

**The pollination ecology of highbush blueberry
(*Vaccinium corymbosum*) in British Columbia**

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Abstract

Agricultural systems often support low beneficial insect diversity because they reduce habitat quality. Agricultural management increases landscape homogeneity resulting in low habitat and resource diversity. Crops that rely on wild pollinators for fruit production or predators and parasitoids for pest control may lose access to these services as the agroecosystem becomes increasingly managed. I used yield data from pollination experiments conducted over four years, along with insect surveys, to better understand the dynamics between insect communities in agroecosystems and their use of the agricultural landscape in highbush blueberry (*Vaccinium corymbosum*) in the Fraser Valley of southern British Columbia, Canada.

Regional land use was identified as being an important component in structuring beneficial insect communities. Semi-natural habitat, such as pasture or fallow, was found to support greater abundances and diversity of all beneficial insects. Land use with greater disturbance, like conventional non-flowering agriculture, reduced pollinator species richness but increased the abundance of generalist predators. The differences between groups in their response to land use types might be driven by variability in access to resources (ex. floral resources or pest insects) in the larger agricultural landscape. However, surrounding landscape composition did not affect blueberry yield deficit, which was instead determined primarily by bumble bee visits and minimum daily temperatures. This finding highlights the importance of weather conducive to pollinator foraging for crop production. Despite the importance of bumble bees for reducing yield deficit, experimental introduction of two managed bumble bee species did not mitigate these deficits. Differences in bumble bee species characteristics associated with reproduction predicted pollen forager recruitment, which when coupled with differences in foraging preferences (blueberry pollen comprised 50% of pollen loads in one species, but less than 20% in the other and in managed honey bees) provides some insight into which managed species is best suited for further commercial development.

My results highlight the complexity associated with predicting crop pollination levels and demonstrate how the impact of wild insects on production will vary with surrounding land-use, species characteristics, and abiotic factors. In crops highly reliant on wild pollinators, like highbush blueberry, understanding the needs of beneficial insects may allow farmers to modify practices to improve ecosystem services.

Keywords: Pollination; ecosystem service; agricultural production; biodiversity; landscape analysis.

For Mémère

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Chapter 1. General Introduction

1.1. Agroecosystems and biodiversity

Agroecosystems are ideal study systems in which to analyze the variability of habitat use by local insect communities, as farmland is rapidly becoming the most common global terrestrial landscape. In the past 300 years, land dedicated to agriculture has increased fivefold across the planet, with more than 1,471 million hectares of cropland being recorded in 1990 (Goldewijk, 2001). Current estimates identify 38.4% of the ice free terrestrial land on the planet as being dedicated to agriculture (FAOSTAT, 2015). This ever growing global agricultural landscape results from the need to keep pace with earth's population, however, by 2050 it is predicted that an additional 1 billion hectares of agricultural land and increased intensification of current agricultural production will be necessary (Tilman et al., 2011). These increases in agricultural area and intensification of land use may have serious biodiversity implications at multiple levels. The complexity of soil food webs has diminished in agricultural systems (Tsiafouli et al., 2015), and nutrient run-off into nearby water sources can result in eutrophication of aquatic habitats, reducing their diversity (Tilman, 1999). Agricultural intensification can also diminish habitat diversity reducing invertebrate prey species for both mammal and avian predators (Vickery et al., 2001; Wickramasinghe et al., 2004). These deleterious effects of agriculture are context dependent with species responses varying in different agricultural systems. In western Europe, for example, pollinator communities experience a decrease in diversity and abundance as agricultural land use intensifies, but crop production areas display a greater diversity of pollinators compared to landscapes characterized by livestock rearing (Le Féon et al., 2010). Identifying the relationship between landscape elements and insect communities in distinct agricultural systems is necessary to better understand the long term effects of habitat modification on biodiversity.

1.2. Ecosystem service and biodiversity

The study and use of ecosystem (or ecological) services is relatively new. The term itself has only increased in usage in scientific journals in the past 25 years (Fisher et al., 2009). Since the mid 1960s the value of ecological functions to human society has been

well documented (De Groot et al., 2002). Multiple definitions of an ecosystem service exist with its descriptions revolving around the services, processes, or functions performed by ecosystems and the species therein that benefit society (Costanza et al., 1998; Daily et al., 1999; Fisher et al., 2009). Ecosystem services include functions such as soil formation, primary productivity, water regulation, pollination, and pest control and are valued globally between \$124-\$145 trillion per year (Costanza et al., 2014, 1998). The total value of services is system dependant. The estimated value of services provided by open oceans and woodlands is approximately 1% of more diversified systems such as coral reefs or coastal wetland (de Groot et al., 2012). Identifying and maintaining species that are integral to the delivery of ecosystem services is essential to ensuring their continued benefit to the planet.

As the term suggests, ecosystem services are evaluated at broad scales, whereas the interactions resulting in ecosystem service delivery occur at smaller scales, between organisms. The differences in the ability of each species to perform a particular function or serve a role in an ecological process accounts for much of the variability in ecosystem service delivery. Generally, greater biodiversity results in greater ecosystem service delivery and stability (Balvanera et al., 2006). This has lead to a variety of projects focused on restoring diversity to disturbed and degraded habitats to re-establish biotic communities that support particular ecosystem functions (Rey Benayas et al., 2009). Diversification of agricultural land through the incorporation of hedgerows or semi-natural habitat in farm areas is a common practice that benefits entire communities of organisms that drive primary production, soil formation, carbon sequestration, pest predation and pollination, among many others (Jonsson et al., 2015; Morandin and Kremen, 2013; Smukler et al., 2010). Similarly, forests with more tree species maximize the delivery of multiple ecosystem services as tree species complementarity in particular ecosystem functions allows the community to mitigate weaknesses in service delivery of certain species (Gamfeldt et al., 2013). Differences in the contribution of species to ecosystem functions can also result in weak biodiversity-ecosystem service relationships as relatively small groups of species can provide a disproportionate amount of the ecosystem function. In particular, cropping systems that rely on pollination may not always benefit from pollinator diversity. Meta-analysis of 90 studies that measured the contributions of wild species to crop pollination demonstrated that common species, representing only 2% of regional species pool, were responsible for 80% of the crop visits (Kleijn et al., 2015). Diversity has

also been shown to be a poor predictor for other services such as nutrient cycling and both pest and weed biocontrol, where indices based on species traits were much more effective at predicting service delivery levels (Díaz and Cabido, 2001; Gagic et al., 2015; Wilby et al., 2005). Therefore, the importance of biodiversity for ecosystem function depends on the species and the function under consideration.

Functional groups can be defined by behaviour, physiology, or even taxonomy, and such groups may be complementary to each other, enhancing the overall delivery of ecosystem services (Díaz and Cabido, 2001). For example, pest predator communities can exhibit complementary behaviours based on differences in hunting location and life stage (Wilby et al., 2005). In strawberry pollination, honey bees tend to pollinate apical stigmas, while smaller solitary bee pollination results in pollen deposition on basal stigmas, more frequently resulting in improved fertilization (Chagnon et al., 2013). Species or functional group complementarity can therefore result in improved delivery of an ecosystem service due to partitioning of the function among multiple species.

1.3. Pollen limitation in *Vaccinium*

Flowering plants make up nearly 90% of all known plant species on the planet (Crepet and Niklas, 2009). Estimates suggest that approximately 87.5% of global flowering plant species require animal mediated pollination (Ollerton et al., 2011). This reliance on animal mediated pollination has explained much of the species diversification in angiosperms (Van der Niet and Johnson, 2012; Sargent, 2004; Vamosi and Vamosi, 2010). The co-evolution between pollinators and plants has serious implications for the reproductive fitness of many plant species. The inability to receive sufficient conspecific pollen is thought to be a major cause of low reproductive success among plant species (Ashman et al., 2004; Burd, 1994). Among agricultural species, in 115 crops that account for 99% of global food production, 87 species rely on animal mediated pollination, representing 35% of total food production (Klein et al., 2007). The loss or reduction of animal pollination might lead to only a relatively small reduction in total agricultural production, but will likely lead to much greater agricultural intensification, to compensate for the inefficiencies of production (Aizen et al., 2009). This may result in increased pollen limitation, as agricultural intensification is among the major drivers of wild pollinator species loss (Kennedy et al., 2013; Kremen et al., 2002; Potts et al., 2017; Tscharntke et al., 2005). Crop species that are reliant on wild pollinators will likely be affected

disproportionately by these cascading effects, as their pollination requirements may not be met by generalist managed pollinators.

Highbush blueberry (*Vaccinium corymbosum*) is one of approximately 22,000 species of plants that is reliant on sonicating bees for sexual reproduction (Vander Kloet 1988, Cardinal et al. 2018). Only particular species of pollinators are capable of vibrating their body through decoupling of the wing muscles in order to induce pollen release from poricidal anthers (King et al. 1996, King and Buchmann 2003). This adaptation may have played a significant role in the diversification of plant-pollinator relationships, as sonication has evolved on average 45 times in bee lineages, with bee genera containing sonicating species being more species rich compared to those that do not (Cardinal et al., 2018). Certain species of bumble bees (*Bombus* sp.) are capable of modulating this behaviour to adjust for environmental variables and different plant species (Switzer and Combes, 2017). The pendulous urceolate flowers that require floral sonication for pollen expulsion results in wild pollinators, specifically, *Bombus* species, being important and frequent visitors to both wild and managed members of *Vaccinium* (Kevan et al. 1983, Cane et al. 1985, Jacquemart 1993, Javorek et al. 2002, Usui et al. 2005), in contrast to managed honey bees (*Apis mellifera*) which cannot sonicate effectively. Floral adaptations of *Vaccinium* likely play a role in the yield deficits seen due to pollen limitation in highbush blueberry (Button and Elle, 2014; Courcelles et al., 2013).

Pollen compatibility issues are also common in cultivated *Vaccinium* species (Hokanson and Hancock 2000). In both lowbush blueberry (*Vaccinium angustifolium*) and cranberry (*Vaccinium macrocarpon*), outcrossed pollination results in better fruit and seed set (Saraccino and Vorsa 1991; Usui et al. 2005). *Vaccinium corymbosum* exhibits significant inbreeding depression in the form of seed abortion (Hokanson and Hancock 2000), and many other reproductive parameters (% fruit set, seed number, seed germination) are negatively affected by self fertilization (Vander Kloet and Lyrene 1987). Reductions in these reproductive parameters likely result from increased homozygosity for sub lethal mutations, and vary based on the genetic load or accumulation of mutations in particular individuals (Krebs and Hancock 1991). In large plants like highbush blueberry, self pollination can be exacerbated by pollinators, whose behaviours include sequential pollination of adjacent flowers to gather resources efficiently (Heinrich 1975). The combination of inbreeding depression along with the large size of highbush blueberry floral

displays increases the difficulty in developing pollination management strategies allowing farmers to maximize highbush blueberry production.

1.4. Pollinator diversity for agricultural pollination

The perception of managed honey bees as valuable agricultural pollinators is relatively recent, as prior to the past century production of honey and wax was their main value (Ransome 1937, vanEngelsdorp and Meixner 2010). In the United States, it is estimated that honey bees have increased yield by 36.3% to \$14.6 billion USD between 1989 and 2000 (Morse and Calderone, 2000). Wild pollinators may potentially be more important agricultural pollinators, as a study of 41 global crop systems found that honey bees only improved fruit set in 14% of systems, while wild pollinators benefited each crop (Garibaldi et al., 2013). The estimated total global value of insect-pollinated crops is approximately \$973 billion, of which \$238 billion is estimated to be a product of improved yields due to pollination (Gallai et al., 2009). The ability of both wild pollinators and commercially managed pollinators to add value to agricultural production offers opportunities to develop new managed pollinator species for agricultural pollination.

Since the early 20th century, researchers have domesticated bumble bee species and exported wild colonies to non-native countries due to their perceived potential as agricultural pollinators (Velthuis and van Doorn, 2006). Only within the past 30 years have domesticated bumble bees been empirically shown to be valuable pollinators in agricultural applications like greenhouse tomatoes (Van Ravestijn and Van Der Sande 1990). Bumble bees have also been identified as having pollination behaviours that result in better field crop pollination relative to honey bees (Javorek et al., 2002; Kendall and Smith, 2016; Thomson and Goodell, 2001; Willmer et al., 1994). Increases in land dedicated to pollinator dependant crops has resulted in greater demand for and decreased availability of honeybee colonies globally, and regional reductions in honey bee colony growth have lead to a need for more options for alternative managed pollinators (Aizen and Harder, 2009; Potts et al., 2010).

1.5. Bloom period and weather

Highbush blueberry in British Columbia (BC) is an early spring blooming crop with a relatively short bloom period during which weather conditions are not often conducive to

pollination (MacKenzie, 1997). The early bloom coincides with bumble bee queen emergence, the most commonly seen wild pollinators in highbush blueberry (Button and Elle, 2014; Mackenzie and Winston, 1984; Ratti et al., 2008). Research suggests that queen bumble bees may be especially tolerant to cold temperature stress (Owen et al., 2013). Temperature during bloom is an important consideration in crop pollination due to bee species having distinct thermal ranges in which they can fly. Bumble bee species typically have lower minimum temperature thresholds relative to honey bees (Corbet et al., 1993), and these foraging windows (dictated by environmental variables) can affect pollinators' ability to pollinate. In Michigan (United States of America, USA), highbush blueberry fields have honey bees as the dominant flower visitors during favorable weather, while bumble bees are more common in poor, wet and cold conditions (Tuell et al., 2009). Depending on environmental variables during the bloom period (such as precipitation and average daily temperatures), seasonal community composition of pollinators visiting highbush blueberry may vary sufficiently to cause variation in yield.

Weather may also affect other aspects of pollinator foraging behaviour that can result in the variable pollination of crops. In warmer temperatures, the pollen and nectar loads of some solitary bees have been shown to be larger than those gathered during cooler conditions (Stone, 1994). The rate of flower nectar secretion and sucrose concentration are also influenced by environmental variables such as humidity and temperature, allowing the plant to modulate the quality of the resource (Bertsch, 1983; Corbet et al., 1993; Southwick et al., 2016). These changes in the quantity and concentration of nectar produced throughout the day can affect the diversity of flower visitors, as well as foraging choices of individuals that will focus on either nectar or pollen (Corbet, 1978).

The highbush blueberry bloom period represents one of the first mass flowering resources of the season in BC and has likely become an important foraging resource for bumble bees in the agricultural landscape. This may be especially true for queens that are beginning to initiate colonies and whose future reproductive success will depend on the bloom (Bowers 1986). Flowering phenology in Canada is shifting towards an earlier bloom, with this change being driven by mean annual temperature (Gonsamo et al., 2013). The early nature of the blueberry bloom and its potential for shifting even earlier, coupled with variable pollination due to changing environmental variables, creates plant-pollinator relationships that are likely sensitive to even minor perturbation.

1.6. Resources in the agroecosystem landscape

The landscape surrounding a farm represents a potential refuge from farm practices such as pesticide use and contains a variety of resources, making this habitat ideal for many of the beneficial insects in agroecosystems. The practice of enhancing habitat in order to increase the biodiversity of beneficial insects in farm landscapes is becoming increasingly popular, and research has demonstrated the potential to enhance beneficial insect biodiversity through increasing landscape resource diversity with the planting of hedgerows and other non-crop species (Morandin and Kremen, 2013; Pontin et al., 2006; Tews et al., 2004). Larger farm landscapes with a high proportion of wooded habitat, low management grassland or agriculture, and increased semi-natural habitat, are also linked to more diverse and abundant insect communities (Giulio et al., 2001; Holland and Fahrig, 2000; Holzschuh et al., 2010, 2007; Marino et al., 2013). Enhancements and conservation of semi-natural land can result in greater levels of ecosystem service delivery, as pollination and/or pest control is improved when a sufficient amount of semi-natural land is present to support beneficial insects (Landis et al., 2005; Menalled et al., 2015; Ricketts et al., 2008). To better preserve or enhance beneficial insects, the effects of land use types on different guilds of insects must be understood for more agroecosystems, and with an explicit consideration of scale.

In a study of insect communities in cereal crops and grassland, functional groups of predators and herbivores responded to landscape features at different scales (Batáry et al., 2012). Differences in the ability of different insects to exploit resources in a landscape can be a product of behaviour, physiology, foraging ranges or other characteristics unique to a species. Even among relatively similar species exploiting the same type of resource, species characteristics can alter their use of a landscape. Pollinator foraging studies demonstrate that honey bees have the ability to communicate areas of high floral resource diversity via waggle dancing (Couvillon et al., 2014). This ability does not exist in *Bombus* species, as foragers can only induce foraging on resource-rich patches via an increase in the generalized foraging activity of their colony mates by moving across the nest while vigorously fanning their wings (Dornhaus and Chittka, 2001). Variability in the response to elements in the landscape by beneficial insects is important in the context of ecosystem service delivery.

1.7. Field selection and layout

My research was performed in the lower Fraser River Valley of British Columbia, Canada. Highbush blueberry is a major fruit crop cultivated between Richmond in the west into Abbotsford and Chilliwack in the East of the Fraser River Valley. Because weather and landscape vary over this region, I selected multiple fields for study in each of six broadly defined municipalities for study (Fig 1.1). Final sample size was reliant on identifying farmer-cooperators that grew a particular cultivar ('Bluecrop') chosen both to standardize the study and because it was known to experience pollination deficits (Button and Elle 2014). Sample size was also dependent on our ability, with two teams of researchers, to collect adequate data to meet my objectives over the short (3-4 weeks) bloom period of this crop.

Fields were selected based on having multiple acres of the cultivar 'Bluecrop'. A one hectare square plot was delineated within each field for all insect collection and pollination experiments. Plots were chosen within larger blocks of 'Bluecrop', with one side of the plot being along a farm edge adjacent to unmanaged land (roads, dykes, natural habitat, etc.). Sampling occurred on four transects, at this semi-natural edge (0m) and at 25m, 50m, and 100m into the crop (Figure 1.2). These four transects represent the areas where the majority of data was gathered for insect surveys and pollination deficit experiments, as described in subsequent chapters.

1.8. Thesis aims

In this thesis I investigate the pollination ecology of highbush blueberry to better understand the multiple factors that might affect the yield and pollination of the crop in the BC lower mainland. In Chapter 2, I utilize surveys of pollinators, terrestrial predators, and aerial predators to determine whether landscape composition at different scales is linked to beneficial insect community composition. In Chapter 3, I use four years of pollination experiment data to investigate the relationships between highbush blueberry yield deficits, pollinator diversity, landscape composition and weather variables. Using Akaike's Information Criterion (AIC) alongside model averaging, I identify the components of the blueberry agroecosystem most likely to predict variation in blueberry yield deficit. Chapter 4 consists of a two year trial of two newly developed commercial bumble bee pollinator species, where I determine whether the addition of these new managed pollinators

mitigates yield deficits in highbush blueberry, as well as identify whether colony growth characteristics are predictive of pollen foraging recruitment. To better understand pollen foraging in three managed pollinators species in highbush blueberry, Chapter 5 explores differences in the composition of pollen loads being returned to honey bee and bumble bee colonies. My research aims to advance the capacity of farmers and agricultural consultants to develop pollination strategies that are responsive to the greater landscape in which farms are imbedded, as well as to the yearly variability in weather during the bloom period. In addition, through studying the managed pollinators available to highbush blueberry, we can inform future developments of new commercially managed pollinators to meet the growing needs of highbush blueberry pollination.

1.9. References

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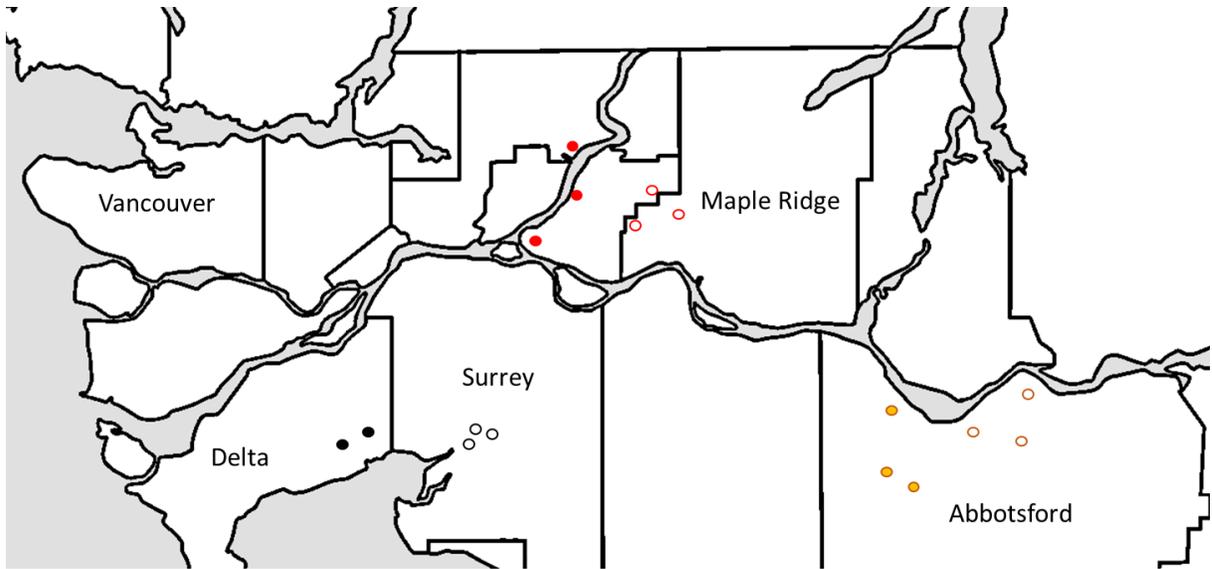


Figure 1.1 Map of blueberry field site locations. Each group (colour and fill) represents one of the major municipalities where highbush blueberry is grown in the Fraser Valley.

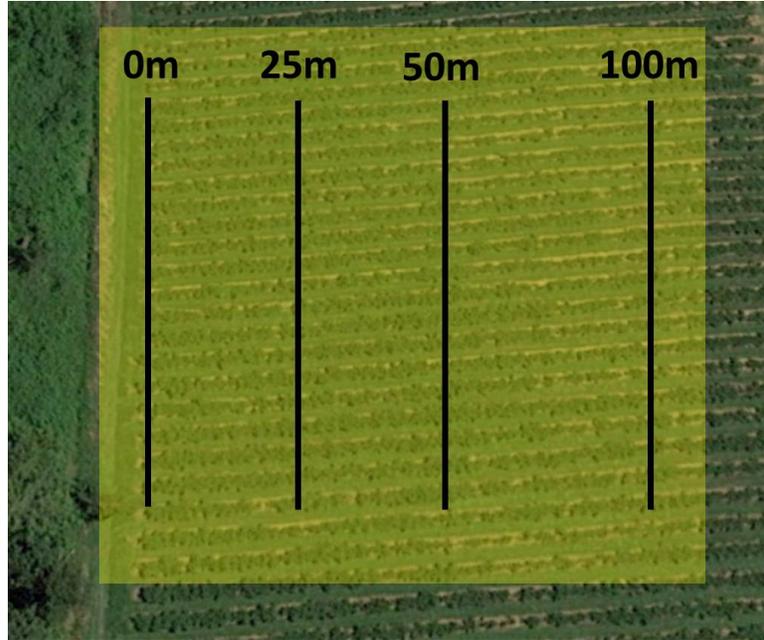


Figure 1.2 Field layout for insect and pollination experiments. Shaded square represents a one hectare plot containing four transects starting at 0m (farm edge) and progressing into the interior of the crop at 25m, 50m and 100m intervals. In some farms the sampling was “across” rows as shown here, and at others sampling was “along” rows, depending on the location of the most natural farm edge.

Chapter 2. Scale and functional group interactions affect insect community composition in agroecosystems

2.1. Introduction

The relationship between habitat and insect community composition is key to understanding biodiversity patterns, as well as the ecosystem services insects might provide. A key feature of many insect communities is the positive response in diversity or abundance with increasing proximity to natural areas such as forest fragments or areas with low management intensity (Hendricks et al. 2007, Tscharrntke et al. 2008). Across a wide range of vertebrate and arthropod species, habitat heterogeneity and particular key elements (i.e. richness) in vegetation found in the landscape are the most common positive drivers of animal diversity (Tews et al. 2004). However, when arthropod diversity responses to landscape are analyzed across multiple functional groups, opposing responses can be found among different groups and study regions (Jeanneret et al. 2003, Tews et al. 2004, Menalled et al. 2015). This complicates conservation planning in natural habitat remnants as species occupying different trophic levels may respond differently to conservation practices (Stoner and Joern 2014). Increasingly, the enhancement of habitat biodiversity on farmland is being pursued to improve ecosystem service delivery to crops (Swinton et al. 2007, Isaacs et al. 2009, Wratten et al. 2012) and other degraded ecosystems (Benayas et al. 2009). The most common methods for this involve restoring farmland to a previous state or enhancing particular characteristics (ex. vegetation diversity) of a landscape to recruit or maintain biodiversity (Bullock et al. 2011).

Farms benefit from a variety of insects that provide services to agricultural production such as pollination and pest predation. In the U.S. it has been estimated that farmers could face increases in production costs or losses in production that would total up to \$57 billion USD in a scenario of no or reduced beneficial insect service provision to agriculture (Losey and Vaughan 2006). Beneficial insects fill various ecological roles on farms. Flower visiting insects like bees can provide pollination service to crops, and low pollinator diversity or low visit rates are associated with low crop yield (Hoehn et al. 2008, Garibaldi et al. 2014). Predators, parasitoids and pathogens provide natural pest control; for instance, in the absence of terrestrial predators, yield losses caused by barley aphids

can be as high as 52%, (Östman et al. 2003), and experiments on alfalfa (*Medicago sativa*) have demonstrated that certain multispecies combinations of pea aphid predators can control the pest at levels higher than would be predicted additively (Cardinale et al. 2003). Providing a landscape that is capable of sufficiently supporting abundant and diverse insect communities can maximize the value received from the local beneficial insect species. However, the maintenance of this beneficial relationship has been put at risk by contemporary land development and intensification.

The link between biodiversity and ecosystem function has been explored and supported in a wide range of systems (Swift and Anderson 1994, Loreau et al. 2001, Tilman et al. 2013). Agricultural landscapes present a useful study system to develop our understanding of insect responses to changes in habitat due to the ubiquitous nature of agriculture and varying degrees of intensity across the globe. Agroecosystems are readily accessible as agricultural intensification is the most common modification of the planet's terrestrial biosphere with 22% of land cover being occupied by pasture, while 15% of land is dedicated to crops (Ramankutty et al. 2008). Increasing proportions of agricultural land in a landscape have been linked to decreases in species richness (Gibbs et al. 2009). More specifically, intensifying agricultural practices on a farm has been demonstrated to reduce species diversity of beneficial insects (Hendricks et al. 2007). This decrease in beneficial insect species richness can reduce potential gains in production, because ecosystem function diminishes with species or abundance loss.

The variety of landscapes in which farms are embedded also allows researchers to identify a variety of insect diversity and ecosystem service delivery trends related to landscape diversity (Kennedy et al. 2013), patch isolation (Jonsen and Fahrig 1997, Kruess and Tscharntke 2000), landscape complexity (Marino et al. 2013), management intensity (House and Stinner 1983) or patch size (Tscharntke et al. 2002). The influence of landscape elements on beneficial insect behaviour varies with foraging range, likely linked to both insect perception of the landscape and access to surrounding areas. From the perspective of different beneficial insects, the same landscape may be offering vastly different resources and presenting unique challenges, linked to foraging ability. As central place foragers, bees minimize their energy expenditure by foraging at fairly predictable distances from their nests. The relative size of a bee is a good predictor of foraging range (Greenleaf et al. 2007). Smaller solitary bees commonly forage at ranges under 400m (Zurbuchen et al. 2010) while some species of bumble bees forage at ranges beyond

500m and as far 1750m (Walther-Hellwig et al. 2000). Basically, bumble bees are foraging at a regional scale. Less work has focused on foraging distance of predators and parasitoids. Radio transmitter studies of carabids (ground dwelling predators) indicate daily movement within the landscape to be no greater than 200m (Hedin and Ranius 2002). Parasitoids like ichneumonid wasps are also difficult to track in the landscape, but studies of yearly expansion of introduced species has shown the potential for species to expand their range by up to 8.6 km per year, most of which is done via walking (Price, 2000). Thus predators and parasitoids are likely foraging more locally. By studying a range of beneficial insects with a variety of foraging ranges we can identify land-use types at various scales that influence the composition of insect communities that can benefit farmers.

The aim of this research is to determine whether highbush blueberry farms (*Vaccinium corymbosum*) in British Columbia's Lower Mainland differ in their beneficial insect communities, and whether those differences are related to the landscapes within which the farms are embedded. To accomplish this, I sampled insects from 11 different fields using three trapping methods (netting, pitfall, and sticky traps) that sampled pollinators, ground-dwelling predators, and parasitoids respectively. I compared beneficial insect species composition among sites and analyzed the surrounding landscape at local and regional scales to evaluate whether the landscape surrounding farms influenced the composition of insect communities. Specifically, I tested the following predictions:

- i) Natural habitats near farms are stronger predictors of insect community composition than disturbed habitats.
- ii) Agricultural intensification reduces beneficial insect abundance and diversity.
- iii) Pollinators will respond to landscape elements at a regional scale.
- iv) Predators and parasitoids will respond to landscape elements at a local scale.

2.2. Materials and Methods

2.2.1. Study Area

Our study area ranged from farms located in the Greater Vancouver area to the Southwestern portion of the Fraser Valley in British Columbia, Canada. In the Fraser Valley, 70% of farmland is comprised of forage and pasture, with blueberry fields being the second most common agricultural land use type at 16% of cultivated land (Fraser Valley Regional District, 2016). In our study, focal blueberry farms varied in size from 2 to 9.1 hectares and were separated by a minimum of 1.8 kilometers. The areas sampled for beneficial insects on each farm were within 1 hectare blocks of the highbush blueberry variety 'Bluecrop', a common mid-season cultivar in the region.

2.2.2. Insect Sampling

Pollinators

During the 2014 and 2015 highbush blueberry bloom we sampled floral visitors with 10 minute surveys on each of four 50 m transects per field, where pollinators were collected with aerial nets at the farm edge (0m), 25, 50 and 100 meters into the crop (Figure 1.2). Insect collection was conducted during suitable bee foraging weather (>15.5°C, minimal wind and no precipitation) with all observed floral visitors collected except the managed honey bee, *Apis mellifera*. Three collections were conducted at each site on different days during the highbush blueberry bloom between mid-April and the middle of May (total sample time = 3 dates x 4 transects x 10 min = 120 min per field). The three collections at a site were rotated among morning (10 AM – 12 PM), midday (12 PM – 2 PM), and afternoon (2 PM – 4 PM), with the timing of sampling and order of sampling of multiple fields randomized among collection dates to account for any variation in the foraging timing of insects. Insects were euthanized, and timers were stopped during insect processing. Insects were later identified in the lab to the lowest taxonomic level possible.

Aerial Pest Predators

Sticky traps have been demonstrated to be an effective method to trap pest predators (Maredia et al., 1992; Stephens and Losey, 2004). Pest predator collections were made at 11 of 12 highbush blueberry fields using 25 x 15 cm double-sided yellow

sticky traps (Bugscan brand). Nine sticky traps were placed on the same transects where pollinator sampling occurred, with three sticky traps placed along each of the three transects. Sticky traps were placed in the field in the morning (day 0) and remained in the field until day 7. Collections were conducted at three time points during the growing season: end of bloom, mid-summer and late summer. Once the traps were collected, they were frozen until insects were counted and assigned to the lowest taxonomic level possible via morphological identification.

Ground Dwelling Pest Predators

At each of the 11 sites, three 8.9 cm diameter plastic cups were placed along each of the three transects used for sticky trap and pollinator sampling. The traps were filled with ethylene glycol and placed under the canopy of highbush blueberry plants. Pitfall traps were installed early morning (day 0) and remained in the field till day 4. Two collections occurred during the 2014 season during the end of bloom and during mid-summer. In 2015, three collections were made: end of bloom, mid-summer and end of summer. Samples were sorted in the field and identified to the lowest taxonomic level possible in the lab.

2.2.3. Landscape Characterization

To understand the effects of regional and local landscape composition on the diversity and abundance of insects found in our fields, we identified land cover in circles of 2000m (regional) and 300m (local) radii extending from the center of each 1-ha block where insects were sampled on farms. Using land cover layers for the region (GeoBase Canada, NRC 2015), we categorized landscape in six categories for our 2000m radius: pollinator 'Rewarding agriculture' (crops frequented by bees), 'Forest', 'Other agriculture', 'Pasture/fallow', 'Wetland' and 'Urban' (Table 2.1). Using ArcGIS (ESRI Inc, 2015) and maps of our farm fields at a 1:2000 scale, we hand digitized land use for the 300m radius into one of five categories: 'Rewarding agriculture' (crops frequented by bees), 'Forest', 'Other agriculture', 'Wetland' and 'Urban' (Table 2.2). At the local scale no pasture or fallow fields were detected resulting in one fewer category at this scale. These major land use categories were condensed from 17 predetermined more specific land use types to allow a comparison of more naturalized landscapes ('Forest', 'Pasture' and 'Wetland') with disturbed landscapes ('Agriculture' and 'Urban').

2.2.4. Analysis

We used three Multivariate ANOVAs (SAS Institute 2016), one for each sampling method, to examine whether insect community composition varied among our 11 sites. This analysis was performed using site and year as random effects. Insect diversity is represented by a total of 31 insect categories (Tables 2.3) encompassing species or morphospecies pooled from each site with each category having a minimum of 5 insects. Species were categorized into functionally similar groups to reduce loss of specimens, and rarer species that could not be incorporated into a generalized insect category were omitted from the analysis.

To analyse similarity in species composition among our farms we performed Non-Metric Multidimensional Scaling (NMDS) using the Vegan package in R (version 3.4). We conducted the NMDS using the abundance of 31 classes of beneficial insects collected across two years from 11 farms. We added vectors using the proportion of landscape occupied by the six land-use types at the regional scale, and five land-use types at the local scale (Tables 2.1 and 2.2). Landscape vectors were fitted to the NMDS plot using the envfit function (Oksanen et al, 2013).

NMDS analyses were then further refined to include only species that are the most likely to provide ecosystem services in sufficient quantities to highbush blueberry (Table 2.4). Among pollinator species only bees from the genus *Bombus* were selected due to being effective *Vaccinium* pollinators (Javorek et al., 2002) and sufficiently abundant in our fields. Predators and parasitoids species captured via sticky and pitfall trapping were only included in the refined NMDS based upon providing a life long pest reduction services (ex. *Amara* sp. are not included due to only larva being insect predators and adult seed predators).

To aid in interpretation of the NMDS, we additionally performed linear regressions using the lme4 function in R to evaluate whether the abundance and richness of insects caught using each collection method was related to the proportion of the 11 land-use types present at our two distances, regional (2000m) and local (300m).

2.3. Results

Pollinators were the most abundant and diverse of the beneficial insects captured, with the most diverse field having 26 species of pollinators (Figure 2.1). Species captured via pitfall traps were less diverse (11 morphotypes or species) consisting primarily of Carabidae and other Coleoptera, and a smaller number of predaceous Hemiptera. Insects sampled via sticky traps were the least diverse, primarily due to our inability to differentiate Ichneumonidae species due to the trapping method. The sticky cards were effective in capturing 7 morphotypes aerial predators and parasitoids, a variety of Coleoptera (Coccinellidae, Staphylinidae and Carabidae), and hemipterans, but given the sticky substance on the cards anatomical differences were obscured. Because some species were rarely collected, we categorized insects into groupings (e.g. all small syrphids were amalgamated). Pollinator captures were classified into 13 groups, while insects from pitfall traps were classified in 11 and insects captured on sticky traps were classified into 7 groups (Table 2.3). Our MANOVA analysis of these groups indicated that farms differed significantly in the composition of: pollinators (Wilks' Lambda=0.13, $F_{11,143} = 2.58$, $P < 0.001$), insects from pitfall traps (Wilks' Lambda=0.39, $F_{11,121} = 3.29$, $P < 0.001$) and insects obtained via sticky trapping (Wilks' Lambda=0.34, $F_{10,90} = 3.29$, $P < 0.001$).

At the regional scale, 'Urban' was the most common landscape type, taking up 41.1 ± 9.0 %, while 'Other agriculture' remained uncommon, at 5.4 ± 4.0 %. At the local scale, 'Rewarding agriculture' (which includes highbush blueberry) was the most common landscape type, occupying 47.6 ± 7.9 % of the entire area, while 'Other agriculture' was the least common landscape type and the most variable, occupying 11.7 ± 10.9 % (Table 2.1).

Using nonmetric multidimensional scaling (NMDS) at the regional scale we found both 'Pasture/fallow' ($p=0.028$) and 'Other Agriculture' ($p=0.04$) were significantly correlated with the differences in community composition among sites (Figure 2.2). When looking at only the 20 most abundant beneficial insects present in sufficient quantities to provide agronomic measurable levels of ecosystem services only 'Other Agriculture' ($p=0.017$) is significantly correlated with differences in the community composition of insects at the regional scale (Figure 2.4). Linear regression predicts that 'Pasture/fallow' was associated with greater total beneficial insect abundance, and greater pollinator abundance, while pitfall species richness was only marginally positively associated with it

at 2000m (Table 2.5). 'Other agriculture' was significantly positively associated with total pitfall species richness and marginally negatively associated with pollinator species richness at 2000m. 'Forest' was also marginally associated with increases in pollinator species richness at 2000m.

At 300m, 'Forest' had the largest coefficient of determination ($r^2=0.46$, Table 2.5), however, no land-use type was significantly correlated with the insect community composition dissimilarity on farms in our NMDS analysis (Figure 2.3). When looking at only the 20 most abundant beneficial insects present in sufficient quantities to provide agronomic measurable levels of ecosystem services 'Other Agriculture' ($r^2=0.5$, $p=0.056$) had the highest coefficient of determination though it was marginally non-significantly correlated with differences in the community composition of insects (Figure 2.5). Linear regression models illustrated a negative relationship between total beneficial insects and proportion of 'Rewarding agriculture' at the local scale. Pollinator species abundances also decreased with increasing 'Other agriculture' at 300m (Table 2.1). In contrast, total pitfall insects increased as 'Other agriculture' increased. The proportion of 'Wetland' was positively associated with total species richness and total pollinators also increased with a greater proportion of 'Forest' at the local scale.

2.4. Discussion

Highbush blueberry agroecosystems vary in beneficial insect diversity

Beneficial insect communities are present in the highbush blueberry agroecosystem despite the relatively high management intensity required to manage pests and pathogens throughout the year. Pollinator species richness varied the greatest between field sites, as one single field had double the number of species as the other 10 fields and five times the species richness of the field with the lowest pollinator biodiversity. Variations of this magnitude did not occur in our other functional groups of beneficial insects (ground predators or aerial predators and parasitoids). The large variability in pollinator diversity can potentially be a product of sampling from differentially sized species pool in regions with the most rich pollinator communities occurring in areas with greater diversity. However, a more likely scenario deduced via our observations and previous work done in the area suggests that the uniqueness of the non-crop habitat surrounding particular speciose fields might play a larger role.

Insect communities largely respond to regional landscapes

Our sampling methods demonstrate that beneficial insects respond to landscape elements in different ways. In our study, we found that netted (pollinators) and pitfall-trapped (predators) insects had significant responses to different landscape elements, but we did not find significant results for sticky-trapped insects. Only at a regional scale were any of our land-use types found to be significant predictors of insect community dissimilarity on our blueberry farms. 'Pasture' represents a relatively low management land use type in our region, while 'Other agriculture' consists of heavily managed agriculture lacking in floral resources. The significance of landscape on community composition at regional scales was predicted to have a strong effect on pollinator communities due to their larger foraging range and ability to access and evaluate habitat at the regional scale. However, our results suggest that regional land use is just as likely to affect terrestrial predators with limited mobility such as carabids. The differences in mobility between pollinators (flight) and terrestrial predators (primarily walking) coupled with the differences in their resource use and natural history might help us understand the response of various diversity metrics to particular land use types at both regional and local scales.

Abundances of different types of beneficial insects respond differently to different landscape elements at the regional scale (2000m)

'Pasture/fallow' land on a regional scale was a significant predictor for the abundance of total beneficial, netted and pitfall trapped insects, and marginally related to sticky trapped insects. Our results correspond with other studies that have found that grasslands and low management pastures have a greater abundance of beneficial insects (Hymenoptera, Lepidoptera) relative to pastures that are frequently grazed (Kruess and Tschardtke, 2002). In areas where major agricultural resource pulses occur, bumble bees become more abundant in areas rich in pasture, fallow and floral resources as these landscapes represent areas with resource constancy (Persson and Smith, 2013). The value of 'Pasture/fallow' landscapes is amplified in highbush blueberry agricultural regions as the bloom duration is approximately a month in early spring, resulting in a major landscape feature being bereft of floral resources throughout the rest of the growing season and under constant disturbances due to farm management. Low management intensity agriculture land-use like pasture has also been shown to positively influence pollinator diversity and abundance at larger landscape scales (700m) relative to smaller

ones (Hines and Hendrix, 2005). Interactions at the regional scale should be expected as pollinators exhibit greater foraging range than terrestrial predators with modeled foraging distances of bumble bees being economical at spans of several kilometers (Cresswell et al., 2000). As such, relationships with floral resources and their diversity (Ghazoul, 2006) or distribution (Essenberg, 2012) occur over a wider range of space and potential land-use types than found for natural enemies.

Despite their relatively poor mobility, the abundance of insects captured using pitfall traps increased in response to an increase of 'Pasture/fallow' land at the regional scale. The importance of landscape on carabid species composition is higher in farm areas with high disturbance and management intensity, such as field cropped to cereals (Weibull and Östman, 2003). Previous work has shown that ground beetles tend to be more diverse and abundant in pasture that is not heavily cultivated or treated with pesticides (Luff and Rushton 1989, House and All 1981), while other coleopteran predators such as coccinellids respond to habitat fragmentation at regional scales (Stoner and Joern, 2014). In our region, 'Pasture-fallow' areas are among the least disturbed habitat types. The regional effects of increased pasture on the number of ground predators in relation to pasture suggest that the value of low managed agricultural land is increasingly high due to the lack of nearby natural or semi-natural areas.

The influence of 'Other agriculture' on beneficial insects at the regional scale differed for our functional groups, likely due to the resources made available by different cropping systems. 'Other agriculture' was significantly positively correlated with the total abundance of ground predators while pollinator species richness declined (the latter was marginally non-significant). Carabid beetles are relatively common in conventional agricultural fields (Weibull and Östman, 2003) with farm practices such as tillage having little to no effect on species richness (Cárcamo et al., 1995). In other common ground predators, such as spiders, habitat complexity and organic agriculture enhanced predator density (Schmidt et al., 2005) offering a greater variety of resources. The mechanism for increasing ground predators with higher proportions of 'Other agriculture' in our study is not known, and further work could aim to determine this. We had anticipated that 'Other agriculture', which by our definition is crops that do not provide resources for pollinators, would be negatively related to pollinator abundance. Indeed, our data suggest that increasing agricultural density with crops of little to no value for pollinators may result in a decrease in pollinator species richness regionally.

At a regional scale, the relationship between the proportion of forest in the landscape and the species richness of pollinators was positive but marginally non-significant, in contrast to previous work (Gibbs et al., 2016). In coffee agroecosystems, the social bee species diversity declines in crop fields further from forests (Klein et al., 2003). The relationship between forest fragments and high pollinator diversity is highly valuable, significantly enhancing the stability and quantity of pollination services (Taylor H. Ricketts, 2004). In these agroecosystems, forests provided important nesting resources for pollinators important to coffee (Klein et al., 2003), however, differences in nesting strategies among bees in specific communities might influence the role or strength of the relationship of forests with bee diversity. The importance of natural habitat on species composition in communities likely varies based on species identity. The foraging resource value of forested areas surrounding blueberry fields in our region is poor relative to that of floral resource rich areas such as meadows and grassland. However, forest edges are likely areas of high floral diversity due to less canopy cover and have been shown to be important nesting areas to particular bumble bee species (Kells and Goulson, 2003). Further studies on how our regional pollinator community interacts with forest boundary habitat may clarify the lack of strong relationship between this land-use type and pollinator communities.

Agriculture at small scales (300m) may dilute beneficial insect abundance, with different responses by different insect groups to landscape elements

At local scales the presence of rewarding agriculture with an abundance of floral resources resulted in a dilution in the total number of beneficial insects we found on farms. The strong dilution effect of total beneficial insects seen in our data at 300m is similar to dilutions seen in previous studies, where pollination of both a crop and a native species decreased in the presence of mass flowering canola in Germany (Holzschuh et al., 2011). The presence of extensive mass flowering crops can also result in higher bumble bee densities (Westphal et al., 2003), but not in our study, where the high floral density of 'Rewarding agriculture' was not sufficient to mediate the negative correlation between total beneficial insects and rewarding agriculture. Our findings may reflect the documented poor value of floral resources provided by highbush blueberry (Somerville and Nicol, 2006), resulting in a landscape of abundant but low quality resources.

In contrast, total beneficial insect abundance increased with the amount of wetland in the local landscape. In British Columbia's lower mainland, highbush blueberry field

margins often abut drainage ditches, dykes and sloughs. These unmanaged areas frequently have greater floral diversity relative to cropland, often being representative of the pre-development flora (Herzon and Helenius, 2008), and their minimal management by farmers can result in a wide array of other resources (alternative prey, nesting sites, overwintering sites, etc.). Woody wetlands have also been shown to be among the most suitable habitats for pollinators in a model developed to determine the effects of landscape composition on bee species richness (Kennedy et al., 2013) .

Similar to trends at the regional scale, ground predator insect abundance increased with 'Other agriculture' and pollinator abundance decreased (this time highly significantly). Though positive responses were seen with 'Other agriculture' at both scales for predators, responses to 'Other agriculture' may differ in predators of different size classes, with larger, less mobile beetles being more susceptible to habitat degradation than smaller, more mobile species who tend to increase in abundance at degraded sites. At the 300m scale, these smaller carabid species may in fact be those benefitting from the increase in 'Other agriculture' near our blueberry farms, while the larger species, or those more sensitive to habitat disturbance, increase in areas of highly unmanaged pasture at the regional scale. The effect of low management pasture, or the presence of other forms of agriculture may also be benefitting carabids through enhancing sources of prey within the fields, providing a richer diversity of natural prey and pest items in a diverse pasture (Holopainen, 1986). In contrast, increasing agricultural intensity reduces the availability of resources for pollinators (Le Féon et al., 2010). Higher agricultural intensity also increases the likelihood of more frequent pesticide application, which is strongly associated with a reduction in pollinator diversity (Brittain et al., 2010). The difference in local access to resources for ground predators (resources increase) and pollinators (resources decrease) is likely a key driver in their differential responses to increased amount of 'Other agriculture' at local scales.

At the local scale, unlike at the regional scale, the amount of 'Forest' in the landscape was a strong positive predictor of pollinator abundance. The increasing complexity and heterogeneity added to landscapes by unmanaged forests and marshy habitat benefit pollinators, as their mobility allows them to perceive and access a greater area of the resource landscape relative to less mobile beneficial insects (Tscharntke et al., 2005). Increases in 'Forest' at the local scale may result in a greater proportion of

pollinator species (local and regional foragers) being able to access important nutritional resources and potentially remain near agricultural crops that benefit from pollination.

Increasing intensification of the BC lower mainland agricultural landscape

Beneficial insects respond differently to different landscape types surrounding agroecosystems. In general, natural or semi-natural land (pastures, wetlands, forests) has a positive effect on insect abundance, but 'Rewarding' agriculture has a negative effect, and beneficial insect types respond differently to 'Other' agriculture. Since 2001, there has been a 322% increase (9,545 ha in 2017) in land dedicated to highbush blueberry agriculture in Canada (Statcan 2017). The increasing acreage of highbush blueberry and other forms of intensely managed agriculture in British Columbia's lower mainland risks reducing some functional groups of beneficial insects and the ecosystem functions provided by these insects. Agricultural development strategies should consider the effect of land modification at multiple scales on agricultural landscapes in order to allow the maintenance of biodiversity and continuance of ecosystem service provision.

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Table 2.1 Land-use type groupings and proportion of area occupied used for analysis obtained using ArcGIS at 2000m radii surrounding blueberry farms in British Columbia.

Distance	Initial GIS categorization	Land-use type group	Mean percentage of land use type (\pm S.D.)
2000m	Broadleaf	Forest	13.0 \pm 5.5
	Coniferous		
	Mixed wood		
	Shrubland		
	Fallow	Pasture/fallow	17.5 \pm 5.8
	Grassland		
	Pasture/Forages		
	Sod		
	Berries	Rewarding agriculture	42.1 \pm 9.1
	Blueberry		
	Cranberry		
	Fruits		
	Orchards		
	Other Fruits		
	Agriculture (undifferentiated)	Other agriculture	5.4 \pm 4.0
	Barley		
	Beans		
	Corn		
	Other Crops		
	Other Vegetables		
	Potatoes		
	Sunflower		
	Vineyards		
	Water		
	Wetland		
	Exposed Land/Barren	Urban	42.1 \pm 9.0
	Greenhouses		
Nursery			
Urban/Developed			

Table 2.2 Land-use type groupings and proportion of area occupied used for analysis obtained using ArcGIS at 300m radii surrounding blueberry farms in British Columbia

Distance	Initial GIS categorization	Land-use type group	Proportion of land use
300m	dev_wooded_low_IS	Forest	13.7 ± 9.9
	Shrub		
	sparse_scrub_weedy		
	wooded_deciduous		
	wooded_mixed		
	woodland_open		
	pasture_grazed	Pasture/fallow	0
	planted_non_ag		
	orchard_rewarding	Rewarding agriculture	47.6 ± 7.9
	annual_crop_non_flwring	Other agriculture	11.7 ± 10.8
	riparian_closed	Wetland	13.2 ± 3.9
	riparian_open		
	Water		
	Bare	Urban	13.9 ± 7.2
	dev_high_IS		
	dev_open_low_IS		
roads_paved			

Table 2.3 Identity of the insects collected through three sampling methods (pitfall trapping, sticky trapping and netting). The 'Identified' column represents that the level to which samples were identified post collection and 'Categorized' represents the grouping in which it was placed into for analysis.

Method	Identified (Species or morphospecies)	Categorized
Pitfall trapping	<i>Amara sp.</i>	<i>Amara sp.</i>
	<i>Carabus fuscipes</i>	<i>Carabus fuscipes</i>
	<i>Carabus granulatus</i>	<i>Carabus granulatus</i>
	<i>Carabus nemoralis</i>	<i>Carabus nemoralis</i>
	Coccinellidae	Coccinellidae
	<i>Harpalus affinis</i>	<i>Harpalus affinis</i>
	Hemipteran	Hemipteran
	<i>Pterostichus melanarius</i>	<i>Pterostichus melanarius</i>
	Staphylinidae	Staphylinidae
Sticky traps	Anthocoridae	Anthocoridae
	Carabidae	Carabidae
	Coccinellidae	Coccinellidae
	Hemiptera	Hemiptera
	Ichneumonidae and Vespidae	Ichneumonidae and Vespidae
	Odonata	Odonata
	Staphylinidae	Staphylinidae
	Syrphidae	Syrphidae
Netting	<i>Andrena angustifarsata</i>	<i>Andrena</i>
	<i>Andrena hemileuca</i>	
	<i>Andrena laminibucca</i>	
	<i>Andrena saccate</i>	
	<i>Andrena salicifloris</i>	
	<i>Andrena transnigra</i>	
	<i>Andrena vicina</i>	
	<i>Andrena w-scripta</i>	
	<i>Bombus flavifrons</i>	<i>Bombus flavifrons</i>
	<i>Bombus impatiens</i>	<i>Bombus impatiens</i>
	<i>Bombus melanopygus</i>	<i>Bombus melanopygus</i>
	<i>Bombus mixtus</i>	<i>Bombus mixtus</i>
	<i>Bombus vosnesenskii</i>	<i>Bombus vosnesenskii</i>
	<i>Halictus rubicundus</i>	Halictidae
	<i>Lasioglossum cressonii</i>	
	<i>Lasioglossum pacatum</i>	
	<i>Lasioglossum pacificum</i>	
	<i>Lasioglossum planatum</i>	
	<i>Lasioglossum zonulum</i>	
	<i>Osmia lignaria</i>	<i>Osmia lignaria</i>
<i>Platycheirus sp.</i>	Small Syrphid	
<i>Sphaerophoria philanthus</i>		
<i>Sphaerophoria sulphuripes</i>		
<i>Syrirta pipiens</i>		

<i>Eupeodes latifasciatus</i>	Medium Syrphid
<i>Eupeodes perplexus</i>	
<i>Eupeodes sp.</i>	
<i>Eupeodes volucris</i>	
<i>Helophilus fasciatus</i>	
<i>Helophilus latifrons</i>	
<i>Scaeva pyrastris</i>	
<i>Sphaerophoria sulphuripes</i>	
<i>Syritta pipiens</i>	
<i>Syrphus opinator</i>	
<i>Syrphus ribesii</i>	
<i>Syrphus torvus</i>	Large Syrphid
<i>Criorhina sp.</i>	
<i>Eristalis anthophorina</i>	
<i>Eristalis brousii</i>	
<i>Eristalis dimidiata</i>	
<i>Eristalis flavipes</i>	
<i>Eristalis tenax</i>	
<i>Merodon equestris</i>	Vespidae
<i>Dolichovespula arenaria</i>	
<i>Dolichovespula maculate</i>	
<i>Polistes dominula</i>	

Table 2.4

Identity of the insects collected through three sampling methods (pitfall trapping, sticky trapping and netting) that are the most likely to contribute towards ecosystem service (pollination and predation). The 'Identified' column represents that the level to which samples were identified post collection and 'Categorized' represents the grouping in which it was placed into for analysis.

Method	Identified (Species or morphospecies)	Categorized
	<i>Carabus fuscipes</i>	<i>Carabus fuscipes</i>
	<i>Carabus granulatus</i>	<i>Carabus granulatus</i>
	<i>Carabus nemoralis</i>	<i>Carabus nemoralis</i>
	Coccinellidae	Coccinellidae
	Hemipteran	Hemipteran
	<i>Pterostichus melanarius</i>	<i>Pterostichus melanarius</i>
	Staphylinidae	Staphylinidae
Sticky traps	Anthocoridae	Anthocoridae
	Carabidae	Carabidae
	Coccinellidae	Coccinellidae
	Hemiptera	Hemiptera
	Ichneumonidae and Vespidae	Ichneumonidae and Vespidae
	Odonata	Odonata
	Staphylinidae	Staphylinidae
	Syrphidae	Syrphidae
Netting	<i>Bombus flavifrons</i>	<i>Bombus flavifrons</i>
	<i>Bombus impatiens</i>	<i>Bombus impatiens</i>
	<i>Bombus melanopygus</i>	<i>Bombus melanopygus</i>
	<i>Bombus mixtus</i>	<i>Bombus mixtus</i>
	<i>Bombus vosnesenskii</i>	<i>Bombus vosnesenskii</i>

Table 2.5 *Linear regression of diversity and abundance metrics with proportion area of land use types in circles surrounding farms at either the regional (2000m) and local scale (300m). Only linear regressions with p-values < 0.07 are shown.*

Scale	Variables	r ²	p
2000m	Total beneficial insects ~ Pasture-Fallow	+ 0.26	0.049
	Total pollinators ~ Pasture-Fallow	+ 0.30	0.039
	Total pitfall insects ~ Pasture-Fallow	+ 0.24	0.056
	Total pitfall insects ~ Other agriculture	+ 0.78	<0.001
	Pollinator species richness ~ Other agriculture	- 0.22	0.067
	Pollinator species richness ~ Forest	+ 0.22	0.068
300m	Total beneficial insects ~ Rewarding agriculture	- 0.27	0.047
	Total species richness ~ Wetland	+ 0.43	0.01
	Total pitfall insects ~ Other agriculture	+ 0.73	<0.001
	Pollinator species richness ~ Other agriculture	- 0.32	0.031
	Total pollinators ~ Forest	+ 0.61	0.002

Table 2.6 *Linear regression of diversity and abundance metrics with proportion area of the top two land use types in circles surrounding farms at either the regional (2000m) and local scale (300m) for the land. Only land use types with the top two highest correlation coefficients from the NMDS analysis are shown for both scales.*

Scale	Variables	r ²	p
2000m	Total beneficial insects ~ Pasture-Fallow	+ 0.26	0.049
	Total species richness ~ Pasture-Fallow		0.48
	Total pollinators ~ Pasture-Fallow	+ 0.30	0.039
	Total pitfall insects ~ Pasture-Fallow	+ 0.24	0.056
	Total sticky trap insects ~ Pasture-Fallow		0.92
	Pollinator species richness ~ Pasture-Fallow		0.55
	Pitfall species richness~ Pasture-Fallow		0.28
	Sticky trap richness ~ Pasture-Fallow		0.44
	Total beneficial insects ~ Other Agriculture		0.09
	Total species richness ~ Other Agriculture		0.07
	Total pollinators ~ Other Agriculture		0.48
	Total pitfall insects ~ Other Agriculture	+ 0.78	<0.001
	Total sticky trap insects ~ Other Agriculture		0.55
	Pollinator species richness ~ Other Agriculture		0.067
	Pitfall species richness Other Agriculture		0.19
	Sticky trap richness ~ Other Agriculture		0.87
300m	Total beneficial insects ~ Other Agriculture		0.07
	Total species richness ~ Other Agriculture		0.27
	Total pollinators ~ Other Agriculture		0.51
	Total pitfall insects ~ Other Agriculture	+ 0.73	<0.001
	Total sticky trap insects ~ Other Agriculture		0.65
	Pollinator species richness ~ Other Agriculture	- 0.32	0.031
	Pitfall species richness Other Agriculture		0.13
	Sticky trap richness ~ Other Agriculture		0.5
	Total beneficial insects ~ Rewarding Agriculture	-0.27	0.047
	Total species richness ~ Rewarding Agriculture		0.61
	Total pollinators ~ Rewarding Agriculture		0.17
	Total pitfall insects ~ Rewarding Agriculture		0.16
	Total sticky trap insects ~ Rewarding Agriculture		0.82
	Pollinator species richness ~ Rewarding Agriculture		0.87
	Pitfall species richness ~ Rewarding Agriculture		0.77
	Sticky trap richness ~ Rewarding Agriculture		0.32

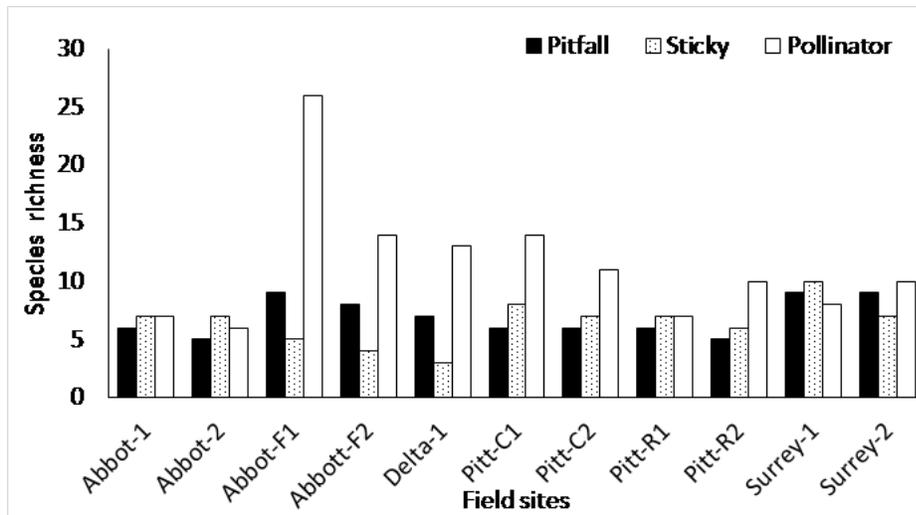


Figure 2.1

Total species richness of arthropods captured at 11 sites using three methods (netting off flowers, pitfall trapping, sticky trapping).

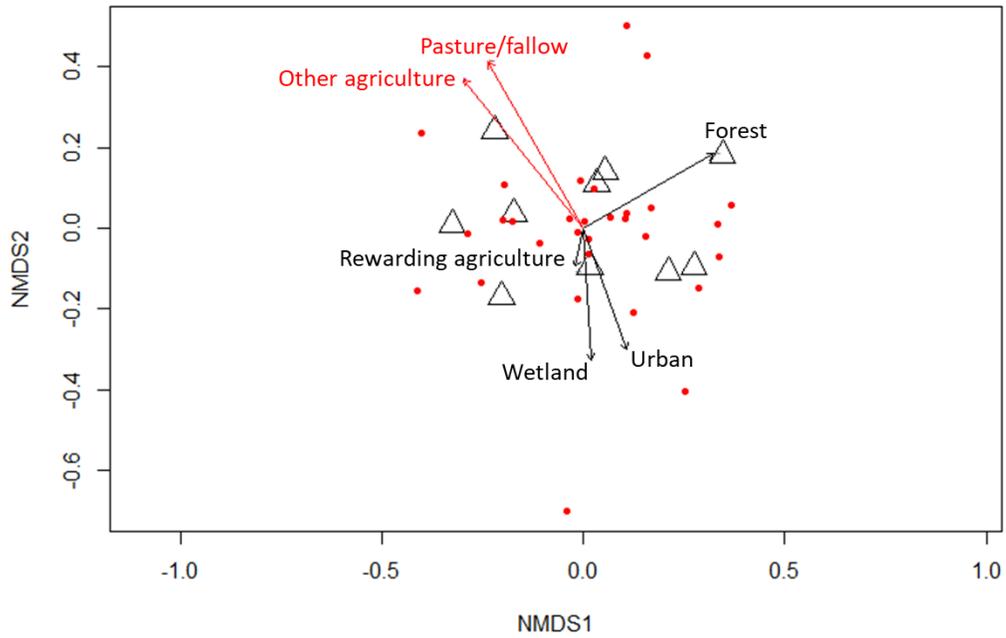


Figure 2.2 NMDS ordination plot (stress=0.19) of insect communities (triangles) at 11 field sites across 2 years with vectors of major landscape composition at a 2000m radius from the field. In red are 'Pasture/fallow' ($r^2=0.56$, $p=0.028$) and 'Other Agriculture' ($r^2=0.56$, $p=0.04$) which were the only significant environmental vectors correlated with insect community dissimilarity. Points represent the 31 classes of beneficial insect species

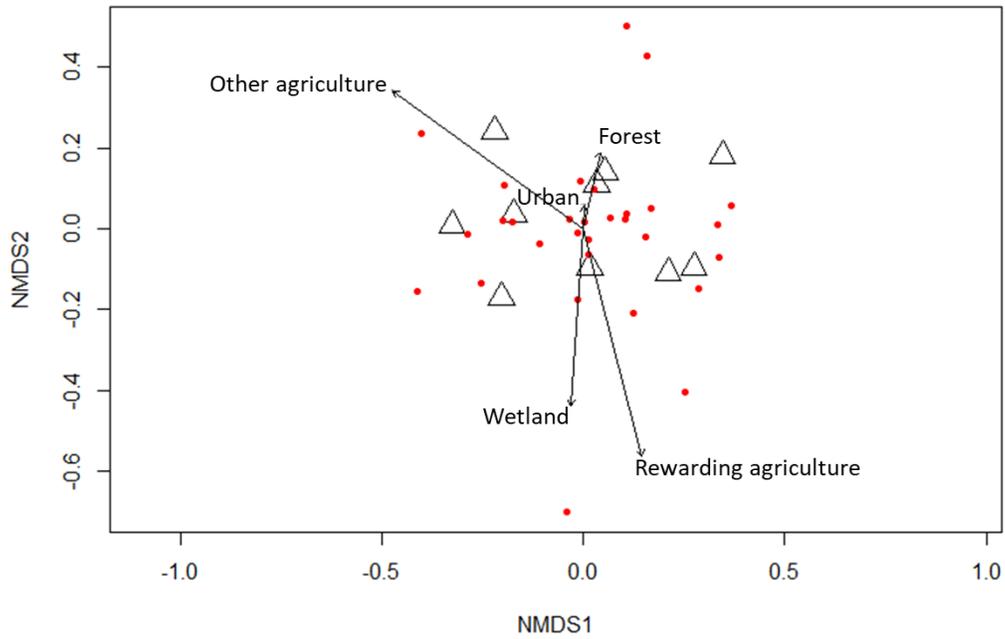


Figure 2.3 *NMDS ordination plot (stress=0.15) of insect communities (triangles) at 11 farms across 2 years with vectors of major landscape composition at a 300m radius from the field. The environmental factor with the highest coefficient of determination was 'Forest', however, it was not significantly correlated with insect community dissimilarity ($r^2=0.46$, $p=0.85$). Points represent the 31 classes of beneficial insect species.*

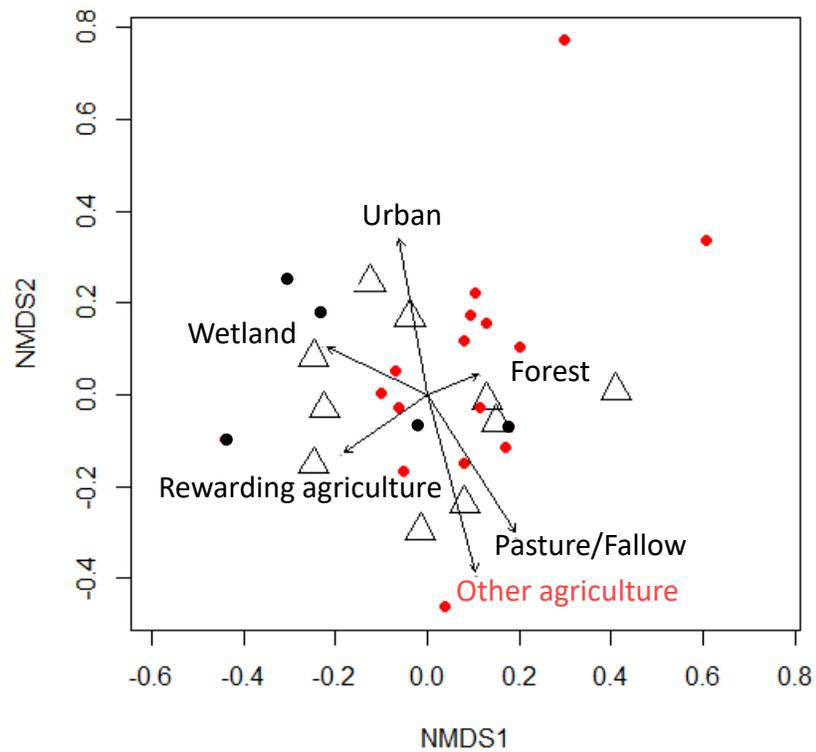


Figure 2.4 *NMDS ordination plot (stress=0.20) of insect communities (triangles) at 11 blueberry field sites across 2 years in British Columbia with vectors of major landscape composition at a 2000m radius from the field. In red is 'Other Agriculture' ($r^2=0.59$, $p=0.017$) which was the only significant environmental vectors correlated with insect community dissimilarity. Points represent the 20 classes of the most important beneficial insect species. Black points represent pollinators and red points represent pest predators.*

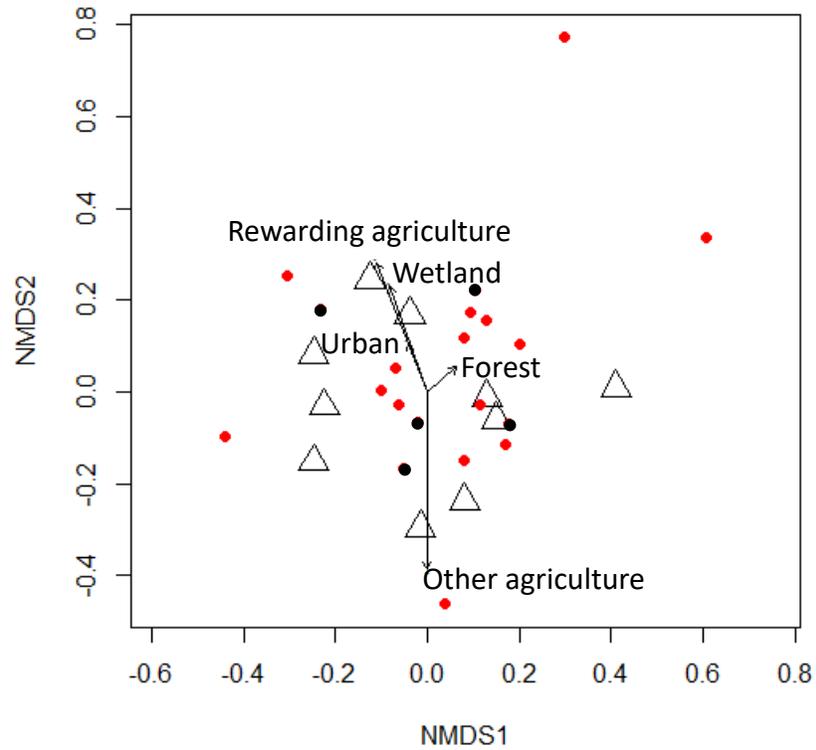


Figure 2.5 NMDS ordination plot (stress=0.17) of insect communities (triangles) at 11 farms across 2 years with vectors of major landscape composition at a 300m radius from the field. The environmental factor with the highest coefficient of determination was 'Other agriculture', however, it was not significantly correlated with insect community dissimilarity ($r^2=0.50$, $p=0.056$). Points represent the 20 classes of the most important beneficial insect species. Black points represent pollinators and red points represent pest predators.

Chapter 3. Bumble bee visit rates are predictive of yield deficits in highbush blueberry over four years

3.1. Introduction

Agricultural production in Canada is becoming increasingly diversified with a greater focus on fruit production. Since 2012, there has been a 6.2% increase in farmland dedicated to fruits, and a 7.1% increase in fruit farmgate value (Agriculture Canada 2016). Historically, fruit production and crop diversity have been limited in Canada relative to other growing regions due to cooler climate and lack of cold hardy varieties. Current global warming models predict a 3-5 week elongation of frost free seasons in Canada, potentially removing some climactic constraints of fruit and vegetable farming (Motha and Baier, 2005). These projections suggest that over time changes in the climate may allow even greater growth in the quantity and variety of fruit crops being farmed in Canada (Rochette et al., 2004). These changes in climate may have unforeseen consequences for fruit agriculture that depends on insect mediated pollination.

Many plant-animal mutualisms are reliant upon predictable phenology between both actors, such that shifts in life-history timing might result in pollinators without resources or plants without pollen distribution. Estimates of shifts in phenology due to climate change have demonstrated that resulting asynchrony between plants and pollinators can result in reductions in floral resource availability as high as 50% (Memmott et al., 2007). Mismatches in bloom and pollinator emergence are most problematic in early season plant-insect interactions as bloom time often correlates with snowmelt and unpredictable spring weather conditions (Hegland et al., 2009; Inouye, 2008; Thomson, 2010). Early flowering phenotypes are therefore especially sensitive to phenological mismatches, resulting in more frequent pollen deficits resulting from poor pollination (Thomson, 2010). These phenological shifts and differences in the ability of plants and pollinators to track preferred climactic envelopes threaten the stability in pollination service delivery to both wild and cultivated plants. For example, in Europe and North America, bumble bee distributions have not expanded to more northerly latitudes or up elevation gradients as distributions shrink in the warming southern extents of their range (Kerr et al., 2015).

Complementarity in pollinator service has been experimentally shown to be a product of diversity in the traits of pollinators, specifically when different species prefer to forage in distinct temperature ranges or on distinct flowers (Frund et al., 2013). Foraging behaviour can also change with other environmental variables; in Californian almond, honey bees preferentially visit flowers in the upper canopy but retreat downward in high wind condition (Brittain et al. 2010). This behaviour results in fields primarily stocked with honey bees having low yield when compared to fields with high pollinator diversity, which mitigates the loss of honey bee pollination in the upper canopy during periods of high wind in which honey bee foraging (and pollination) is reduced due to wind speeds (Brittain et al., 2010). Seed set in pumpkins has also been shown to be a product of diversity in functional traits with spatial, temporal and behavioural differences among pollinators the best predictor for success crop pollination (Hoehn et al., 2008). Understanding the response of agricultural pollinators to environmental variables is necessary to understand the variability in agricultural production systems, especially in a time of changing and variable climate.

Globally, there are indications of potential shortages of pollinators for agricultural pollination. The production of new honey bee (*Apis mellifera*) colonies is approximately three times less than the rate of demand for honey bees from new pollinator-dependent crop plantings (Aizen and Harder, 2009). Honey bees have become a necessity in much of North America's pollinator-dependent agriculture, despite wild pollinators being effective and sufficient pollinators in many cropping systems (Garibaldi et al., 2013; Holzschuh et al., 2012; Mallinger and Gratton, 2015). Much of the current increase in Canadian fruit production is due to increases in blueberry and cranberry acreage (AgCan 2016), both of which are highly dependent on managed and wild pollinators (especially bumble bees, *Bombus* spp.) to produce optimal yields (Aras et al., 1996; Button and Elle, 2014; Gibbs et al., 2016; Spivak, 2006).. Increased agricultural acreage in highbush blueberry therefore increases both the demand for managed honey bees, and minimizes habitat for wild pollinators that support fruit production (StatCan 2017). Numerous studies have demonstrated the importance of natural habitats near farms to support wild pollinators on-farm in agricultural systems (Carvalho et al., 2010; Gibbs et al., 2016; Kremen et al., 2004; Taylor H Ricketts, 2004). Furthermore, a study evaluating historical versus contemporary records of North American bumble bee species demonstrated a drastic decline in the ranges and abundances of multiple species (Cameron et al., 2011).

Biodiversity can mitigate phenological shifts as there is species overlap to cover any gaps in pollination delivery (Bartomeus et al., 2013), however, due to the relatively species poor pollinator community in Canada compared to the United States (Moisset and Buchmann, 2011; Richards and Kevan, 2002), pollination service delivery may not be resilient to change. Species poor communities, like those found in BC agriculture, may suffer inordinately in climate change scenarios due to the similarity in response by pollinators to changes in environmental variables. In blueberry, phenological mismatches or reductions in wild bumble bees have important consequences, as the most effective pollination occurs with bee species capable of sonication such as bumble bees (Javorek et al., 2002). To ensure sustainable production of highbush blueberry a thorough understanding of the dependence of blueberry yield on both managed and wild pollinators and the environmental variables associated with pollination service delivery is necessary.

Our study aims to characterize pollination deficits and variables that predict these deficits in highbush blueberry. We measured yield deficits for 17 fields of highbush blueberry cultivar “Bluecrop”. We use AIC model selection methods to evaluate the contribution of visit patterns by wild and managed bees, weather (temperature, rainfall), and surrounding landscape on inter-year variability in yield.

3.2. Materials and Methods

3.2.1. Field Sites

We conducted our study over 4 years (2013 – 2016) across the British Columbia Lower Mainland. Our field sites consist of conventional highbush blueberry farms extending from Delta, B.C. to Abbotsford, B.C. In the first three years of the project, 17 fields were surveyed; 11 fields were surveyed in the final year. Fields were chosen to ensure a minimal distance of 1.8km between field sites, and all farms grew the same cultivar, “Bluecrop”, which has a strong reliance on pollinators for fruit production (Button and Elle, 2014; Gibbs et al., 2016; Isaacs and Kirk, 2010). Farms ranged from 2 ha to 10 ha, with multiple cultivars grown alongside “Bluecrop”. In our region, highbush blueberry blooms in early spring (late April through May), when weather is rainy and cool creating conditions that are difficult for wild and managed pollinators. Managed honey bee colonies are installed shortly after the start of bloom when approximately 10% of flower buds are

open and moved between cultivars as the bloom period progresses (BC Ministry of Agriculture, 2014).

3.2.2. Pollinator Observations

To determine the rate of pollinator visits to blueberry, each field was surveyed a minimum of three times each year during blueberry bloom. Each field survey consisted of a 10 minute observation in each of the four transects used in the pollination experiment, at 0m (most natural field edge), 25m, 50m, and 100m into the field (Fig. 1.2). The 10 minute observation consists of selecting a random bush within a 40m transect and observing it for 30 seconds counting and identifying every flower visitor, moving 2 meters along the transect, and repeating the observation. A total of 20 randomly selected bushes were observed for a total of 10 min observation time per transect, leading to a grand total of 80 bushes and 40 min observation per field per survey date. All surveys were done on sunny to slight overcast days when the temperature was greater than 13°C with wind speed below 10km/h. The majority of visits in our region are by managed honey bees and wild bumble bees, with a small fraction (2.8%) by other bees and flies. We focussed on the honey bee and bumble bee visits for this paper.

3.2.3. Yield Deficits

To establish whether poor pollination in highbush blueberry results in yield deficits, hand pollination experiments were conducted at each field in each year. We selected forty bushes per field, with 10 bushes randomly chosen along each of four, 40 meter transects. The transects were placed at the edge of the field (0m), then at 25m, 50m and 100m away from the edge towards the field centre. On each bush we selected two clusters of 10-25 flowers, assigned as either open pollinated (OP) or supplementally pollinated (SP). Open pollinated flowers were exposed to the local pollinator community to represent the typical yield due to that sites pollinator community and supplementally pollinated flowers received additional outcross pollen from the same cultivar, collected via sonication using an electric toothbrush then applied to stigmas with a paintbrush. Hand pollinations were done three times during the bloom each year to ensure each flower received a minimum of one supplemental pollination treatment. Post bloom, once fruit began to form, clusters were covered in mesh bags to ensure no fruit loss. Fruit was collected during late summer with percent fruit set (%) and weight per berry (g) measured for each cluster. Yield is the

product of these two variables, and yield deficit is calculated as Yield SP – Yield OP, as SP clusters represent the maximal amount of fruit capable of being produced.

3.2.4. Determining the Proportion of Semi-natural Habitat

We analyzed landscape composition in circles of 300m and 2000m radii surrounding each field. The central point of the circles was designated as of the centre of a one hectare ha block that was initially delineated for the pollination experiment. At a scale of 1:2000, the area within each 300 m circle was hand digitized using ArcGIS (ESRI Inc.) and classified as one of 26 land-use types (Table 3.1). The landscape composition within the 2000m radii circles was determined through the use of land cover maps developed from Earth Observation for Sustainable Development of Forests forest cover map produced by Natural Resources Canada (AAFC, 2010). Both data sets were then further grouped into semi-natural vs. disturbed based on assumed quality of habitat for pollinators. Semi-natural habitat included unmanaged landcovers, forest remnants, and marshy areas while disturbed habitat typically consisted of urban or agricultural development.

3.2.5. Weather Variables

Daily temperature data was downloaded from the Environment and Climate Change Canada historical database (http://climate.weather.gc.ca/historical_data/search_historic_data_e.html). We used data from four independent weather stations to represent the four major regions where our 17 highbush blueberry farms were located (station [number of fields assigned that station]: Abbotsford A [6], Delta Burns Bog [2], Pitt Meadows CS [6] and Cloverdale East [3]). Bloom period was defined as ranging from the start of our pollinator collections in fields to the final insect collections during flower dehiscence. We visited fields every two-three days pre-bloom, resulting in any potential underestimate of bloom period being less than three days. Data utilized from the historical record include the following, calculated for the bloom period of each field for each year: total rain (cm), number of heating degree days (18°C) during bloom, mean daily temperature (°C), number of days with rain, mean daily minimum temperature (°C). Temperature during bee observations (°C) was determined through the use of a Kestrel 2000 Pocket Weather Meter (kestrelinstruments.com).

3.2.6. Model Selection

To investigate the influence of: number of bumble bee visits, number of honey bee visits, proportion of semi-natural habitat (2000m), proportion of semi-natural habitat (300m), total rain during bloom (cm), number of heating degree days, mean daily temperature (°C), number of days with rain, mean daily minimum temperature (°C) and temperature during bee observations (°C) on yield deficit (Table 3.2), we used Akaike Information Criterion to compare models. A model set was developed using the dredge function from the MuMin package (Barton 2009) in R (version 3.4.4). To reduce the number of models for parameter significance estimates, we developed a top model set using the criteria of $\Delta AICc < 2$. Using the parameters found in models meeting this criterion we assessed the significance of model parameters and determined whether the confidence intervals of parameter estimates crossed zero.

3.3. Results

Pollinator observations

Honey bee visits varied dramatically between years across our farm sites with a low of 50.9 bees per 40 minutes during 2014 and a high of 305.2 in 2015. The variation between in bumble bee visit rates between years varied less with counts between 12.7 bumblebees in 2014 and 27.3 in 2013 (Table 3.2). Mean maximum daily temperatures were relatively similar across the four years with 2013 having the warmest days $20.9 \pm 0.3^{\circ}\text{C}$, while 2015 was the only year with a temperature under 20°C . Similarly 2015 was also on average the coldest with minimum temperatures of 12.4 ± 0.4 , while 2014 had the warmest 15.1 ± 0.2 mean minimum temperature. Number of rainy days were similar across all years, however, total rain was greatest in 2013 ($37.2 \pm 5.8\text{mm}$) and lowest in 2015 ($16.9 \pm 10.2\text{mm}$).

Yield deficits

Across farms, yield deficits varied from 0.13 ± 0.06 to 1.01 ± 0.01 . The greatest average yield deficits within a year were found in 2014, with yield deficits of 0.49 ± 0.22 , while the smallest yield deficit was in 2015 0.28 ± 0.16 (Figure 3.1).

AIC model selection

The most strongly supported models for predicting yield deficit in highbush blueberry contained 9 parameters, with the number of honey bee visits being the only parameter missing from the global model. The lowest AICc score was found in a model containing number of bumble bee visits (higher visit rates reduce the deficit) and mean minimum daily temperature (°C, where lower temperatures during bloom increase the deficit). Sixteen models met the $\Delta AICc < 2$ criteria (Table 3.3), with number of bumble bee visits being present in all models. Daily minimum temperature was found in 8 of the models. The top model in our set had an R^2 value of 0.19, and based on the confidence intervals of the parameters in our top model set (Figure 3.2), the number of a bumble bee visits and mean daily temperature (°C) are the most likely to influence yield deficits in our highbush blueberry fields.

3.4. Discussion

In British Columbia, yield deficits are consistently present in the highbush blueberry cultivar “Bluecrop”. These deficits represent a large inefficiency in the cropping system. Previous work has shown that the value of loss per hectare due to poor pollination ranges between \$15000-18000/ha (Button and Elle, 2014; Gibbs et al., 2016). However, yield deficits in highbush blueberry seem to be unique to British Columbia, and cv. “Bluecrop” does not exhibit pollen limitation of yield within highbush blueberry’s native range of Michigan (Gibbs et al., 2016). Experiments evaluating pollen limitation of fruit crops are relatively uncommon. The majority of analyses emphasize the proportion of fruit production attributable to pollinators and not the level of fruit production unattainable by the current pollinator community. The value of pollinators to agriculture is estimated to be \$183 billion (Gallai et al., 2009); including the lost farm income due to pollen limitation would likely increase this value substantially.

Through AIC model selection we demonstrated that both pollinator and environmental variables contributed to yield deficit. Despite being observed at only one fifth the rate of honey bees, our data suggest that bumble bee visits are more important for reducing the yield deficit, likely because of their sonication behaviour. In other *Vaccinium* species, such as cranberry (*Vaccinium macrocarpon*) and lowbush blueberry (*V. angustifolium*), *Bombus* species exhibit greater abilities as pollinators due to their

faster handling time of flowers, preference for *Vaccinium* spp. pollen, and greater stigmatic pollen deposition (Bobiwash et al., 2017; Cane and Schiffhauer, 2003; Drummond, 2012; Javorek et al., 2002; Stubbs and Drummond, 2001). In other fruit crops, the effectiveness of *Bombus* species has been shown to vary in comparison to honey bees. In a study of apple (*Malus sp.*) and almond (*Prunus dulcis*, bumble bees increased the deposition of pollen in apple and reduced deposition in almond when honey bees were abundant (Thomson and Goodell, 2001). Focusing on the attributes of particular pollinator behaviours may be valuable in investigating the potential effectiveness of pollinators, but positive trends may not always result in agricultural production gains (Fulton et al., 2015). The integration of both behaviour and plant response (pollinator effectiveness) provides a better understanding of pollinator-plant interactions. Frameworks that combine successful pollen deposition with plant reproductive success have been proposed to improve among-system comparisons of plant-pollinator interactions (Ne'Eman et al., 2010). However, such approaches do not explicitly address variation in the efficacy of interactions that may arise over time.

The most commonly observed wild pollinators in BC highbush blueberry fields are bumble bees (Mackenzie and Winston 1984, Ratti et al. 2008, Button and Elle 2014, Gibbs et al. 2016). Over the course of 4 years we observed 8203 bees visiting highbush blueberry, with five bumble bee species (*Bombus flavifrons*, *Bombus melanopygus*, *Bombus mixtus*, *Bombus vosnesenskii*, and the introduced *Bombus impatiens*) the most common wild species (9.95% of all visits observed). Honey bees were substantially more common, providing 88.6% of observed bee visits. Despite the relatively low diversity of pollinators in highbush blueberry in BC (Gibbs et al., 2016), community composition changes have occurred over the last few decades. *Bombus occidentalis* was once the most common bumble bee species in BC highbush blueberry but it has steadily declined (Colla and Ratti, 2010) and wasn't observed in 4 years of bee observations in the present study. Historical data in our region also do not include the introduced *B. impatiens* (Mackenzie and Winston, 1984) with a single specimen observed in 2003 (Ratti et al., 2008) and multiple observed (9) in the final two years of our study. This compositional change highlights the need to understand the contribution of particular species to pollination, and the role agroecosystems play in pollinator community composition. Changes in community composition over time could impact the levels of pollen limitation in fields.

Our model selection identified minimum average daily temperature during the bloom as a strong contributor to yield deficits, with greater deficits in colder temperatures. On average bumble bee species have a lower temperature threshold at which they can become active relative to honey bees (Corbet et al., 1993). The theoretical lowest temperature threshold at which honey bees can activate flight muscles has been calculated to range between 8.7-11.2 °C; for bumble bees, the range is 1.4-12 °C depending on species (Burrill and Dietz, 1981; Corbet et al., 1993). In years like 2015, the mean minimum daily temperature during bloom was 6.1 °C, well below the temperature threshold estimated for honey bees. A low minimum daily temperature increases the probability that a portion of the bloom day exhibits temperatures at which flight, and subsequent foraging, becomes overly costly for these bees. Coincidentally, 2015 was also the year where the highest number of *Bombus* visits was recorded. In all but a single year, 2014, the mean minimum daily temperature was below 9°C. For most species of bumble bees this is not likely to lead to a significant deterrence to foraging, especially for the queens that are more abundant than workers at the start of bloom. In a study of three alpine/subalpine *Bombus* species, queens were observed flying/foraging at temperatures lower than both workers and males (Lundberg et al. 1980). Cold spring weather may result in bumble bees becoming increasingly important to fruit pollination and crop yield during those periods.

Contrary to previous studies, landscape was only a minor component in the variation of yield deficit over time. Local semi-natural habitat (300m) was found among the top models more often (three vs. one) than regional semi-natural habitat (2000m). Generally, as the proportion of semi-natural habitat near farms decreases, pollinator diversity and visit rates to crops also experience reductions (Ricketts et al., 2008). In large monoculture cropping systems, the value of quality pollinator habitat increases with plant diversity at local scales being especially important for maintaining pollinator diversity (Kennedy et al., 2013). Over the four years of our study there was little variation in the landscape surrounding our farms. The landscape near our farms has long harboured highly managed agriculture, resulting in landscape being an unimportant predictor for yield deficit variation due to its relatively stable nature. However, we might expect particular elements in the landscape to affect pollinator community responses long term. Depending on the plant species composition in the surrounding area, some of which are preferred over blueberry by bumble bees for nest provisioning (Bobiwash et al., 2017), the effects

of climate change on pollinators can be mitigated or enhanced. When exotic plants species are established in species poor communities they can add to the floral resource landscape for pollinators while potentially facilitating pollination of nearby species (Memmott and Waser, 2002; Moragues and Traveset, 2005; Rodriguez, 2006). However, exotic plant species preferentially benefit generalist while specialist species suffer in these novel communities shaped by climate change (Schweiger et al., 2010). Taking into account the way pollinator species utilize the landscape we can develop hypotheses on how communities will adapt to climate change in areas that differ in their level of landscape disturbance.

Poor weather during the bloom has previously been linked to lower yield in Michigan highbush blueberry (Tuell and Isaacs, 2010), however, honey bees were the predominant pollinators in that study. Our model supports bumble bee visits and the average minimum temperature during bloom as predicting yield deficit mitigation in our region. An effect of honey bees on yield may not be present in our analysis due to their per capita ineffectiveness as blueberry pollinators (Javorek et al., 2002) or due to their ubiquity across the landscape. During our 10 minutes observations the rate of honey bee visits varied between 2.4 to 21.7 depending on the year. Preliminary research suggests that 2 bees per minute of observation approaches levels of pollination sufficient for proper fruit set (Lonsdorf, pers. comm.).

Our model is missing a variety of short term and microclimatic variables that are also likely to influence pollinator behaviour and variability in our data. Temperatures, duration of rainy periods, and other aspects of weather likely vary within regions, but we needed to use a single weather station for climate data. More precise hourly weather data for our sites would allow us to better construct the model to determine the proportion of the day where the temperature threshold for activity was met for our two major groups of pollinators. It is also important to note that our landscape variables are only rough estimates of the value of particular landscapes to pollinators. The resources provided to pollinators by semi-natural habitat likely vary in quality and quantity throughout the season. Understanding the degree to which both wild and managed pollinators utilize these land use types would allow for more precise categorization.

Our study supports findings of others that wild pollinators are essential actors in crop-pollinator interactions (Klein et al. 2007, Winfree et al. 2008, Garibaldi et al. 2013,

Allen-wardell et al. 1998). Yield deficits present in BC highbush blueberry are unlikely to be mitigated simply by increasing honey bee stocking density. To optimize pollination of this early flowering crop concerted efforts must be taken to maintain or increase current bumble bee populations and adapt pollination management strategies to climactic variables during the bloom. It is also important to understand that pollinator phenology may not immediately track increasingly earlier bloom periods. The bloom during the final two years of our study started approximately 2 weeks earlier than the previous two. Should trends towards earlier bloom periods continue, identifying whether bumble bee phenology and queen emergence follow suit can be valuable in predicting future yield deficits in early flowering cultivars like “Bluecrop”. Monitoring local wild pollinator diversity, abundance and phenology can assist in developing efficient crop pollination strategies.

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Table 3.1 Land use categories used for hand digitization of the landscape surrounding highbush blueberry farm sites in British Columbia. Adapted from Gibbs et al. (2016.)

Land use categories	Land use explanation	Land use group
Annual crop, non-flowering	Cereal and grain crops	Disturbed/Agriculture
Annual crop, flowering	Flowering crops, e.g. sunflowers	Disturbed/Agriculture
Perennial crop, non-flowering	Orchards, non-rewarding for bees	Disturbed/Agriculture
Perennial crop, flowering	Orchards, rewarding for bees, e.g. apple or cherry	Disturbed/Agriculture
Bare	Non-vegetated ground cover	Disturbed/Agriculture
Marshland	Marshes and vegetated wetlands	Semi-natural
Mown grass	Lawns, mown roadsides	Disturbed/Agriculture
Grazed pasture	Pasture for livestock	Disturbed/Agriculture
Grazed savanna	Savanna grazed by livestock	Disturbed/Agriculture
Savanna, ungrazed	Savanna, undisturbed understory	Semi-natural
Sparse, weedy scrub	Open areas with undisturbed weeds	Semi-natural
Shrub	Shrubland	Semi-natural
Woodland, open	open woodland	Semi-natural
Woodland, deciduous	Woods dominated by deciduous trees	Semi-natural
Woodland, coniferous	Woods dominated by coniferous trees	Semi-natural
Woodland, mixed	Woods with both deciduous and coniferous trees in abundance	Semi-natural
Pavement	roads: paved or heavily driven dirt	Disturbed/Agriculture
High intensity, development	Industrial areas, urban zones	Disturbed/Agriculture
Low intensity, open development	Suburban areas, high density	Disturbed/Agriculture
Low intensity, wooded development	Human dwellings in wooded areas	Disturbed/Agriculture
Low density, open development	Suburban areas, low density	Disturbed/Agriculture
Water	Natural and manmade bodies of water	Disturbed/Agriculture
Riparian, open	Riparian zones with short vegetation	Semi-natural
Riparian, wooded	Riparian zones in wooded areas	Semi-natural
Planted, non-agriculture	Managed plants, e.g., hedges	Disturbed/Agriculture
Planted, native	Managed native plant restorations	Semi-natural

Table 3.2 *Across-field averages for flower visits by honey bees and bumble bees, and for 7 environmental variables (mean \pm standard deviation) between 2013 and 2016. Visits consisted of pollinator visit data were from 17 British Columbia highbush blueberry fields in 2013-2015, and 11 fields in 2016. Environmental data were from four climate stations in each year. Visit means were calculated from three 40 minute samples across each field during the four years of study.*

Variable	Year			
	2013	2014	2015	2016
Honey bee visits (per 40 minutes)	61.4 \pm 27.9	50.9 \pm 32.6	305.2 \pm 203.1	133.1 \pm 91.9
Bumble bee visits (per 40 minutes)	27.3 \pm 38.3	12.7 \pm 16.6	26.0 \pm 40.8	18.9 \pm 34.2
Mean observation temperature ($^{\circ}$ C)	19.5 \pm 2.2	21.1 \pm 1.1	17.3 \pm 1.1	20.3 \pm 3
Mean maximum daily temperature ($^{\circ}$ C)	20.9 \pm 0.3	20.2 \pm 0.3	18.6 \pm 0.4	20.3 \pm 0.4
Mean minimum daily temperature ($^{\circ}$ C)	8.9 \pm 0.9	9.9 \pm 0.5	6.1 \pm 0.4	7.2 \pm 0.8
Mean daily temperature ($^{\circ}$ C)	14.9 \pm 0.6	15.1 \pm 0.2	12.4 \pm 0.4	13.8 \pm 0.4
Heating degree days	3.2 \pm 0.5	3.1 \pm 0.2	5.6 \pm 0.4	4.3 \pm 0.4
Mean total rain (mm)	37.2 \pm 5.8	23.3 \pm 4.6	16.9 \pm 10.2	17.9 \pm 9.0
Mean number of rain days	6.6 \pm 1.3	6.4 \pm 2.2	6.1 \pm 0.8	6.2 \pm 1.4

Table 3.3 Selection of best combination ($\Delta AICc < 2$) of variables to predict Highbush blueberry yield deficit (Yield of supplementally pollinated flowers – Yield of Open pollinated flowers). $\Delta AICc$ represents the difference in AICc relative to the min AICc.

Parameters	Df	AICc	$\Delta AICc$	r^2	Akaike weights
Mean minimum daily temperature + bumble bee visits	4	79.9	0	0.19	0.104
Mean minimum daily temperature + semi-natural habitat (300m) + bumble bee visits	4	80.1	0.21	0.2	0.094
Mean observation temperature + Mean minimum daily temperature + bumble bee visits	5	80.4	0.52	0.2	0.08
Mean minimum daily temperature + # of rainy days + bumble bee visits	5	80.7	0.82	0.19	0.069
Mean minimum daily temperature + # of rainy days + bumble bee visits	5	80.7	0.83	0.19	0.069
Heating degree days + bumble bee visits	4	80.8	0.91	0.20	0.066
Mean daily temperature + bumble bee visits	4	80.9	0.97	0.20	0.064
Mean observation temperature + mean daily temperature + bumble bee visits	5	81	1.11	0.20	0.06
Mean observation temperature + heating degree days + bumble bee visits	5	81	1.11	0.20	0.06
Mean daily temperature + # of rainy days bumble bee visits	5	81.2	1.28	0.19	0.055
# of rainy days + heating degree days + bumble bee visits	5	81.2	1.33	0.18	0.054
Mean observation temperature + bumble bee visits + honey bee visits	5	81.4	1.47	0.18	0.05
Mean observation temperature + mean minimum daily temperature + # of rainy days + bumble bee visits	6	81.5	1.61	0.19	0.047
Mean observation temperature + total rain(mm) + bumble bee visits	5	81.6	1.71	0.18	0.044
Mean minimum daily temperature + mean daily temperature + bumble bee visits	5	81.7	1.8	0.18	0.042
Mean minimum daily temperature + Heating degree days + bumble bee visits	5	81.8	1.87	0.18	0.041

Table 3.4 *Relative importance value and number of models containing each parameter from the 14 top linear models measuring the effects pollinator visits and weather variables on yield deficit in highbush blueberry in British Columbia.*

Variable	Relative importance	N containing Models
Number of bumble bee visits	1	16
Mean daily minimum temperature	0.89	8
Semi-natural habitat (300m)	0.22	3
Number of rain days during bloom	0.21	3
Mean maximum daily temperature (°C)	0.17	3
Mean observation temperature (°C)	0.14	2
Total rain (mm)	0.13	2
Mean daily temperature (°C)	0.11	2
Heating Degree days	0.11	2
Semi-natural habitat (2000m)	0.07	1

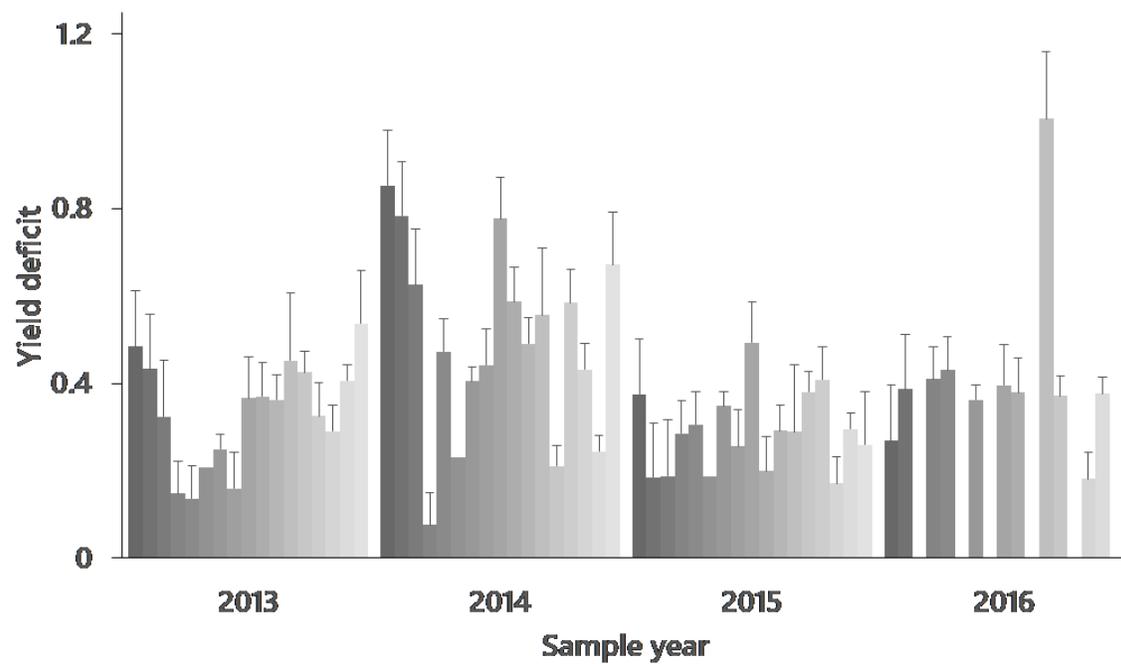


Figure 3.1 Yield deficit (Supplemental yield – Open pollinated yield) over four years in British Columbia highbush blueberry fields. From 2013-2015 yield deficits were calculated for 17 fields. Only 11 fields were studied during 2016 fields. Error bars represent S.E.

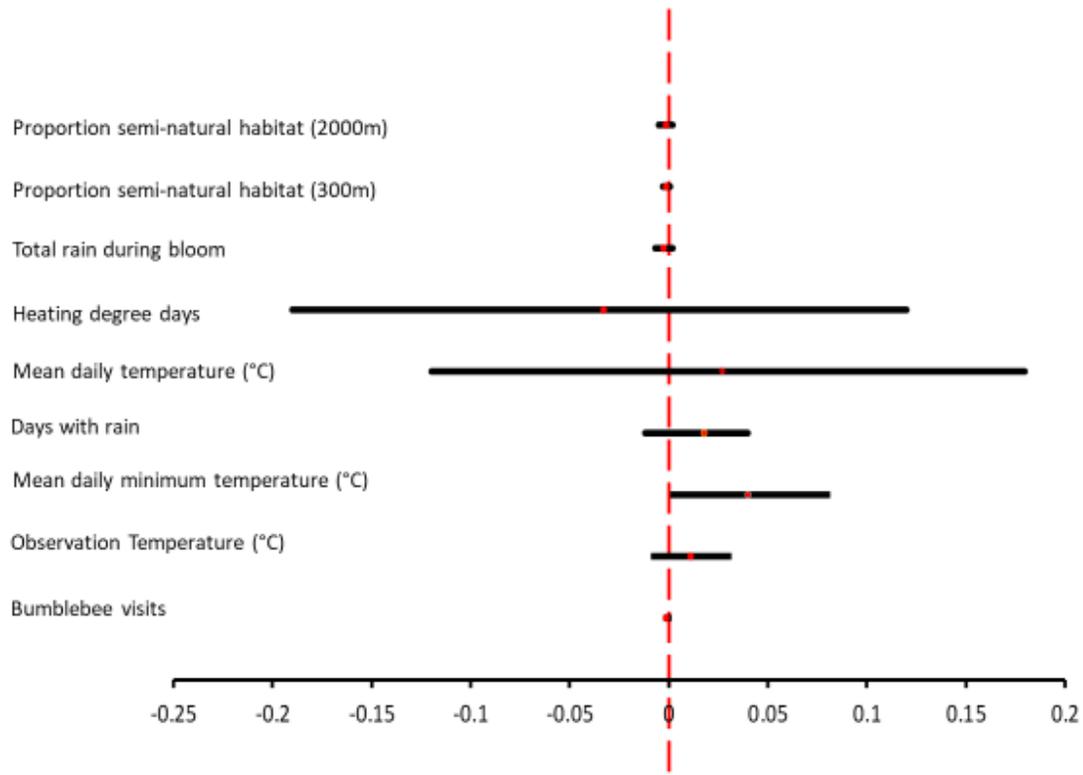


Figure 3.2 Average parameter estimates from linear mixed effects models for model parameters: proportion of semi-natural habitat (2000m), proportion of semi-natural habitat (300m), total rain during bloom (cm), number of heating degree days, mean daily temperature (°C), number of days with rain, mean daily minimum temperature (°C), temperature during bee observations (°C) and number of bumble bee visits on yield deficits of highbush blueberry. Estimates (closed circles) are calculated using the top model set from the model dredging process along with 95% confidence intervals (horizontal lines).

Chapter 4. Bumble bee colony characteristics as predictors for pollen foraging rate

4.1. Introduction

The availability of pollinators for crops has been increasingly limited due to global agricultural trends and anthropogenic disturbances. Since 1961, the total arable land planted to pollinator-dependent crops has increased by 70-100%, with the highest growth seen in underdeveloped countries (Aizen et al. 2008). In developing regions of the planet, human access to certain essential micronutrients is reliant upon pollinator-dependent crops (Eilers et al. 2011, Chaplin-Kramer et al. 2014). Despite 60% of global food production not being dependent on pollination, 75% of the leading 115 crops globally rely on animal mediated pollination (Klein et al. 2007) with more than 900 harvested or planted tropical species benefitting from pollination (Roubik 1995). Current trends in honey bee colony growth have not kept pace with the growing demand for agricultural pollination (Aizen and Harder, 2009). The ongoing conversion of land to pollinator-dependent agriculture ironically may be one of the leading causes of the loss of wild pollinators.

Habitat loss has been implicated in the decline of global pollinator abundance and diversity (Winfree et al. 2009), and is exacerbated by the increasing proportion of the terrestrial biome (40% of total land mass) dedicated to agricultural production (Foley et al. 2005). In many cases, wild pollinators are more effective pollinators of crops, with one study demonstrating wild bees increasing fruit set in all 41 crops surveyed, while benefits from honey bees were only seen in 14% of the crops (Garibaldi et al. 2013). Yet our food systems increasingly rely on managed pollinators like honey bees, because of the vast acreage requiring pollination and lack of sufficient wild pollinators in these landscapes to provide pollination services. Even the growth of apiculture has been surpassed by the proportion of agriculture requiring pollinators (Aizen and Harder 2009). There is clearly a need for new pollination strategies in pollinator-dependent crops.

The reliance and use of honey bee alternatives in managed pollination has a long history with a variety of solitary and social species being used. Late 1800 to early 1900 researchers were the first to identify limitations in the honey bee's capacity to pollinate particular crops, alongside the finding that some species are better adapted to particular crops (Batra 1995). For example, in order to improve red clover seed production in New

Zealand, *Bombus* spp. from England were imported to establish effective pollination (Bohart 1972). It wasn't until the mid-20th century that an alternative solitary pollinator species, *Megachile rotundata*, was reared for use in agriculture (Batra 1995). Since those early beginnings, a variety of bee species are currently being used as alternatives to honey bees for agricultural pollination. *M. rotundata* and other solitary bees such as *Osmia* species are now firmly established as field crop and orchard pollinators (Bosch et al. 2002). Bumble bee species rearing has developed (Plowright and Jay 1966) with five bumble bee species commonly being artificially reared for greenhouse pollination of crops (Velthuis and van Doorn 2006). It is estimated that there are over 900,000 colonies of *Bombus terrestris* reared annually for agricultural pollination (Velthuis and van Doorn 2006). Increasingly, species are being identified as valuable agricultural pollinators due to their effectiveness in accessing and transferring pollen or because of their ability to withstand particular rearing and agricultural practices. Identifying the benefits to the crop and mechanisms by which particular pollinators increase yield is important as we continue to develop techniques to manage and rear new species for agricultural pollination.

In highbush blueberry (*Vaccinium corymbosum*), yield has been demonstrated to be both pollen limited and reliant on a particular group of pollinators (Chapter 3). In British Columbia, bumble bees are the main wild pollinator supplementing managed honey bees, and the fruit loss per hectare due to poor pollination can be valued up to \$15000 USD (Gibbs et al. 2016). Different geographic regions where this crop is grown, in the native range of highbush blueberry, have a more diverse pollinator fauna and blueberry doesn't experience the same levels of yield deficit (Gibbs et al. 2016). The presence of bumble bees on BC farms is associated with lower yield deficits (Button and Elle 2014, Chapter 3), perhaps because they are more efficient at delivering pollen to the crop relative to honey bees in *Vaccinium* species (Javorek et al. 2002). Prior to this research, there were no species of managed bumble bee approved for use outside of greenhouses in British Columbia. Developing managed bumble bee species that can be used in British Columbia has become a priority, in efforts to improve yield in highbush blueberry and other orchard crops. Here, we evaluate how the use of two newly developed bumble bee species affects yield on British Columbia farms.

In addition to evaluating pollination effectiveness, it is useful to consider traits of bee species that might make them useful for development as managed crop pollinators. Bumble bee species have been shown to vary in foraging performance (Raine and Chittka

2005), foraging ranges (Westphal et al. 2006) and overall colony size (Spaethe and Weidenmüller 2002). We expect that characteristics associated with pollen need, specifically those associated with larval production will result in increased foraging. In lowbush blueberry, queen bumble bees were shown to be the most efficient pollen foragers (Javorek et al., 2002). This behavioural adaptation likely results from the evolutionary pressure associated with founding colonies, as queens must establish sufficient pollen stores to rear the first generation of workers with queen early pollen quantity predictive of colony growth (Westphal et al., 2009). Less frequently evaluated are differences in species that might affect or predict their rate of foraging in crops. Identifying colony characteristics that affect foraging choices in workers can further our understanding of the developmental cues that drive pollinator resource selection and forager recruitment in bumble bee colonies.

In this study, we evaluated colony characteristics and how they relate to foraging strength for two managed bee species. Specifically, we ask:

- 1) Do colony growth characteristics differ between *Bombus huntii* and *Bombus vosnesenskii*?
- 2) Does *Bombus* addition to highbush blueberry fields affect yield deficit mitigation?
- 3) Are colony characteristics associated with pollen need predictive of pollen foraging?

4.2. Materials and Methods

4.2.1. Field Setup

Our sample sizes for this research were constrained by the availability of bumble bee colonies, which were generously provided by Biobest. In 2014 we compared 5 fields supplemented with *Bombus huntii* (+BH) and 1 field supplemented with *Bombus vosnesenskii* (+BV) to 6 control fields without bumble bee additions. In 2015, we compared 6 control fields with 3 fields supplemented with *Bombus huntii* (+ BH) and 3 fields supplemented with *Bombus vosnesenskii* (+ BV). The 2014 stocking density was 2 quads (four colony packages of bumble bee colonies) per field, and the 2015 stocking density

was 4 quads per field. Colonies were placed along the “most natural” edge of the hectare crop block in which the study took place, in the middle of the first row of highbush blueberry. All growers additionally utilized honey bees for pollination, that were placed centrally within farms. Stocking rates for honey bees ranged from 3 to 8 hives per acre for the 12 farms used in this research, and at some farms the stocking rate was changed over the course of the experiment because of the amount of bloom by different cultivars grown at the farm.

4.2.2. Colony Characteristics

Foragers were observed and counted for 5 minutes at each bumble bee colony in every field a minimum of three times over the course of the bloom to determine the number of active pollen and non-pollen foragers returning to the colony. Because time of day can affect foraging rate and behaviour, observations at colonies were conducted once in each of morning (10h00-12h00), midday (12h00-14h00), and afternoon (14h00-16h00). All observations were performed on days above 15.5°C, with low winds, no precipitation and at least partial sun. Managed bumble bee colonies were euthanized once the blueberry bloom was complete and dissected in the lab to determine colony characteristics: (change in colony weight (euthanized weight – deployment weight), # honey pots, # of pollen pots, # of workers, # of queens, # of males, number of queen cells and total number of worker cells produced).

4.2.3. Pollination Experiment

We performed an experiment to evaluate yield deficits due to inadequate pollination on 40 bushes per field, 10 at each of four distances from the ‘most natural’ edge (0m, 25m, 50m, 100m; Figure 1.2, see Chapter 3). On every bush two experimental clusters were designated, one each for ambient and supplemental pollination treatments. We chose clusters within bushes that had similar numbers of flower buds (around 20) and were at a similar phenological stage. “Ambient” clusters were open to the complete pollination environment (managed honey bees, wild bees, and managed bumble bees for the +BH and +BV treatments). “Supplemented” clusters were also open to ambient pollination, but were additionally supplemented by hand with outcross pollen from the same cultivar. Hand pollinations were repeated a minimum of three times over the course of the bloom to ensure all flowers received saturating pollen loads. By comparing the

difference in yield [weight per berry (g) multiplied by fruit set (%)] between ambient (local pollination environment) and supplemental (saturating pollen addition) clusters we can determine the yield deficit. The yield deficit represents the theoretical yield that is not being produced due to pollen limitation (inadequate pollen delivery in the ambient pollination environment). We conducted pollination experiments on control fields (wild pollinators and managed honeybees) and on bumblebee addition fields (wild pollinators, managed honeybees and addition of either *B. huntii* or *B. vosnesenskii*). If managed bumble bees contribute enough to crop pollination to improve yields, we expect lower yield deficits on +BH and +BV fields relative to control fields.

4.2.4. Analysis

Colony Characteristics

A Multivariate ANOVA (SAS Institute 2016) was used to examine the differences among bumble bee species in colony growth and development characteristics. This analysis was performed using bee species as a fixed effect with field sites and year as random effects, to determine whether species differed in colony growth characteristics (number of queens, number of workers, number of males, number of total queens cells, number of total worker/male cells, number of honey pots, number of pollen pots and change in colony weight (g)). Individual colonies were used as our sampling units. To aid interpretation of the MANOVA we subsequently performed univariate ANOVAS on each colony characteristic.

Pollen Deficit Characterization

To determine whether pollination treatment resulted in differential mitigation of pollination deficit we used two generalized linear mixed models to incorporate both fixed (pollination treatment and species) and random effects (site and year). Because previous work found no difference in bumble bee abundance with distance into the field at the scale of our study, we do not include distance in our models (Button and Elle 2014). For this analysis we used the “lme4” package (Bates 2017) in R (3.4.2). Using the normal approximation we determine p-values from our mixed model to measure the probability of a false positive. Two comparisons were completed to compare the size of the blueberry yield deficit resulting from fields with bumblebee additions (*B. huntii* and *B. vosnesenskii*) relative to control fields in 2014 and 2015. In 2015, both species were available in sufficient

quantity to equally distribute across fields allowing us to compare yield deficit values derived from fields with either *B. huntii* or *B. vosnesenskii*.

Predicting the Rate of Pollen Foraging

To evaluate whether the mean number of pollen foragers returning to colonies during observations varied due to measured colony characteristics or species identity we utilized Akaike information criteria (AIC) obtained using the R package 'MuMin (Barton 2013). Our predictor variables were colony weight change, number of workers, number of males, number of queens, total worker cells, total queen cells, colony weight change, number of pollen pots, number of nectar pots and mean number of nectar foragers. Candidate models consisted of linear mixed effect models with field and year designated as random factors, and colony used as our unit of replication. Significance of model parameters were assessed by whether they appeared in models that fell within the 95% confidence sets of the model averaging process ($\Delta AIC_c < 2$; Burnham & Anderson, 2002), had a significantly high summed Akaike weight (> 0.5) across all models, and parameter estimates for which confidence intervals did not cross zero.

4.3. Results

Bumble Bee Colony Characteristics

Colony characteristics differed significantly between species (Wilks' Lambda=0.71, $F_{10,141} = 5.71$, $P < 0.001$), with number of queens, number of queen cells, number of pollen pots, mean number of nectar foragers and mean number of pollen foragers demonstrating significant differences in univariate ANOVAs used for interpretation (Table 4.1).

The total number of workers counted at the end of the bloom differed between species and between years (Figure 4.2). Significantly more queens were produced in BH colonies in both 2015 and 2014 (Figure 4.1 and Table 4.1), and queen production was doubled in 2015 relative to 2014. The overall production of individual bumble bees (total number worker cells) was also much greater in 2015 compared to 2014. Worker cell production was similar in both years with no significant differences between the species.

Colonies grew significantly more (final weight (g) – initial weight (g)) during the 2015 season compared to the 2014 season, however, colony growth was similar for both

species. A much greater number of pollen pots were counted during 2015, with pollen pot production being significantly higher in BV (Table 4.1). The number of nectar and pollen foragers observed during 5 minute observations was significantly higher for BH in both years (BH = 1.09 ± 0.7 , BV = 0.7 ± 0.6).

Bumble bee yield deficit mitigation

In all experimental fields, supplementally pollinated flowers produced heavier fruit ($t_{2810} = 19.3$, $p < 0.01$), and had higher yields ($t_{2872} = 17.5$, $p < 0.01$) relative to ambient pollinated flowers (Table 4.2). This indicates pollen limitation across all fields used in our study. Percentage fruit set was similar in both pollination treatments, ambient and supplemented ($t_{3026} = 1.2$, $p = 0.24$). To determine the effectiveness of *Bombus* additions, all *Bombus* addition fields were combined and compared to control blueberry fields. Yield deficits varied between year, farm and site, however, the addition of *Bombus* species to fields did not significantly reduce the size of the yield deficit ($t_{975} = -1.4$, $p = 0.14$) in addition no differences in the yield deficit between the fields containing different *Bombus* species were found in 2015 ($t_{317} = 1.6$, $p = 0.12$).

Predicting the Rate of Pollen Foraging

Through our model selection protocol the model with the highest support for predicting the return rate of pollen foragers contained: number of males, number of workers and total queen cells produced (Table 4.3). No other model fell within the $\Delta AICc < 2$ range, providing us with only one set of model parameters to evaluate. The relative importance values of the three parameters contained in our top model were 1.00 (Figure 4.2) and < 0.01 for all other parameters initially included in the global model.

4.4. Discussion

Differences in colony growth characteristics of *Bombus* species are not well studied, as only a small proportion of species are reared in captivity. Our results suggest that the reproductive capacity of species may differ, especially in the production of queens which are the most resource costly caste. The size difference between a queen cell and a worker cell likely necessitates a difference in resource allocation by workers to the cell. Previous research (Pomeroy 1979, 1981) on *Bombus ruderatus* found a linear relationship between cocoon size and pollen intake, with the larger queen cells requiring 330% more

pollen than a worker cell. In queens, the relationship between queen size and fitness is thought to follow a convex function with foraging benefits to large size diminished by the costs of resource investment (Owen 1988). Similarly, feeding trials on different *Bombus* species demonstrate that much of the variation in size is a direct result of food supply provided to the larva (Plowright and Jay 1977, Sutcliffe et al. 1978). Both our species, *B. huntii* and *B. vosnesenskii*, were placed in similar agroecosystems with access to relatively similar floral resources (from both crop and weed species). Similar access to forage in relatively similar agroecosystems suggests that differences in queen cell production may be due to differential foraging efforts and are likely species characteristics. These differences between species may affect aspects of foraging behaviour and pollination effectiveness in highbush blueberry warranting further behavioural studies.

In our study, the average number of workers returning to the colony with pollen over a five minute observation period was higher in BH, which also mirrors the greater number of pollen pots found in BH relative to BV. As demands for protein increase, due to increased queen production, we would predict increases across the suite of characteristics associated with increased storage and acquisition of pollen. Pollinator foraging choices have previously been demonstrated to be affected by the specific resource needs of pollinator species. In honey bees, supplementing colonies with pollen results in foragers switching from pollen foraging to nectar foraging or ceasing foraging activity (Camazine 1993). Similarly, experimental removal of pollen stores from honey bee colonies resulted in increased foraging effort, as well increases in the number of pollen foraging workers (Fewell and Winston 1992). Bumble bees may also respond to colony pollen storage in similar ways. As pollen stores are artificially enhanced in a colony, pollen foraging recruitment decreases but not in colonies with severe pollen depletion (Kitaoka and Nieh 2009). However, in the same study (Kitaoka and Nieh 2009), circulating pollen odor within a nest increased pollen forager recruitment, but only when colonies were pollen poor. This suggests that there is an additional level of processing or signalling that must take place beyond the typical biochemical and physical cues studied thus far. Bumble bee colonies may have the capacity to assess both the current state of their pollen stores and evaluate additional need based on colony features. Pollen pots and queen larvae likely represent a combination of cues that indicate both a current and future need for pollen.

Despite differences in pollen foraging rate, neither of our *Bombus* species improved crop pollination in highbush blueberry. The greatest success of commercial

bumble bee supplementation is seen in greenhouse agriculture. Bumble bee pollination in greenhouse peppers has been shown to increase crop yield by up to 29% (Abak et al. 1997), as well as fruit size and quality (Roldán Serrano and Guerra-Sanz 2006). Greenhouse tomato (Dogterom et al. 1998) overall yield per square meter (Daşgan et al. 2004) also benefitted from bumble bee pollination. A more limited number of studies have demonstrated that bumble bees may be more effective pollinators in certain field crops, such as apple and lowbush blueberry, due to increased pollen deposition and better foraging behaviour relative to honey bees (Thomson and Goodell 2001, Javorek et al. 2002). In lowbush blueberry, the density of managed *B. impatiens* was found to be correlated with fruit set and seed set (Desjardins and de Oliveira 2006). Field experiments in Maine lowbush blueberry fields also demonstrated that fruit yield derived from fields with 10 bumble bee colonies per hectare were similar to those stocked with 7.5-10 colonies of honey bees per hectare (Drummond 2012). However, in a study comparing three managed pollinators (*Apis mellifera*, *Bombus impatiens*, and *Megachile rotundata*), *B. impatiens* did not significantly reduce the pollen limitation seen in New Brunswick lowbush blueberry, and no major effects on fruit or seed set were noted (Fulton et al. 2015).

Previous research in British Columbia highbush blueberry has demonstrated positive correlations between wild bumble bees and yield metrics such as fruit mass (Ratti et al. 2008), and the reduction of yield deficits (Button and Elle 2014), yet our results with managed *Bombus spp.* did not replicate those levels of yield enhancement, even at rates of 16 colonies per field. In comparison to other highbush blueberry growing regions, increased pollination in British Columbia is correlated with wild bumble bee abundance (Chapter 3), while Michigan highbush blueberry pollination is best predicted by managed honey bee abundance (Gibbs et al. 2016). This and the known yield deficits in BC highbush blueberry suggest that bumble bees do play a strong role in mitigating yield deficits. Our inability to reduce the deficit using managed bumble bees may be due to an insufficient forager population. Sizes of colonies range from fewer than 100 individuals in arctic species to larger colonies of over 1000 individuals among tropical species (Spaethe and Weidenmüller 2002), and averaged ~350 workers at the end of bloom in the current study. Compared to the tens of thousands of honey bee workers in an average colony, the foraging strength of managed bumble bees may be low. Even though honey bees are relatively ineffective pollinators of highbush blueberry, they may be sufficiently effective due to their high numbers. This might be especially true in areas with large highbush

blueberry plantings, like the BC lower mainland, since previous research has shown the diminishing importance of wild pollinators as field size increases (Isaacs and Kirk 2010).

The rate of pollen foraging differed between the *Bombus* species added to blueberry fields in our study, and was most strongly predicted by the number of males, the number of workers, and total queen cells. The production of reproductive castes in a bumble bee colony is controlled by a variety of factors that can differ across species and habitats. The production of males is thought to be the most effective use of colony resources in low resource environments as they are the most economical reproductive caste to produce in high numbers (Beekman and van Stratum 1998). However, queen success results in the greatest fitness for workers of the colony, as they share on average 75% of their genes with other females relative to males who share only 25% of their genes with workers. To maintain the same level of colony fitness achieved by producing numerous males, resources must be sufficiently abundant to produce an adequate number of queens to obtain maximize the fitness of workers in the colony (Beekman and van Stratum 1998). Male production may also be a product of worker laying, however, Vaamonde et al. (2002) demonstrated that this does not substantially affect overall queen production. In both scenarios of high and low resource abundance, greater production of reproductive castes is a possible predictors of pollen foraging rate. This creates the possibility of selecting future managed bumble bee species based on characteristics associated with the production of reproductive castes. Despite being present in our model, the parameter estimate obtained for the number of workers in a colony suggest that it is unlikely to strongly affect the rate of increase on pollen foraging. Coupled with our model selection data, the significant differences between species in queen cell production and pollen foraging suggest that identifying species with high rates of queen production investment can potentially allow us to identify future effective managed pollinators.

Identifying potential future species for rearing as managed pollinators for highbush blueberry requires that we identify life history characteristics that are synergistic with the characteristics of the crop. Previous research on these species demonstrate differences in the attractiveness of the target crop, with *B. huntii* pollen loads containing more than double the amount of *V. corymbosum* pollen than *B. vosnesenskii* pollen loads (Bobiwash et al. 2017). In comparison to honey bees, bumble bees may choose to forage on plants with high pollen protein essential amino acid content (Micheu et al. 2000). Developing *Bombus* species for a relatively nutrient poor crop like highbush blueberry (pollen crude

protein content of 13.1%) may be difficult as a result of its low nutritional value. Research on bumble bee foraging choices suggest that foragers may be able to discriminate between plants (both interspecific and conspecific) with differing protein qualities (Robertson et al. 1999, Hanley et al. 2008). Targeting and tracking resources in an ecosystem is important for a central-place forager aiming to maximize fitness. Bumble bees have a well developed spatial memory allowing them to modify forage targets based on their experience with various species in an ecosystem (Cartar 2004). Species with higher demands for protein may not value resource quality as much as quantity. In these species, overall protein demand may result in plant choices that incorporate ease of access and availability. Mass flowering crops like blueberry provide an abundance of lower quality pollen that is readily available. Identifying pollinator species with characteristics indicating high pollen need and turnover might allow the most effective managed pollinators to be developed for crop pollination.

The ideal managed crop pollinator for highbush blueberry would demonstrate a few key characteristics: 1) lifecycle needs can be met in or near the crop, 2) sufficiently high production of foragers, 3) high need of pollen, 4) foraging choices emphasizing abundance over quality. *B. huntii*, exhibits many of the qualities, but is not sufficiently abundant to meet the needs of mass-flowering highbush blueberry. At the stocking rates utilized in our study, no effect of yield deficit mitigation was found. Increasing the stocking density of bumble bee colonies to benefit from the higher foraging rate of *B. huntii* is currently unlikely due to the costs. However, stocking density trials would be highly valuable in order to determine the stocking rate needed to mitigate yield deficits, enabling improved predictions of economic scenarios when managed bumble bees become feasible. Further research and development on bumble bee and other native species as managed pollinators adapted to local agricultural conditions is important for increasing the pollination strategy options for farmers and also to understand the dynamics of species' life-history traits and interactions with plants in an agroecosystem.

4.5. References

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Table 4.1 Colony characteristics for two managed bumble bee species (*Bombus huntii* and *Bombus vosnesenskii*) across two years in British Columbia highbush blueberry fields. Species differed significantly overall, as demonstrated using a MANOVA (Wilks' Lambda=0.71, $F_{10,141}=5.71$, $P<0.001$; year was included as a random effect). The table additionally shows results of univariate ANOVAs to determine which colony characteristics contributed to MANOVA results.

	<i>B. huntii</i> means (± SE)±	<i>B. vosnesenskii</i> means (± SE)	F	P
Number of males	99.7 ± 28.2	104.73 ± 25.6	0.92	0.34
Number of workers	85.6 ± 25.7	93.5 ± 30.8	0.57	0.45
Number of queens	41.8 ± 13.8	17.5 ± 12.1	15.3	< 0.001
Total worker cells	348.1 ± 84.7	369.7 ± 73.8	0.53	0.47
Total queen cells	114.5 ± 45.6	26.1 ± 20.5	33.72	< 0.001
Number of honey pots	181.5 ± 64.6	189.1 ± 49.9	0.69	0.41
Number of pollen pots	12.3 ± 13.1	19.4 ± 24.5	4.23	0.04
Colony weight change (g)	250.2 ± 53.5	242.2 ± 58.6	0.23	0.63
Nectar foragers	1.3 ± 0.4	0.78 ± 0.61	12.97	< 0.001
Pollen foragers	2.2 ± 0.7	1.7 ± 0.5	4.36	0.03

Table 4.2 Berry weight (g), Fruit set (%) and yield (fruit set % * fruit weight(m)) (\pm S.E.) under two field treatments (control and + *Bombus*) and two pollination treatments (ambient and supplemental) in British Columbia highbush blueberry fields across 2014 and 2015. *Bombus* fruit characteristics data represents pooled data from fields with *Bombus huntii* and *Bombus vosnesenskii*.

Year		Control		+ <i>Bombus</i> species	
		Ambient	Supplemental	Ambient	Supplemental
2014	Berry weight (g)	0.82 \pm 0.4	1.3 \pm 0.46	0.94 \pm 0.46	1.37 \pm 0.44
	Fruit set (%)	0.86 \pm 0.32	0.87 \pm 0.29	0.88 \pm 0.27	0.90 \pm 0.25
	Yield	0.82	1.27	0.89	1.32
2015	Berry weight (g)	1.02 \pm 0.46	1.23 \pm 0.5	1.05 \pm 0.4	1.21 \pm 0.43
	Fruit set (%)	0.83 \pm 0.22	0.86 \pm 0.2	0.92 \pm 0.14	0.93 \pm 0.14
	Yield	0.77	1.01	0.95	1.11

Table 4.3 Selection of best combination of variables obtained from *B. huntii* and *B. vosnesenskii* for predicting the number of mean number of pollen foragers (per 5 minutes) returning to a bumble bee colony, using data from British Columbia highbush blueberry fields . *K* represents the number of parameters in the model, $\Delta AICc$ represents the difference in *AICc* relative to the min *AICc*.

Model	K	$\Delta AICc$	Akaike weights
pollen forager ~ queen cells + female + male	3	0	0.998
pollen forager ~ worker cells + queen cells + female + male	4	12.97	0.002
pollen forager ~ worker cells + queen cells + female + male + queens	5	17.21	0
pollen forager ~ worker cells + queen cells + female + male + nectar forager + queens	6	20.79	0
pollen forager ~ worker cells + queen cells + female + male + pollen pots + nectar forager + queens	7	34.10	0
pollen forager ~ species + worker cells + queen cells + female + male + pollen pots + nectar forager + queens	8	45.57	0
pollen forager ~ species + worker cells + queen cells + female + male + pollen pots + nectar forager colony weight change + queens	9	59.74	0
pollen forager ~ species + worker cells + queen cells + female + male + honey pots + pollen pot + colony weight change + nectar forager + queens	10	69.37	0

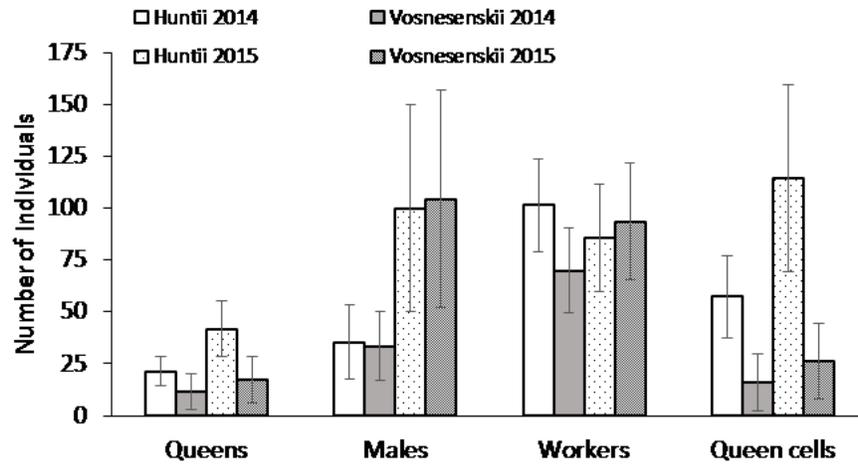


Figure 4.1

Mean number of queens, males, workers and queen cells per colony for two species of bumble bee (*B. huntii* and *B. vosnesenskii*) in 2014 and 2015. 48 *B. huntii* colonies and 24 *B. vosnesenskii* were studied in 2014, and 48 colonies of each species in 2015. Error bars represent standard deviation.

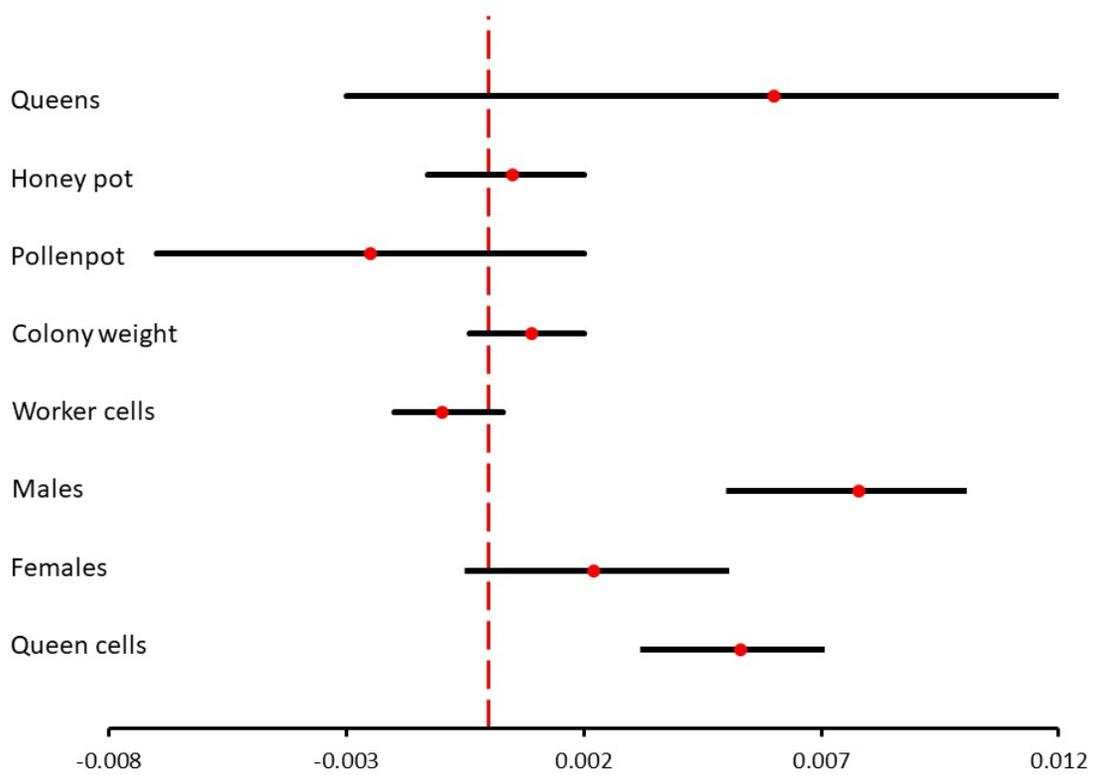


Figure 4.2 Average parameter estimates from linear mixed effects models ('site' held as a random intercept) for model parameters on pollen foraging rate of workers from colonies of two bumble bee species British Columbia. Estimates (red circles) are calculated from combined species data using the top model set from the model dredging process along with 95% confidence intervals (horizontal lines). Only queen cells and males are likely to influence foraging rate as they do not overlap with 0.

Chapter 5. Pollen foraging differences among three managed pollinators in the highbush blueberry (*Vaccinium corymbosum*) agroecosystem¹

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5.1. Introduction

A large proportion of modern agriculture greatly relies on insect mediated pollination (Klein et al., 2007; Aizen et al., 2009; Gallai et al., 2009). Among 200 countries, 75% of the top global commodity crops benefit from pollination (Klein et al. 2007), with some countries having as high as 84% of their crop species benefitting in some way from pollination (Williams, 1994). The integral role played by pollinators in fruits and vegetable production alone is approximated at \$106 billion dollars US (Gallai et al., 2009). Despite the value provided by wild pollinators to agriculture (Garibaldi et al., 2013), they are not sufficient to maintain agricultural production, most of which relies on managed pollinators. The growth rates of managed pollinator colonies have declined across much of the globe while demand for their services has increased (Aizen and Harder, 2009), causing a decrease in the stability and limiting future growth of pollinator dependent crop production (Garibaldi et al., 2011; Potts et al., 2017).

Many agricultural fields offer pollinators a wide range of floral resource diversity in the form of non-crop species. The presence of alternative forage for pollinators on farms is largely dictated by the cropping system and farm management intensity. Beyond the control of farmers, plant diversity outside of cropping areas may also benefit pollinators with sufficient foraging ranges. Previous work has demonstrated that wild bee abundance and species richness are correlated with land cover quality surrounding agricultural land and local farm management practices (Kennedy et al., 2013). When weedy species are found within or surrounding cropland the diversity of pollinators visiting crops as well as the pollination of the crop itself is enhanced (Button and Elle, 2014; Carvalheiro et al., 2011; Nicholls and Altieri, 2013). Managed bees are also known to benefit from diverse agricultural landscapes (Decourtye et al., 2010; Holzschuh et al., 2007). However, in many scenarios additional non-crop floral resources might be detrimental to crop pollination. A high abundance of weed species can reduce crop pollination through competition for

pollinators (Bretagnolle and Gaba, 2015). This competition for pollination in agricultural systems can lead to losses in crop productivity as pollinators neglect foraging for resources on the target crop (Wilcock and Neiland, 2002). Understanding the fidelity of managed pollinators for crop flowers is an important component of their suitability for pollination.

Highbush blueberry, *Vaccinium corymbosum* (Gray), is an important crop in British Columbia, which produces 90% of all highbush blueberries in Canada and 50% of the entire Canadian blueberry crop (Agriculture Canada 2010; Brazelton 2013). Blueberry production is reliant upon pollination to produce economically viable yields, with pollination responsible for 50-66% of fruit total production (Gibbs et al., 2016). Pollination need among BC blueberry farms is particularly high as it has been previously demonstrated that yields could be increased by 33% (\$18400/ha) should sufficient amounts of pollination be present in a field (Button and Elle, 2014). Highbush blueberry requires a specialized behaviour from pollinators for pollen transfer. Buzz pollination, the sonication of anthers, is required for pollen to be released from pores in the anthers and made accessible to pollinators (Buchman 1983). Though common in upwards of 15,000 plant species (Buchman 1983) and 50 genera of bee species (De Luca and Vallejo-Marín, 2013), in British Columbia highbush blueberry fields, only *Bombus* species and not *Apis mellifera* (Linnaeus) are capable of buzz pollination. In addition, particular cultivars such as 'Bluecrop' display floral characteristics (narrow corolla opening) resulting in greater levels of nectar robbing by honey bees (Courcelles et al., 2013), exacerbating the difficulty in receiving sufficient pollen delivery. Farmers still stock their fields with honey bees, however, in order to provide an adequate supply of visitors, even if these visitors are relatively inefficient at pollen movement. Previous research has shown that honey bees make up 70% of highbush blueberry's floral visitors and wild bumble bees approximately 28% (Button and Elle, 2014). The relatively small colony sizes of bumble bee species (100s of bees) relative to honey bee colonies (tens of 1000s of bees) likely limits the ability of wild *Bombus* species to maximize blueberry production in BC. Because of this, two managed bumblebee species, *Bombus huntii* (Greene) and *Bombus vosnesenskii* (Radoszkowski), are in development for use in BC highbush blueberry production.

Pollination effectiveness can vary based on behavioural differences that affect the rate of pollen delivery to flowers and the quality of pollen being delivered (Garibaldi et al., 2011; Herrera, 1987; Javorek et al., 2002). Particular behaviours such as nectar robbing

in highbush blueberry cultivars with small corolla diameters can lead to flower damage and limit the potential of the flower being properly pollinated (Courcelles et al., 2013). Characteristics such as floral visit duration and flight distance between flowers have previously been used to develop metrics to determine the equivalency values of single foragers between pollinator species on one specific crop (Javorek et al., 2002) but neglect to incorporate variability in pollen load composition in diverse agricultural landscapes. Heterospecific pollen receipt can prevent maximum seed set (Ashman and Arceo-Gómez, 2013) which in turn can affect fruit yield or quality (Crane, 1964). Though self-pollen has been demonstrated to result in pollen tube formation, increasing relatedness between plants results in lower seed numbers and more seed abortion in highbush blueberry (Krebs and Hancock 1989). Pollen foraging behaviours that maximize contact with a flower's reproductive organs or enhance movement of pollen between flowers are only valuable to a target crop when the pollen is that of a conspecific. For example, the primary agricultural pollinator, *Apis mellifera*, will collect pollen from up to 19 species of flowers (Girard, 2014) when foraging in *Vaccinium angustifolium* (Aitum). Variation in pollen resources found in agricultural landscapes may lead to deposition of non-crop pollen and reduction in pollination effectiveness.

The purpose of this study is to determine whether and to what degree three managed pollinator species (*Apis mellifera*, *Bombus huntii* and *Bombus vosnesenskii*) are utilizing highbush blueberry as a pollen resource. Increased attractiveness of the target crop to bees, determined through higher incidence of target pollen in corbicular loads, would indicate increased visit rate or visit duration to highbush blueberry. We additionally identified non-crop pollen types in corbicular loads, which provides information about foraging preferences in these landscapes dominated by a single floral resource, *V. corymbosum*. Through determining the crop and wild plant species that are the most targeted for pollen foraging, we can more reliably predict the effectiveness of new managed pollinator species and better understand the agroecosystem as a pollinator resource landscape.

5.2. Materials and Methods

5.2.1. Study Sites

Our study sites consisted of nine commercial production highbush blueberry fields (*V. corymbosum*) in the Lower Mainland of British Columbia. The yield of highbush blueberry is highly dependent on pollination by both managed and wild pollinators (Benjamin and Winfree, 2014; Isaacs and Kirk, 2010). Particular cultivars, such as “Bluecrop”, experience yield deficits due to flower morphology that limits the accessibility of flowers to honey bees (Button and Elle, 2014; Courcelles et al., 2013). All nine fields actively introduce managed pollinators during blueberry bloom with *A. mellifera* being present at all fields. *Bombus huntii* and *B. vosnesenskii* were each present at only 3 fields, providing us with 3 pollinator treatment groups – three *A. mellifera* only fields, three *A. mellifera* + *B. huntii* fields and three *A. mellifera* + *B. vosnesenskii* fields. Each field was a minimum of 1km away from other fields in the study. Highbush blueberry farms in the area generally grow multiple blueberry cultivars, however, our focal fields were all cultivar “Bluecrop”.

5.2.2. Pollen Collection and Slide Preparation

We examined corbicular pollen loads in this study; although destined for nest provisions and unavailable for pollination, the proportion of pollen being returned to colonies can serve as a proxy for the potential for pollination. At each field two bee collections were made between April 16, 2016 and May 14, 2016, the duration of the bloom of this cultivar in our region. Ten bees of the managed species at the site with corbicular pollen loads were sampled during each collection at each field for a sample size of 20 bees per field. Bees were sampled between 10h00 and 14h00, on days above 15.5 °C, with low winds, no precipitation and at least partial sun. *A. mellifera* returning to their colonies with pollen were netted and euthanized, while *Bombus* species returning with pollen were captured and chilled in a cooler so corbicular pollen loads could be removed and the bees released. Bumble bees were then returned to their colonies in order to not adversely effect the number of workers available to contribute to crop pollination.

The 20 corbicular pollen loads from each field were thawed, crushed, suspended in 300 µL of 70% EtOH, and vortexed for 1 minute. We then pipetted 30 µL of the ethanol

mix onto a microscope slide. A small cube of fuschin gelatin (Kearns and Inouye, 1993) was melted over the pollen to stain it.

5.2.3. Pollen Identification

We used a reference pollen collection developed by our group, and pollen grain photographic references from Agriculture and Agri-Food Canada (Girard, 2014) to identify pollen. Pollen was identified to the lowest taxonomic level possible (species in some cases; family for others). Pollen that could not be resolved to family or species was classified into an “unknown” category. We counted 100 pollen grains per slide along randomly placed transects along the slide.

5.2.4. Vegetation Sampling

We sampled non-crop flowers within fields to help us assess whether pollen collected by foraging bees was from within or outside farms. A one hectare plot was delineated within the field, along the edge of the farm. We placed 40 meter long transects at 0, 25, 50 and 100m from the natural edge of each of the fields (a weedy strip, farm row, or hedgerow) to the interior of the crop (Fig. 1.2). We recorded presence/absence of every plant species with open flowers in 10 quadrats placed in a stratified random manner along each 40m transect. Quadrats (100cm x 10 cm) were placed perpendicular to each transect, with one end at the base of a blueberry plant. We summed the number of times a plant species with open flowers occurred for every species at each transect (range of 0-10 occurrences per transect, as we had 10 quadrats per transect). This provided us with relative abundance data at every site for weedy species. In addition we made list of plant species observed along the edges of farms to better understand the floral resource landscape in which the farm was embedded.

5.2.5. Analysis

A Multivariate ANOVA (SAS Institute 2016) was used to examine the differences among bee species in pollen types in corbicular pollen loads. This analysis was performed using bee species as a fixed effect with field sites as random effects, to determine whether differences existed in the composition of pollen collected by the three managed pollinators. Pollen types where less than 5 grains were identified from a single sample were omitted

from the analysis. Tukey HSD post-hoc comparison were used on univariate ANOVA responses to determine species differences in collection of particular pollen types (R Core Team 2013)

To further determine whether non-crop plant species diversity in the fields was related to differences in pollen collection at particular fields we performed a Mantel Test (R package 'ape') (Paradis et al., 2004) comparing the corbicular pollen load collection of bees with the presence of non-crop plant species at each site.

5.3. Results

The two most frequently collected pollen types were that of *V. corymbosum* (41% of bees sampled and > 10% of pollen loads when present) and pollen from species in Rosaceae (in our area, various species of *Rubus*; 42% of bees sampled). *Ranunculus repens* (Lamotte) was the only other plant species represented with any regularity, being present in corbicular pollen loads of 23% of bees sampled (Figure 5.1).

The three managed bee species differed in the profile of pollen types they collected (Wilks' Lambda=0.34, F32,324 =2.58, P<0.001). Univariate ANOVAs indicated that pollen collected from species in Asteraceae (dandelions and hawkweeds, P =0.04), Rosaceae (P =0.03), *Juncus* (rush, normally wind pollinated; P =0.016), *Sambucus racemosa* (red elderberry (Gray); P =0.01), and *V. corymbosum* (P <0.0001), all varied significantly among bee species (Table 5.1). *Bombus huntii* collected more *V. corymbosum* pollen than either of the other species. *Apis mellifera* collected more *Juncus* and *Sambucus* than either *Bombus* species. *Bombus vosnesenskii* collected more Asteraceae and Rosaceae than *A. mellifera* (Table 5.2 and Figure 5.2).

On average the number of plant species represented in corbicular pollen loads differed significantly among bee species ($\chi^2=10.92$, P <0.01), with *A. mellifera* collecting fewer pollen types (1.3 ± 0.56) than either *Bombus* species, *Huntii*: 1.85 ± 1.0 ; *Vosnesenskii*: 1.88 ± 0.88 .

A Mantel test comparing the similarities between non-crop vegetation present within fields and the pollen types collected by bees showed no relationship (test statistic P = 0.95).

5.4. Discussion

We expected blueberry pollen to be prevalent in pollen loads given the abundance of this resource during crop bloom. A typical field of *V. corymbosum* may have more than 2500 blueberry bushes per hectare and upwards of 20 million flowers. The corbicular pollen loads of our species ranged from 15 to 52% *V. corymbosum*, demonstrating that it is far from a preferred resource for nest provisioning. The lack of collection of *V. corymbosum* pollen may be due to its poor nutritional value. For example, forage choice in *Bombus impatiens* has been shown to be influenced by the pollen's protein to lipid ratio (Vaudo et al., 2016), and in highly managed farm systems, foraging honey bees have been shown to collect a wide variety of non-crop floral resources based on the nutritional value of the collected pollen (Requier et al., 2015). The crude protein content of blueberries (13.9%) is generally considered below the level required to sustain honey bee nutrition (Kleinschmidt and Kondos, 1976). The low protein content and availability of alternate forage may reduce the value of *V. corymbosum* pollen to bees despite its prevalence in the landscape.

Pollen from the Rosaceae was frequently collected by all three managed bee species. In our region, the Rosaceae pollen type likely represents wild *Rubus* species (*R. spectabilis*, *R. parviflorus*, and *R. ursinus*), all species with bloom times overlapping that of *V. corymbosum* (E. Elle, pers. obs). These shrubs are not located within fields and are rare in edge vegetation surveys of our fields, but are reasonably common across the landscape in southern BC. Pollen from species in the Rosaceae is much more nutritionally rich than blueberry pollen, with among the highest crude protein (24.43%) of pollen commonly collected by honey bees (Forcone et al., 2011). Similarly, weed species from our fields such as *Ranunculus repens* and species in Fabaceae (*Trifolium repens*, *Trifolium pratense* and *Trifolium pratense*), also have high crude protein content, 21% (*T. repens*) and 23.7% (Fabaceae; (Somerville, 2001) and these types were collected in moderate frequency by *A. mellifera* and *B. vosnesenskii*. Our findings suggest that *A. mellifera* and *B. vosnesenskii* preferentially forage for pollen from species with high protein contents, as has been found with other bees (Leonhardt and Blüthgen, 2012), but that *B. huntii* does not. Further evidence for variation in protein preferences comes from differences in the collection of *V. corymbosum* pollen among the three managed pollinators, with *B. huntii* collecting more than three times the amount of this low-protein

pollen than collected by *B. vosnesenskii* and *A. mellifera*. Protein content preferences may be related to differences in colony characteristics of the species, which determine nutritional requirements. For example, *B. impatiens* colonies with low pollen stores or high need may ignore the nutritional profile of pollen relative to colonies whose pollen needs are met (Francis et al., 2016). If *B. huntii* had low stores or high need, these colonies may have been less discriminatory, a hypothesis that could be tested in future work. The lack of particular amino acids in a resource landscape may also increase the value of plant species in which the amino acid occurs, increasing the likelihood they will be visited by pollinators. Ericaceae have low cystine and histidine content, but average contents of leucine and valine (McLellan, 1977). Whether amino acid compositions drive pollen foraging in our study is unknown, but further study into composition differences between species in a landscape can further elucidate trends in pollen collection by worker bees.

Pollen foragers at our sites tended to forage for pollen from a single species; 55% of our samples were single-species samples. This trend is primarily driven by *A. mellifera* as 75% of workers returned to the colony with only one type of pollen, while the majority of workers among both bumble bee species returned with multiple pollen types (55%). *A. mellifera* workers tended to gather pollen from fewer species per foraging trip relative to workers from both *Bombus* species. This difference in the mean number of pollen types gathered per foraging bout between *Apis* and *Bombus* species may simply be a by-product of the difference in foraging communication between species. Pollinator species communicate with each other using a variety of mechanical, visual and chemical signals. The *A. mellifera* waggle dance was described more than 60 years ago (von Frisch and Lindauer, 1956) and is known to result in targeted foraging on particular plant species. In addition, it has been suggested that inspector honey bees can enhance a colonies response to changes in floral resource value (Granovskiy et al. 2012). The ability to communicate specific location information and relative value of foraging areas does not exist in *Bombus*, though their behaviour in the nest can increase foraging activity of colony mates (Dornhaus and Chittka, 2001). These differences could lead to more specificity of pollen collection by *Apis* relative to *Bombus*.

Our study demonstrates that managed pollinator species may differ in how much they are attracted to our target crop. The sampling of corbicular pollen loads represents pollen that is being provisioned for larva, and is generally not accessible for crop pollination, but does provide us with an idea of the relative attractiveness of different floral

species in our agroecosystem. For bees, pollen quality is determined via the composition of nutrients, with higher pollen quality associated with health and immune system responses (Di Pasquale et al., 2013). On highbush blueberry farms, blueberry pollen is among the least nutritionally robust, presenting the issue of pollination competition from non-crop plant species. Our results also suggest that the non-crop species present in pollen loads are from plants from outside farms, indicating that managed bees are leaving farms to forage elsewhere. This is not good from the perspective of farm managers.

The study of pollen load composition also furthers our understanding of the suitability of different bee species as managed pollinators. Pollinator species with relatively small worker populations need to have some degree of attractiveness or specialization to the pollen or pollination syndrome of the target crop species to overcome their lack in numbers. This is especially true in species requiring specialized pollination, such as *Vaccinium* species, where sonication is required to remove pollen from flowers. Plants with less stringent pollination requirements may benefit from workers that are nectar foraging through inadvertent pollen transfer. In an easily pollinated plant sheer number of low to average quality pollinators may be sufficient to meet pollination needs, while crops with more specialized pollination requirements may need to prioritize particular pollinator species adapted to the characteristics of the crop.

Farmers and land managers may also play a role in mitigating the siphoning of pollinators away from the target crop. In our study, honey bees gather pollen from a wide variety of weedy plants located within the field (*Fabaceae*, *Juncus spp.*, *Ranunculus repens*), suggesting a strong preference to diversify pollen resources at a farm level scale. Alternatively, *Bombus* species are foraging afield from the farm to collect pollen from Rosaceae. These trends introduce multiple problems for the farm manager in terms of managing non-crop species within and surrounding farms. The removal of non-crop floral resource may not have the intended consequences of promoting pollen foraging on a sub-optimal pollen such as that of blueberry. The maintenance of weedy edges or strips within an agricultural field may facilitate the diversification of pollen resources collected by honey bee colonies, potentially leading to increased pollen foraging on abundant crop flowers once a theoretical pollen diversity quota is reached. *Bombus* species in our study target Rosaceae, plants that are recommended for removal around farms due to being alternate hosts for the invasive berry pest *Drosophila suzukii* (Matsumura). Despite removal efforts, Rosaceae species exist in unmanaged land surrounding farms constituting a significant

proportion of the pollen being returned by managed bumble bee species, and potentially wild *Bombus* as well. A more thorough understanding of the flexibility of pollen foraging choices and plant characteristics that drive plant target selection can lead to an improvement in landscape management to improve crop pollination. In selecting managed pollinators for particular crops, or domesticating new species, pollen preference in agroecosystems is as important as more direct measures of pollinator effectiveness such as visits per minute and pollen deposition. Our findings demonstrate that based on pollen foraging of the candidate *Bombus* species, *B. huntii* is likely to be a more efficient pollinator of *V. corymbosum*.

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Table 5.1 Differences among three managed bee species (*A. mellifera*, *B. huntii*, *B. vosnesenskii*) in pollen types collected as assessed from corbicular pollen loads. A MANOVA indicated significant differences among the three species in their pollen profile, and these univariate ANOVAs illustrate the pollen types collected differentially by the three species. See also figure 5.2

Variables	Df	F	P
Asteraceae	2	3.2	0.042*
Fabaceae	2	1.92	0.14
Rosaceae	2	3.56	0.03*
<i>Cornus</i>	2	0.92	0.4
<i>Juncus</i>	2	4.21	0.016*
<i>Rumex</i>	2	0.24	0.78
<i>Sambucus racemose</i>	2	4.68	0.0103*
<i>Ranunculu repens</i>	2	2.98	0.053
<i>Vaccinium corymbosum</i>	2	16.63	<0.0001**
Unknown	2	1.2	0.3

* p < 0.05, ** p < 0.01

Table 5.2 Tukey HSD post-hoc comparisons of corbicular pollen loads from three pollinator species (*Apis mellifera*, *Bombus huntii*, *Bombus vosnesenskii*). Only significant differences are shown. Mean differences represent the estimated difference in the number of pollen grains between two species for a particular pollen type.

Pollen	Species A	Species B	Mean difference (A - B)	P value	95 % confidence interval	
					Lower bound	Upper Bound
Asteraceae	<i>B. vosnesenskii</i>	<i>A. mellifera</i>	5.45	0.05	-0.06	10.9
Rosaceae	<i>B. vosnesenskii</i>	<i>A. mellifera</i>	20.9	0.02	2.7	38.9
<i>S. racemosa</i>	<i>B. huntii</i>	<i>A. mellifera</i>	-8.3	0.02	-15.4	-1.1
	<i>B. vosnesenskii</i>	<i>A. mellifera</i>	-7.5	0.04	-14.6	-0.4
<i>V. corymbosum</i>	<i>B. huntii</i>	<i>A. mellifera</i>	37.1	> 0.001	20.3	53.9
	<i>B. huntii</i>	<i>B. vosnesenskii</i>	35.1	> 0.001	18.7	51.9

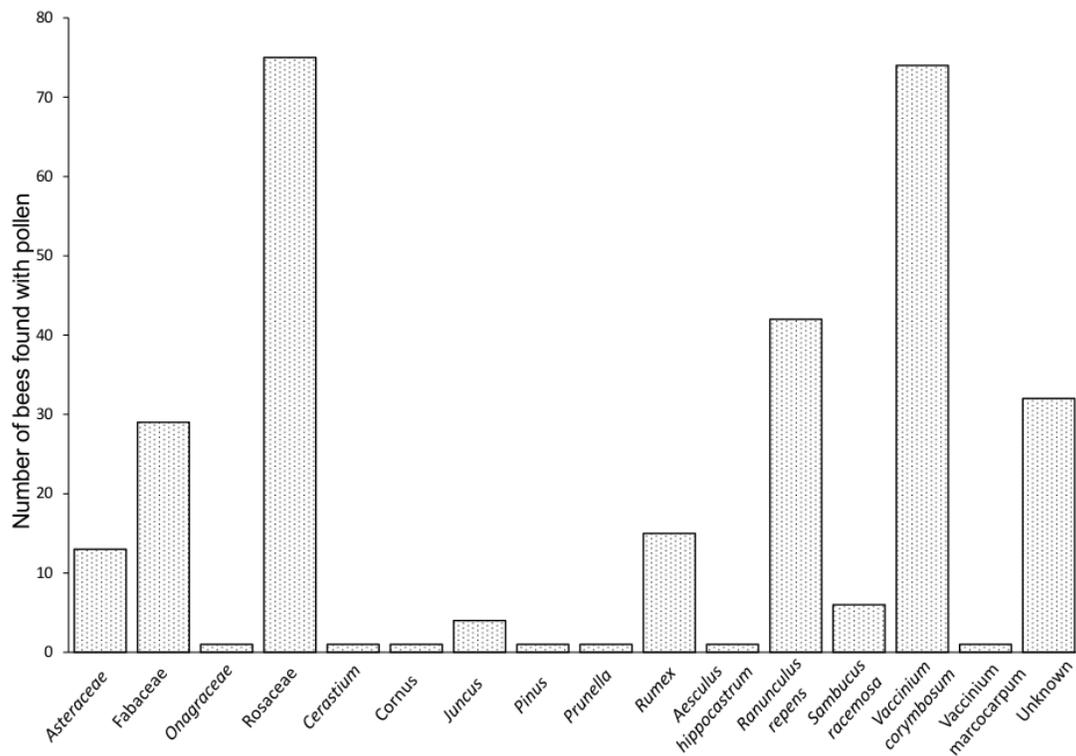


Figure 5.1 Total number of bees on which pollen from indicated species or group was detected in corbicular pollen loads. Three managed bee species were collected from three fields each for this analysis (n=180).

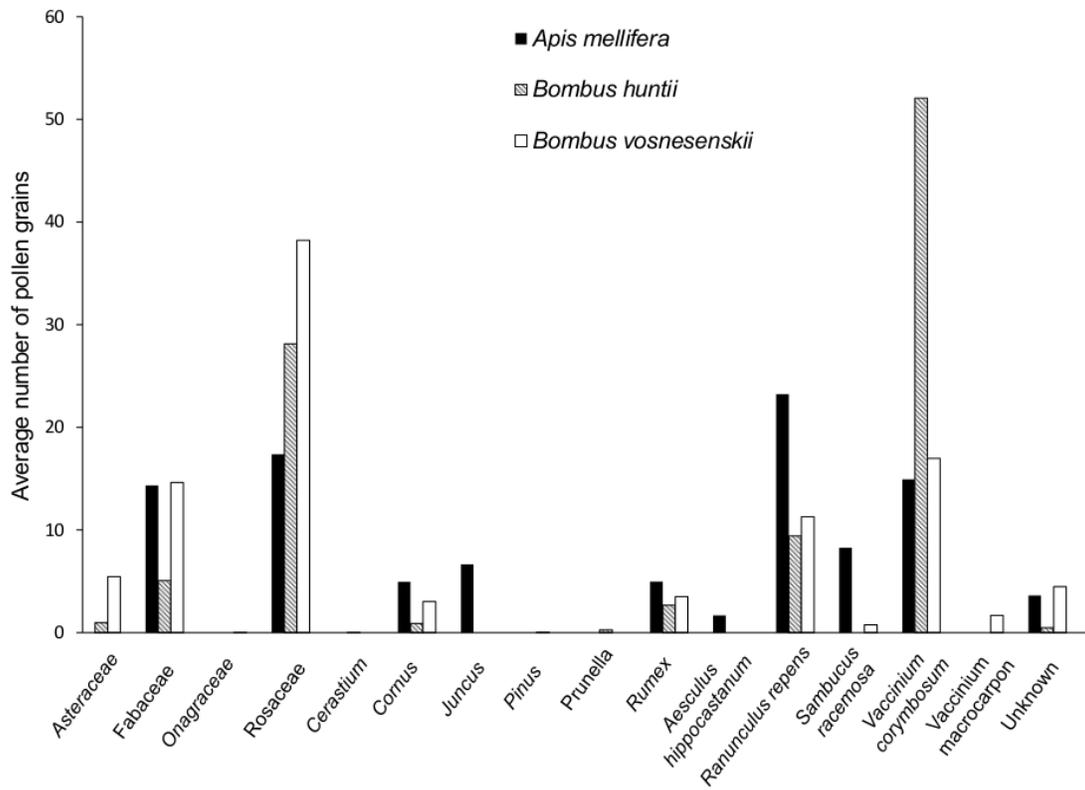


Figure 5.2 Average number of pollen grains of distinct plant species found in corbicular loads of three species of managed pollinators, each collected from three fields (n=180).

Chapter 6. General Conclusions

6.1. Landscape influences insect diversity

The composition of the landscape surrounding agricultural fields plays an important role in determining the availability of beneficial insects in crop fields. The effect of regional land use had a bigger influence on insect communities than land use at smaller scales, although abundance of particular guilds of beneficial insects was influenced by land use at local scales. My results corroborate previous studies that support the presence of semi-natural habitat at regional scales as an important component in maintaining insect biodiversity in agroecosystems (Holland and Fahrig 2000, Steffan-Dewenter et al. 2002, Thies et al. 2003, Holzschuh et al. 2007). My results also identify the variability in responses to various landscape elements by different functional groups of beneficial insects. Foraging range may serve as an effective predictor when estimating the scale at which organisms quantify the quality of habitat or resources. Differences in the scale at which species evaluate a landscape are further complicated by differential responses of functional groups to land use types. Pollinators likely benefit from foraging resources that are more frequently present in low management land use types, while pest predators or parasitoids may benefit from increased pest prey concentration resulting from agriculture. In addition, habitat that we may perceive as being beneficial, such as flowering agriculture, was identified as resulting in lower pollinator abundance. This may be more indicative of pollinator dilution over the large mass flowering agricultural landscape during blueberry bloom rather than a reduction due to the deleterious effects of flowering agriculture. Optimizing an agricultural landscape for beneficial insect conservation must consider and balance the opposing responses between different insect guilds.

6.2. Yield deficits as a product of bumble bee pollination and weather during bloom

My results corroborate previous work in highbush blueberry that illustrated the importance of bumble bees to crop pollination (Button and Elle 2014, Gibbs et al. 2016). Yield deficits are consistently present in highbush blueberry in British Columbia, a phenomenon that does not occur in its native area of Michigan (Gibbs et al. 2016). Differences in pollinator communities, or environmental conditions during bloom might be

responsible for the persistence in yield deficit. Mean minimum daily temperature was identified along with bumble bee visits as being predictive of yield deficit. The relationship between these two elements, and the exclusion of honey bee visits as an important predictive variable, reinforces the importance of wild pollinators in crop pollination (Garibaldi et al. 2013). Bumble bees generally have a lower temperature threshold at which they can fly and forage relative to honey bees, providing them with an expanded pollination window. Coupled with their effectiveness as *Vaccinium* pollinators, bumble bees play a disproportionate role in blueberry production.

6.3. Managed bumble bee species do not mitigate yield deficits

Neither of the managed *Bombus* species stocked in highbush blueberry fields resulted in the mitigation of yield deficits due to poor pollination. Despite being identified as an effective pollinator in *Vaccinium* crops (Stubbs and Drummond 2001, Javorek et al. 2002) the introduction of *Bombus* colonies into the field does not always improve yields in blueberry (Fulton et al. 2015). Bumble bee colonies rarely surpass a couple hundred workers, an amount which may be insufficient to successfully alter the number of flowers receiving saturated pollen levels in a highbush blueberry field. In my pollinator surveys it was rare to observe any of my managed bumble bee species in the field, despite their stocking directly into the hectare we studied. The small size of managed bumble bee colonies likely negates their superior ability as a pollinator of blueberry; instead, supporting populations of wild bumble bees is important (Chapter 3). Measurement of bumble bee colony metrics suggests that the two bumble bee species studied may recruit pollen foragers at different rates, with *B. huntii* higher than *B. vosnesenskii*. My model selection suggests that the most important predictive variables for pollen forager recruitment are the total production of gynes and number of males in the colony. The production of queens requires substantially more resources than workers due to size differences, necessitating the gathering and investment of more floral resources. Species with colonies that enter a reproductive state early, or for a prolonged period of time, may be better suited as effective crop pollinators. The increased demand of floral resources for the rearing of reproductive castes may benefit flowering crop pollination if they have an abundance of nearby pollen protein and nectar.

6.4. Managed species differ in pollen foraging targets

My results suggest that despite the relative abundance and proximity of floral resources, managed bee species forage predominantly outside of the blueberry agroecosystem for pollen. This is consistent with previous work that shows bumble bee species selecting pollen of higher protein and essential amino acid content (Leonhardt and Blüthgen 2012). Blueberry pollen is considered to be a relatively low quality pollen resource due to its low protein and essential amino acid content (Kleinschmidt and Kondos 1976). However, approximately 50% of all pollen collected from one managed pollinator species, *B. huntii*, was from highbush blueberry. Highbush blueberry pollen in both *B. vosnesenskii* and *A. mellifera* pollen loads was less than 20% of the total amount of pollen collected. Bumble bees are much more selective in pollen foraging choices relative to honey bees (Leonhardt and Blüthgen 2012), however, in my study both honey bees and one species of bumble bee preferentially foraged on non-crop flowers. Pollen from *Rubus* and *Ranunculus* species were the most common non-crop species in pollen loads. These flowers are easier to access than those of highbush blueberry, and their pollen is estimated to be within the proper threshold of protein content to be considered an good resource (Kleinschmidt and Kondos 1976). These results highlight the importance of species differences in ecosystem service delivery. Though not available for pollination due to being packed in corbiculae, pollen load compositions likely represent flower species that are benefitting from insect mediated pollination. Linking foraging choices with species characteristics might better explain these choices. *B. huntii* colonies tend to recruit pollen foragers at a greater rate as queen production increases. This increased protein need may result in *B. huntii* sacrificing pollen quality for pollen quantity. Characteristics of pollinator species that induce foraging on nearby floral resources are important in developing future pollinators for highbush blueberry.

6.5. Management recommendations

The increases in agricultural development in BC, specifically in flowering berry crops, has likely resulted in early flowering crop species like blueberry becoming increasingly important major resource pulses for wild *Bombus* species. Bumble bee colonies that are sufficiently fed grow not only larger in size, but in reproductive capacity as well, with larger colonies experiencing higher reproductive rates (Pelletier and Mcneil

2012). The early emerging nature and large resource requirement of foundress bumble bee queens is an ideal phenological overlap with highbush blueberry bloom, benefitting both mutualists in the plant-pollinator interaction. Wild bumble bee species may be more frequent highbush blueberry visitors than my bumble bee trial data suggests, as queens and early workers condition foragers on a similar search and reward system (Heinrich 1975). Wild bumble bee colonies are also not likely to be facing the same nutritional pressures as commercial colonies because wild colonies are typically much smaller than those reared artificially. Wild bumble bees may also use floral resources in the landscape much differently than the commercial species utilized in my trial. Further understanding of how wild pollinators are utilizing resources on and off the farm will allow us to better understand the ecological dynamics between pollinators and their habitat. Despite the BC blueberry production guide advocating for the removal of non-crop flowering weeds during bloom, my results suggest that maintaining within-farm floral resource diversity might ensure that more pollinators remain in the field to pollinate or at the very least acquire the necessary nutritional resources more efficiently.

In addition to changes regarding on-farm flowers, other management changes may be in order. Precautions should be taken regarding pesticide application post bloom when beneficial insects (primarily pollinators) are thought to have vacated blueberry fields. Pest predators and parasitoid species likely remain within crops year-round, since agricultural landscapes provide some degree of habitat and resources if the cropping structure is diverse enough to serve as refugia against pesticide application. It is also recommended that growers track bloom date and record first appearance of bumble bees on farms. Changes in the bloom period might be costly to highbush blueberry farmers if wild pollinator communities do not respond to changes in environmental variables at the same rate. This can risk both productivity and profitability of blueberry farms as well as affect the development and sustainability of nearby pollinator populations that have grown accustomed to an early bloom mass flowering crop. Finally, largescale conservation of semi-natural habitat should also be considered to maintain insect diversity. The blueberry agroecosystem is a large part of BC's lower mainland landscape, but semi-natural land near those farms is an essential component of on-farm production. Land managers should recognize that farms are an important part of the resource landscape for beneficial insect diversity, and so on-farm practices should minimize impact to non-target pests. It is

possible that enhancement of wildlife habitat on farms could improve biodiversity conservation throughout the agroecological landscape of southern BC.

6.6. References

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