and Bluett, C. 2001. Honeybee pollination of buckwheat (*Fagopyrum esculentum* Moench) cv. Manor. Aust. J. Exp. Agric. **41**: 1217-1221.

Goulet, H. 2003. Biodiversity of ground beetles (Coleoptera: Carabidae) in Canadian agricultural soils. Can. J. Soil Sci. **83**: 259-264.

Goulson, D., Lye, G. C. and Darvill, B. 2008. Decline and conservation of bumble bees. Annu. Rev. Entomol. **53**: 191-208.

Government of Canada. 2016. Historical data. [Online] Available: http://climate.weather.gc.ca/historical_data/search_historic_data_e.html [2016 Dec. 9].

Gradish, A. E., Cutler, G. C., Frewin, A. J. and Scott-Dupree, C. D. 2016. Comparison of buckwheat, red clover, and purple tansy as potential surrogate plants for use in semi-field pesticide risk assessments with *Bombus impatiens*. Peer J **4**: 1-17.

Gradish, A. E., Scott-Dupree, C. D. and Cutler, G. C. 2012a. Susceptibility of *Megachile rotundata* to insecticides used in wild blueberry production in Atlantic Canada. J. Pest Sci. **85**: 133-140.

Gradish, A. E., Scott-Dupree, C. D., Frewin, A. J. and Cutler, G. C. 2012b. Lethal and sublethal effects of some insecticides recommended for wild blueberry on the pollinator *Bombus impatiens*. Can. Entomol. **144**: 478-486.

Greenleaf, S. S. and Kremen, C. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. Proc. Natl. Acad. Sci. **103**: 1389-13895.

Guisse, J. K. and Miller, D. G. 2011. Distribution and habitat preferences of *Osmia lignaria* (Hymenoptera: Megachilidae) and associated cavity-nesting insects in California's Sierra Nevada foothills adjacent to the Sacramento Valley. Pan-Pac. Entomol. **87**: 188-195.

Hanes, S. P., Collum, K. K., Hoshide, A. K. and Asare, E. 2013. Grower perceptions of native pollinators and pollination strategies in the lowbush blueberry industry. Renew. Agric. Food Syst. **30**: 124-131.

Hanley, M. E., Franco, M., Pichon, S., Darvill, B. and Goulson, D. 2008. Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. Func. Ecol. **22**: 592-598.

Hayat, R. 1997. Prey of some robber flies (Diptera: Asilidae) in Turkey. Zool. Middle East **51**: 87-94.

Heinrich, B. 2004. Bumblebee economics. Functional Ecology. Harvard University Press, Cambridge.

Hendriksma, H. P. and Shafir, S. 2016. Honey bee foragers balance colony nutritional deficiencies. Behav. Ecol. Sociobiol. **70**: 509-517.

Hickman, J. M. and Wratten, S. D. 1996. Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. J. Econ. Entomol. **89**: 832-840.

Hicks, B. 2009. Observations of the nest structure of *Osmia inermis* (Hymenoptera: Megachilidae) from Newfoundland, Canada. J. Acadian Entomol. Soc. **5**: 12-18.

Hicks, B. J. 2011. Pollination of lowbush blueberry (*Vaccinium angustifolium*) in Newfoundland by native and introduced bees. J. Acadian Entomol. Soc. **7**: 108-118.

Hoehn, P., Tscharntke, T., Tylianakis, J. M. and Steffan-Dewenter, I. 2008. Functional group diversity of bee pollinators increases crop yield. Proc. R. Soc. B **275**: 2283-2291.

Hopwood, J. L. 2008. The contribution of roadside grassland restorations to native bee conservation. Biol. Conserv. **141**: 2632-2640.

Hunt, J. H., Brown, P. A., Sago, K. M. and Kerker, J. A. 1991. Vespid wasps eat pollen (Hymenoptera: Vespidae). J. Kansas Entomol. Soc. **64**: 127-130.

Inouye, D. W. 1980. The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. Oecologia **45**: 197-201.

Irvin, N. A., Wratten, S. D., Frampton, C. M., Bowie, M. H., Evans, A. M. and Moar, A. T. 1999. The phenology and pollen feeding of three hover fly (Diptera: Syrphidae) species in Canterbury, New Zealand. New Zealand J. Zool. **26**: 105-115.

Isaacs, R. and Kirk, A. K. 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. J. Appl. Ecol. **47**: 841-849.

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M. and Landis, D. 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. Front. Ecol. Environ. **7**: 196-203.

Javorek, S. K., Mackenzie, K. E. and Vander Kloet, S. P. 2002. Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). Ann. Entomol. Soc. Am. **95**: 345-351.

Jonsson, A. M., Ekroos, J., Danhardt, J., Andersson, G. K. S., Olsson, O. and Smith, H. G. 2015. Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. Biol. Conserv. **184**: 51-58.

Karem, J., Woods, S. A., Drummond, F. and Stubbs, C. 2006. Sampling native wasps along both vertical and horizontal gradients in the Maine lowbush blueberry landscape. Environ. Entomol. **35**: 1083-1093.

Karem, J., Woods, S. A., Drummond, F. and Stubbs, C. 2010. The relationships between Apocrita wasp populations and flowering plants in Maine's wild lowbush blueberry agroecosystems. Biocontrol Sci. Technol. **20**: 257-274.

Kearns, C. A. and Inouye, D. W. 1997. Pollinators, flowering plants, and conservation biology. Bioscience **47**: 297-307.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhoffer, J. H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S. K., Jha, S., Klein, A. M., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L., Neame, L. A., Otieno, M., Park, M., Potts, S. G., Rundlof, M.,

Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B. F., Westphal, C., Wilson, J. K., Greenleaf, S. S. and Kremen, C. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. **16**: 584-599.

Kerr, J. T., Pindar, A., Galpern, P., Packer, L., Potts, S. G., Roberts, S. M., Rasmont, P., Schweiger, O., Colla, S. R., Richardson, L. L., Wagner, D. L., Gall, L. F., Sikes, D. S. and Pantoja, A. 2015. Climate change impacts on bumblebees converge across continents. Science **349**: 177-180.

Kevan, P. G. 1973. Parasitoid wasps as flower visitors in the Canadian high arctic. J. Pest Sci. **46**: 3-7.

Kevan, P. G. 1977. Blueberry crops in Nova Scotia and New Brunswick- pesticides and crop reductions. Can. J. Agric. Econ. **254**: 61-65.

Kevan, P. G. and Phillips, T. P. 2001. The economic impacts of pollinator declines: An approach to assessing the consequences. Ecol. Soc. **5**: 1-17.

Kinsman, G. 1993. The history of the lowbush blueberry industry in Nova Scotia 1950-1959. The Blueberry Producers' Association of Nova Scotia.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'gonigle, L. K., Rader, R. and Ricketts, T. H. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. **6**: 7414-7421.

Klein, A. M., Brittain, C., Hendrix, S. D., Thorp, R., Williams, N. and Kremen, C. 2012. Wild pollination services to California almond rely on semi-natural habitat. J. Appl. Ecol. **49**: 723-732.

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. and Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops. Proc. Natl. Acad. Sci. U.S. A. **274**: 303-313.

Koh, I., Lonsdorf, E. V, Williams, N. M., Brittain, C., Isaacs, R., Gibbs, J. and Ricketts, T. H. 2015. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl. Acad. Sci. U.S. A. **113**: 140-145.

Kotze, D. J., Brandmayr, P., Casale, A., DAuffy-Richard, E., Dekoninck, W., Koivula, M. J., Lovei, G. L., Mossakowski, D., Noordijk, J., Paarmann, W., Pizzolotto, R., Saska, P., Schwerk, A., Serrano, J., Szyszko, J., Taboada, A., Turin, H., Venn, S., Vermeulen, R. and Zetto, T. 2011. Forty years of carabid beetle research in Europe- from taxonomy, biology, ecology and population studies to bioindication, habitat assessment and conservation. ZooKeys **100**: 55-148.

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vazquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., Keitt, T. H., Klein, A. M., Regetz, J. and Ricketts, T. H. 2007. Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. Ecol. Lett. **10**: 299-314.

Kromp, B. 1999. Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. Agric. Ecosyst. Environ. **74**: 187-228.

Landis, D. A., Wratten, S. D. and Gurr, G. M. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. **45**: 175-201.

Laverty, T. M. and Harder, L. D. 1988. The bumble bees of eastern Canada. Can. Entomol. **120**: 965-987.

Losey, J. E. and Vaughan, M. 2006. The economic value of ecological services provided by insects. Bioscience **56**: 311-323.

Loureiro, A. M. M. C. and Cutler, G. C. 2016. Parasitism of blueberry spanworm (Lepidoptera: Geometridae) by Ichneumonidae and Tachinidae in Nova Scotia blueberry fields. J. Acad. Entomol. Soc. **12**: 31-34.

Lovei, G. L. and Sunderland, K. D. 1996. Ecology and behaviour of ground beetles (Coleoptera: Carabidae). Annu. Rev. Entomol. **41**: 231-256.

Lundgren, J. G. 2009. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. Biol. Control **51**: 294-305.

M'gonigle, L. K., Ponisio, L. C., Cutler, K. and Kremen, C. 2015. Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. Ecol. Appl. **25**: 1557-1565.

MacIvor, J. S. 2016. Cavity-nest boxes for solitary bees: a century of design and research. Apidologie. **47**: 1-17.

MacIvor, J. S. and Packer, L. 2015. "Bee hotels" as tools for native pollinator conservation: A premature verdict? PLoS One **10**: 1-13.

Majka, C. G. and Bousquet, Y. 2008. Maritime provinces Carabidae: a correction. Zootaxa **1755**: 68.

Majka, C. G. and McCorquodale, D. B. 2006. The Coccinellidae (Coleoptera) of the Maritime provinces of Canada: new records, biogeographic notes, and conservation concerns. Zootaxa **1154**: 49-68.

Majka, C. G., Bousquet, Y. and Westby, S. 2007. The ground beetles (Coleoptera: Carabidae) of the Maritime provinces of Canada: review of collecting, new records, and observations on composition, zoogeography, and historical origins. Zootaxa **1590**: 1-36.

Marshall, S. 2007. Insects: Their Natural History and Diversity: With a Photographic Guide to Insects of Eastern North America. Firefly Books Ltd. Ontario, Canada. pp 736.

Martin, E. A., Reineking, B., Seo, B. and Steffan-Dewenter, I. 2013. Natural enemy interactions constrain pest control in complex agricultural landscapes. Proc. Natl. Acad. Sci. U.S. A.**110**: 5534-5539.

Martin, E. A., Reineking, B., Seo, B. and Steffan-Dewenter, I. 2015. Pest control of aphids depends on landscape complexity and natural enemy interactions. Peer J **3**: 1-22.

McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R. and Wood, D. M. 1987. Manual of nearctic Diptera. Agriculture Canada.

McKechnie, I. M., Thomsen, C. J. M. and Sargent, R. D. 2017. Forested field edges support a greater diversity of wild pollinators in lowbush blueberry (*Vaccinium angustifolium*). Agric. Ecosyst. Environ. **237**: 154-161.

Memmott, J., Craze, P. G., Waser, N. M. and Price, M. V. 2007. Global warming and the disruption of plant-pollinator interactions. Ecol. Lett. **10**: 710-717.

Melathopoulos, A. P. 2015. Ecosystem services, context and the social basis for conservation: the case of insect pollination benefits to lowbush blueberry. PhD thesis. Faculty of Science. Dalhousie University.

Meyer, S., Unternahrer, D., Arlettaz, R. and Humbert, J.- Y. 2017. Promoting diverse communinties of wild bees and hoverflies requires a landscape approach to managing meadows. Agr. Ecosyst. Environ. **239**: 376-384.

Michener, C. D. 2007. The Bees of the World. 2nd edition. The John Hopkins University Press, Baltimore.

Minckley, R. L., Wcislo, W. T., Yanega, D. and Buchmann, S. L. 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. Ecology **75**: 1406-1419.

Mitchell, T. B. 1962. Bees of the eastern United States: Family Megachilidae. [Online] Available: https://projects.ncsu.edu/cals/entomology/museum/downloads/Megachilidae.pdf [2016 Nov. 24].

Moisan-DeSerres, J., Chagnon, M. and Fournier, V. 2014a. Influence of windbreaks and forest borders on abundance and species richness of native pollinators in lowbush blueberry fields in Québec, Canada. Can. Entomol. **147**: 432-442.

Moisan-Deserres, J., Girard, M., Chagnon, M. and Fournier, V. 2014b. Pollen loads and specificity of native pollinators of lowbush blueberry. J. Econ. Entomol **107**: 1156-1162.

Morandin, L. A. and Kremen, C. 2013. Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecol. Appl. **23**: 829-839.

Morandin, L. A. and Winston, M. L. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. Agric. Ecosyst. Environ. **116**: 289-292.

Morandin, L. A., Winston, M. L., Abbott, V. A. and Franklin, M. T. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? Basic Appl. Ecol. **8**: 117-224.

Mullins, A. 2014. Field-edge planting to deter white-tailed deer and attract carabid beetles in soybean fields. M.Sc. Thesis. Faculty of Agriculture. Dalhousie University.

pp. 90.

Nielsen, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S. G., Roberts, S. P. M., Settele, J., Szentgyörgyi, H., Vaissière, B. E., Vaitis, M., Woyciechowski, M., Bazos, I., Biesmeijer, J. C., Bommarco, R., Kunin, W. E., Tscheulin, T., Lamborn, E. and Petanidou, T. 2011. Assessing bee species richness in two Mediterranean communities: Importance of habitat type and sampling techniques. Ecol. Res. **26**: 969-983.

Norfolk, O., Eichhorn, M. P. and Gilbert, F. 2016. Flowering ground vegetation benefits wild pollinators and fruit set of almond within arid smallholder orchards. Insect Conserv. Divers. **9**: 236-243.

O'Neal, M. E., Mason, K. S., and Isaacs, R. 2005a. Seasonal abundance of ground beetles in highbush blueberry (*Vaccinium corymbosum*) fields and response to a reduced-risk insecticide program. Environ. Entomol **34**: 378-384.

O'Neal, M. E., Zontek, E. L., Szendrei, Z., Landis, D. A. and Isaacs, R. 2005b. Ground predator abundance affects prey removal in highbush blueberry (*Vaccinium corymbosum*) fields and can be altered by aisle ground covers. BioControl **50**: 205-222.

Obrycki, J. J. and Kring, T. J. 1998. Predaceous Coccinellidae in biological control. Annu. Rev. Entomol **43**: 295-321.

Ollerton, J., Winfree, R. and Tarrant, S. 2011. How many flowering plants are pollinated by animals? Oikos **120**: 321-326.

Packer, L., Genaro, J. A. and Sheffield, C. S. 2007. The bee genera of Eastern Canada. Can. J. Arthropod Identif. **3**: 1-32.

Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E. and Danforth, B. N. 2015. Negative effects of pesticides on wild bee communities can be buffered by landscape context. Proc. Natl. Acad. Sci. U.S. A. **282**: 1-9.

Pernal, S. F. and Currie, R. W. 2000. Pollen quality of fresh and 1-year-old single pollen diets for worker honey bees (*Apis mellifera* L.). Apidologie **31**: 387-409.

Pernal, S. F. and Currie, R. W. 2001. The influence of pollen quality on foraging behavior in honeybees (*Apis mellifera* L.). Behav. Ecol. Sociobiol. **51**: 53-68.

Persson, A. S. and Smith, H. G. 2013. Seasonal persistence of bumblebee populations is affected by landscape context. Agric. Ecosyst. Environ. **165**: 201-209.

Peters, V. E., Carroll, C. R., Cooper, R. J., Greenberg, R. and Solis, M. 2013. The contribution of plant species with a steady-state flowering phenology to native bee conservation and bee pollination services. Insect Conserv. Divers. **6**: 45-56.

Pettis, J. S., Lichtenberg, E. M., Andree, M., Stitzinger, J., Rose, R. and VanEngelsdorp, D. 2013. Crop pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen *Nosema ceranae*. PLoS One **8**: 1-9.

Pitts-Singer, T. L. and James, R. R. 2008. Do weather conditions correlate with findings in failed, provision-filled nest cells of *Megachile rotundata* (Hymenoptera:

Megachilidae) in western North America? J. Econ. Entomol. **101**: 674-685.

Platt, J. O., Caldwell, J. S. and Kok, L. T. 1999. Effect of buckwheat as a flowering border on populations of cucumber beetles and their natural enemies in cucumber and squash. Crop Prot. **18**: 305-313.

Ponisio, L. C., M'Gonigle, L. K. and Kremen, C. 2016. On-farm habitat restoration counters biotic homogenization in intensively managed agriculture. Global Change Biol. **22**: 704-715.

Pontin, D. R., Wade, M. R., Kehrli, P. and Wratten, S. D. 2006. Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. Ann. Appl. Biol. **148**: 39-47.

Popic, T. J., Davila, Y., C. and Wardle, G. M. 2013. Evaluation of common methods for sampling invertebrate pollinator assemblages: net sampling out-performs pan traps. Plos One **8**: 1-9.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. and Kunin, W. E. 2010. Global pollinator declines: Trends, impacts and drivers. Trends Ecol. Evol. **25**: 345-353.

R Development Core Team. 2016. Vienna, Austria.

Racys, J. and Montviliene, R. 2005. Effect of bees-pollinators in buckwheat (*Fagopyrum esculentum* Moench) crops. J. Apic. Sci. **49**: 47-51.

Rao, S. and Strange, J. P. 2012. Bumble bee (Hymenoptera: Apidae) foraging distance and colony density associated with a late-season mass flowering crop. Environ. Entomol **41**: 905–915.

Renkema, J. M., Christopher Cutler, G. and Rutherford, K. 2014. Molecular analysis reveals lowbush blueberry pest predation rates depend on ground beetle (Coleoptera: Carabidae) species and pest density. BioControl **59**: 749-760.

Renkema, J. M., Cutler, G. C., Lynch, D. H., Mackenzie, K. and Walde, S. J. 2016. Organic mulches in highbush blueberries alter beetle (Coleoptera) community composition and improve functional group abundance and diversity. Agric. For. Entomol. **18**: 119-127.

Renkema, J. M., Lynch, D. H., Cutler, G. C., MacKenzie, K. and Walde, S. J. 2012. Predation by *Pterostichus melanarius* (Illiger) (Coleoptera: Carabidae) on immature *Rhagoletis mendax* Curran (Diptera: Tephritidae) in semi-field and field conditions. J. Biol. Control **60**: 46-53.

Renkema, J. M., Manning, P. and Cutler, G. C. 2013. Predation of lowbush blueberry insect pests by ground beetles (Coleoptera: Carabidae) in the laboratory. J. Pest Sci. **86**: 525-532.

Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A. and Viana, B. F. 2008. Landscape effects on crop pollination services: Are there general patterns? Ecol. Lett. **11**: 499-515.

Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B. E. and Henry, M. 2013. Differences of floral resource use between honey bees and wild bees in an intensive farming system. Agric. Ecosyst. Environ. **179**: 78-86.

Roubik, D. W. 2001. Ups and downs in pollinators populations: when is there a decline? Conserv. Ecol. **5**: 2.

Rundlof, M., Persson, A. S., Smith, H. G. and Bommarco, R. 2014. Late-season mass-flowering red clover increases bumble bee queen and male densities. Agric. Biol. Conserv. **172**: 138-145.

Rusch, A., Chaplin-Kramer, R., Gardiner, M. M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharntke, T., Weisser, W. W., Winqvist, C., Woltz, M. and Bommarco, R. 2016. Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. Agric. Ecosyst. Environ. **221**: 198-204.

Russo, L., DeBarros, N., Yang, S., Shea, K. and Mortensen, D. 2013. Supporting crop pollinators with floral resources: network-based phenological matching. Ecol. Evol. **3**: 3125-3140.

Russo, L., Park, M., Gibbs, J. and Danforth, B. 2015. The challenge of accurately documenting bee species richness in agroecosystems: Bee diversity in eastern apple orchards. Ecol. Evol. **17**: 3531-3540.

Sardiñas, H. S. and Kremen, C. 2015. Pollination services from field-scale agricultural diversification may be context-dependent. Agric. Ecosyst. Environ. **207**: 17-25.

Sarver, M. J. 2007. Farm Management for Native Bees: A Guide for Delaware. USDA NRCS and Delaware Department of Agriculture. Dover, DE.

SAS Institute Inc. 2014. Cary, NC.

Saunders, M. E., Luck, G. W. and Mayfield, M. M. 2013. Almond orchards with living ground cover host more wild insect pollinators. J. Insect Conserv. **17**: 1011-1025.

Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G. and Kleijn, D. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss - a meta-analysis. Ecol. Lett. **16**: 912-920.

Senapathi, D., Biesmeijer, J. C., Breeze, T. D., Kleijn, D., Potts, S. G. and Carvalheiro, L. G. 2015. Pollinator conservation - The difference between managing for pollination services and preserving pollinator diversity. Curr. Opin. Insect Sci. **12**: 93-101.

Sheffield, C. S., Kevan, P. G., Pindar, A. and Packer, L. 2013. Bee (Hymenoptera: Apoidea) diversity within apple orchards and old fields in the Annapolis Valley, Nova Scotia, Canada. Can. Entomol. **145**: 94-114.

Sheffield, C. S., Kevan, P. G. and Smith, R. F. 2003. Bee species of Nova Scotia, Canada, with new records and notes on bionomics and floral relations

(Hymenoptera: Apoidea). J. Kansas Entomol. Soc. **76**: 357-384.

Sheffield, C. S., Kevan, P. G., Westby, S. M. and Smith, R. F. 2008. Diversity of cavity-nesting bees (Hymenoptera: Apoidea) within apple orchards and wild habitats in the Annapolis Valley, Nova Scotia, Canada. Can. Entomol. **140**: 235-249.

Sheffield, C. S., Wilkes, M. A., Christopher Cutler, G. and Hermanutz, L. 2014. An artificial nesting substrate for *Osmia* species that nest under stones, with focus on *Osmia inermis* (Hymenoptera: Megachilidae). Insect Conserv. Divers. **8**: 189-192.

Sloggett, J. J. and Majerus, M. E. N. 2000. Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): an evolutionary perspective. Biol. J. Linnean Soc. **70**: 63-88.

Spivak, M., Mader, E., Vaughan, M. and Euliss, N. H. 2011. The plight of the bees. Environ. Sci. Technol. **45**: 34-38.

Spradbery, J. P. 1973. Wasps: An account of the biology and natural history of solitary and social wasps. University of Washington Press, Seattle.

Sprague, R., Boyer, S., Stevenson, G. M. and Wratten, S. D. 2016. Assessing pollinators' use of floral resource subsidies in agri-environment schemes: An illustration using *Phacelia tanacetifolia* and honeybees. Peer J **4**: 2677-2692.

Somerville, D. 2000. Honey bee nutrition and supplementary nutrition. [Online] Available: http://www.dpi.nsw.gov.au/__data/assets/pdf_file/0008/117494/honey-bee-nutrition-supplementary-feeding.pdf [2017 Mar. 02].

Somerville, D. 2001. Nutritional value of bee collected pollens. [Online] Available: https://rirdc.infoservices.com.au/downloads/01-047 [2016 Oct. 24].

Statistics Canada. 2016. Table 001-0009. Area, production and farm gate value of fresh and processed fruits, by province annual. CANSIM (database). [Online]. Available: http://www5.statcan.gc.ca/cansim/a05?lang=eng&id=0010009 [201717 June 06].

Stephens, M. J., France, C. M., Wratten, S. D. and Frampton, C. 1998. Enhancing biological control of leafrollers (Lepidoptera: Tortricidae) by sowing buckwheat (*Fagopyrum esculentum*) in an orchard. Biocontrol Sci. Technol. **8**: 547-558.

Stireman, J. O., O'Hara, J. E. and Wood, D. M. 2006. Tachinidae: Evolution, behaviour, and ecology. Annu. Rev. Entomol. **51**: 525-555.

Stubbs, C. S. and Drummond, F. A. 1997. Management of the alfalfa leafcutting bee, *Megachile rotundata* (Hymenoptera: Megachilidae), for pollination of wild lowbush blueberry. J. Kansas Entomol. Soc. **70**: 81-93.

Stubbs, C. S. and Drummond, F. A. 2001. *Bombus impatiens* (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for lowbush blueberry pollination. J. Econ. Entomol **94**: 609-616.

Stubbs, C. S., Drummond, F. A. and Allard, S. L. 1997. Bee conservation and conserving *Osmia* spp. in Maine lowbush bleuberry fields. Northeast. Nat. **4**: 133-144.

Stubbs, C. S., Jacobson, H. A., Osgood, E. A. and Drummond, F. A. 1992. Alternative forage plants for native (wild) bees associated with lowbush blueberry, *Vaccinium* spp., in Maine. Orono. [Online] Available: http://digitalcommons.library.umaine.edu/aes_techbulletin. [2017 Jan. 31].

Taki, H., Boone, J. W., Viana, B. F., Silva, F. O., Kevan, P. G. and Sheffield, C. S. 2004. Effect of shading on trap nest utilization by hole-nesting aculeate Hymenoptera. Can. Entomol. **136**: 889-891.

Taki, H., Okabe, K., Makino, S., Yamaura, Y. and Sueyoshi, M. 2009. Contribution of small insects to pollination of common buckwheat, a distylous crop. Ann. Appl. Biol. **155**: 121-129.

Theodore Munyuli, M. B. 2013. Is pan-trapping the most reliable sampling method for measuring and monitoring bee biodiversity in agroforestry systems in sub-Saharan Africa? Int. J. Trop. Insect Sci. **33**: 14-37.

Thomson, L. J. and Hoffmann, A. A. 2009. Vegetation increases the abundance of natural enemies in vineyards. Biol. Control **49**: 259-269.

Torchio, P. F. 1987. Use of non-honey bee species as pollinators of crops. Proc. Entomol. Soc. Ontario **118**: 111-124.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I. and Thies, C. 2005. Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. Ecol. Lett. **8**: 857-874.

Tuell, J. K., Ascher, J. S. and Isaacs, R. 2009. Wild bees (Hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. Ann. Entomol. Soc. Am **102**: 275-287.

Vander Kloet, S. P. 1988. The genus *Vaccinium* in North America. Agriculture Canada, Wolfville, Nova Scotia.

vanEngelsdorp, D. and Meixner, M. D. 2010. A historical review of managed honey bee populations in Europe and the United States and the factors that may affect them. J. Invertebr. Pathol. **103**: 80–95.

Vaughan, M. and Black, S. H. 2008. Native pollinators: How to protect and enhance habitat for native bees. Native Plants J. **9**: 80-91.

Venturini, E. M., Drummond, F. A., Hoshide, A. K., Dibble, A. C. and Stack, L. B. 2017. Pollination reservoirs in lowbush blueberry (Ericales: Ericaceae). J. Econ. Entomol. **109**: 1-14.

Vickery, V. R. 1991. The honey bee: A guide for beekeepers. Particle Press, Westmount, Quebec, Canada.

Walton, N. J. and Isaacs, R. 2011. Influence of native flowering plant strips on natural enemies and herbivores in adjacent blueberry fields. Environ. Entomol. **40**: 697-705.

Wei, X., Xu, X. and Deloach, C. J. 1995. Biological control of white grubs (Coleoptera: Scarabaeidae) by larvae of *Promachus yesonicus* (Diptera: Asilidae) in China. Biol. Control **5**: 290-296.

Westerfelt, P., Widenfalk, O., Lindelöw, Å., Gustafsson, L. and Weslien, J. 2015. Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. Insect Conserv. Divers. **8**: 493-504.

Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. J. Appl. Ecol. **46**: 187-193.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitat in the Conservation of Bees. Academic Press, London.

Whidden, T. L. 1996. The fidelity of commercially reared colonies of *Bombus impatiens* Cresson (Hymenoptera: Apidae) to lowbush blueberry in southern New Brunswick. Can. Entomol. **128**: 957-958.

Williams, N. M., Minckley, R. L., and Silveira, F. A. 2001. Variation in native bee faunas and its implications for detecting community changes. Ecol. Soc. **5**: 1-22.

Williams, P. H., Thorp, R. W., Richardson, L. L. and Colla, S. R. 2014. Bumble bees of North America: An Identification Guide. Princeton University Press, Princeton.

Wilson, J. S., Griswold, T. and Messinger, O. J. 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: Are pan traps sufficient? J. Kansas Entomol. Soc. **81**: 288-300.

Winfree, R. 2010. The conservation and restoration of wild bees. Ann. N. Y. Acad. Sci. **1195**: 169-197.

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G., V, D. P. and Aizen, M. A. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. Ecology **90**: 2068-2076.

Winfree, R., Gross, B. J. and Kremen, C. 2011. Valuing pollination services to agriculture. Ecol. Econ. **71**: 80-88.

Winfree, R., Williams, N. M., Dushoff, J. and Kremen, C. 2007. Native bees provide insurance against ongoing honey bee losses. Ecol. Lett. **10**: 1105-1113.

Woltz, J. M., Isaacs, R. and Landis, D. A. 2012. Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. Agric. Ecosyst. Environ. **152**: 40-49.

Wood, G. W. 1968. Self-fertility in the lowbush blueberry. Can. J. Plant Sci. **48**: 431-433.

Wood, G. W., Crozier, L. M. and Neilson, W. T. A. 1983. Monitoring the blueberry maggot, *Rhagoletis mendax* (Diptera: Tephritidae), with Phercon AM traps. Can. Ent **115**: 219-220.

Wood, T. J., Holland, J. M. and Goulson, D. 2015a. Pollinator-friendly management does not increase the diversity of farmland bees and wasps. Biol. Conserv. **187**: 120-126.

Wood, T. J., Holland, J. M. and Goulson, D. 2015b. A comparison of techniques for assessing farmland bumblebee populations. Oecologia **177**: 1093-1102.

Wood, T. J., Holland, J. M. and Goulson, D. 2017. Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. J. Appl. Ecol. **54**: 323-333.

Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E. and Desneux, N. 2012. Pollinator habitat enhancement: Benefits to other ecosystem services. Agric. Ecosyst. Environ. **159**: 112-122.

Wratten, S. D., White, A. J., Bowie, M. H., Berry, N. A. and Weigmann, U. 1995. Phenology and ecology of hover flies (Diptera: Syrphidae) in New Zealand. Environ. Entomol. **24**: 595-600.

Yarborough, D. E. 1997. Production trends in the wild blueberry industry in North America. Acta Hortic. **446**: 33-35.

Yarborough, D. E. 2004. Factors contributing to the increase in productivity in the wild blueberry industry. Small Fruits Rev. **3**: 33-43.

Yarborough, D. E. 2012. Establishment and management of the cultivated lowbush blueberry (*Vaccinium angustifolium*). Int. J. Fruit Sci. **12**: 1-3.

Ziska, L. H., Pettis, J. S., Edwards, J., Hancock, J. E., Tomecek, M. B., Clark, A., Dukes, J. S., Loladze, I. and Polley, H. W. 2016. Rising atmospheric CO_2 is reducing the protein concentration of a floral pollen source essential for North American bees. Proc. Natl. Acad. Sci. U.S.A. **283**: 1-7.