

**Pollination in highbush blueberry  
(*Vaccinium corymbosum* L.) and the effects of  
surrounding landscape on wild bee abundance**

**by**

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Requirements for the Degree of  
Master of Science

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## **Abstract**

Over one third of the world's crops rely on pollination, primarily provided by bees, for production. I examined wild and managed pollinator contributions to yield in highbush blueberry in BC's lower mainland, and how local and landscape factors influence pollinator abundance. Honey bees made up the majority of flower visits, but half the visits to cultivar 'Bluecrop' were made by wild bumble bees. Pollination deficits declined with either increasing bumble bee visits or increasing total visits (honey bees and bumble bees combined). Bumble bee abundance increased with surrounding semi-natural land and declined with surrounding 'bee-friendly' agriculture. Local effects on bumble bee abundance disappeared in the absence of landscape influences. This work supports a growing body of literature that suggests wild bees are important crop pollinators that must be incorporated into agricultural management strategies in order to maximize potential crop yields.

**Keywords:** pollination deficit; mixed pollinator strategy; landscape; agricultural sprays; pollinator forage; blueberry

The most exciting phrase to hear in science,  
the one that heralds new discoveries,  
is not "eureka!" but "that's funny...!"

- Isaac Asimov

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# Chapter 1.

## General Introduction

One third of the world's agricultural crops rely on animal pollinators for some component of their production (Klein *et al.* 2007). Agricultural pollination is provided primarily by bees (Free 1993) both managed (National Research Council 2007; Mader, Spivak & Evans 2010) and wild (Kremen, Williams & Thorp 2002; Goulson 2003; Greenleaf & Kremen 2006), and has been valued at over \$210 billion globally (€153 billion; Gallai *et al.* 2009). However, agricultural intensification has increased at a pace that outmatches our ability to provide managed honey bee populations to fulfill pollination needs (Aizen & Harder 2009). It is important for us to know, then, how well crops are currently being pollinated, and the extent to which managed vs. wild pollinators are providing pollination services.

When pollen delivery to crop flowers is insufficient for the fertilization of all ovules, and so insufficient for either the production of maximum fruit number or fruit weight, the crop is considered to have a pollination deficit (Knight *et al.* 2005). These deficits are often measured using pollen supplementation experiments, wherein the deficit is measured as the difference in yield between flowers pollinated by bees and flowers additionally pollinated with excess pollen by hand (as in Ashman *et al.* 2004, Knight *et al.* 2005 or similar). Deficits are fairly common and have been studied extensively in wild plants (63% of 482 wild plant species examined experienced deficits; Knight *et al.* 2005), but deficits in agricultural crops have received substantially less attention (59% of only 17 examined crop species experienced deficits; Mayfield 1998). Deficits can be reduced by increasing pollinator visits, and thus pollen delivery, to crop flowers. This can be done either by increasing the number of honey bee hives hired and placed in a field (termed the “stocking rate”), or by implementing management strategies aimed at increasing the abundance of wild pollinators present in the agricultural landscape.

European honey bees are currently the most common managed pollinator in the world (National Research Council 2007), but many crops are also pollinated by wild bees (Kremen *et al.* 2002; Garibaldi *et al.* 2013). Wild pollinators in particular are receiving increasing recognition in agricultural systems as essential players in the reduction of pollination deficits (Holzschuh, Dudenhöffer & Tschardtke 2012; Garibaldi *et al.* 2013). This is in part because in some cases wild pollinators possess behaviours that can make them more efficient crop pollinators than honey bees. Tomatoes and peppers for example require their anthers to be sonicated in order to release pollen (Free 1993). This sonication (termed 'buzz pollination') is a behaviour that can be performed by bumble bees, but not by honey bees (Buchmann 1983). Wild pollinators are also more likely to fly and forage in cool wet conditions than honey bees (Javorek, Mackenzie & Vander Kloet 2002), and can provide pollination insurance for potential honey bee colony losses due to parasites and disease (Winfree *et al.* 2007). However, wild pollinators themselves are declining on a global scale (Potts *et al.* 2010). Understanding the contributions of wild pollinators to agricultural yields and factors that affect wild pollinator abundances in agroecosystems is therefore essential not only to determine how we can maximize crop yield and grower income, but also to provide a means by which industry can be encouraged to engage in pollinator conservation.

Wild pollinator abundances are strongly predicted by the availability of nesting sites (Potts *et al.* 2005) but also rely on available forage (Korpela *et al.* 2013). Wild bees are central place foragers and bumble bees can travel between 100m and 1750m from their nest to forage (Walther-Hellwig & Frankl 2000; Darvill, Knight & Goulson 2004; Osborne *et al.* 2008), suggesting both nest sites and food must be available at these scales. In agricultural landscapes, most crops bloom for short periods which may not completely overlap with the flight and foraging periods of wild insects. A consideration of both non-crop forage at the local scale, and alternative forage (crop or non-crop) at the landscape scale, is therefore useful for predicting wild pollinator use of agroecosystems.

When considering forage availability to bees in agricultural landscapes it is important to note that increased diet diversity can increase colony growth in honey bees (Sagili & Breece 2010). This diversification in diet can be facilitated by non-crop flowers (weeds) for pollinators foraging in primarily monocultured landscapes. Grassy field margins, weeds within fields, and margins sown with pollen and nectar-producing flowers

are known to enhance pollinator abundance within fields (Fussell & Corbet 1992; Morandin & Winston 2005; Pontin *et al.* 2006; Pywell *et al.* 2006; Hannon & Sisk 2009; Haaland, Naisbit & Bersier 2011; Korpela *et al.* 2013). Of course, agricultural intensification can reduce the diversity and availability of forage at the landscape scale (Kearns, Inouye & Waser 1998; Kremen *et al.* 2002; Goulson 2003), negatively impacting pollinator populations.

In this thesis I investigate pollination services to highbush blueberry (*Vaccinium corymbosum* L.), a buzz-pollinated crop (Free 1993) for which growers facilitate pollination by renting managed honey bee colonies. In Chapter 2 I focus on pollinator community composition and measure the relative visit rates of honey bees vs. wild bees to blueberry flowers as well as the level of pollination success in two cultivars of highbush blueberry. I also investigate how deficits are related to the type of visiting pollinator (managed honey bees and wild bees). In Chapter 3 I ask how the abundance of wild pollinators in blueberry fields is influenced by the composition of the surrounding landscape, as well as the intensity of local (on-farm) management. By understanding how important wild pollinators are to blueberry pollination, and which factors most strongly influence their abundance in this crop, growers will be able to implement management strategies that both enhance crop yields and possibly help to conserve wild pollinators in British Columbia's lower mainland.

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## **Chapter 2.**

# **Wild bumble bees reduce pollination deficits in a crop mostly visited by managed honey bees<sup>1</sup>**

### **Introduction**

Over one third of the world's crops rely on animal pollinators for some component of yield (Klein *et al.* 2007). Pollination of global agriculture has been estimated to value \$210 billion (€153 billion: Gallai *et al.* 2009) and is primarily provided by bees (Free 1993); both wild (Goulson 2003; Greenleaf & Kremen, 2006; Kremen *et al.* 2002) and managed (Mader *et al.* 2010; National Research Council 2007; Potts *et al.* 2010).

European honey bees (*Apis mellifera*), the most common managed pollinators in modern agriculture (National Research Council 2007; Potts *et al.* 2010), are often used to maximise pollination and yield (Kearns *et al.* 1998). Globally, managed honey bee populations have increased by 45% over the last 50 years, but this has not been enough to meet the demand imposed by the simultaneous rapid >300% expansion of pollinator-dependent crops (Aizen & Harder 2009). Existing managed honey bee populations have also been stressed by various factors including parasitic mites and disease (National Research Council 2007). Given these challenges to managed honey bee pollination, a greater understanding of the contributions of wild pollinators to agriculture is vital. In this chapter I investigate the contributions by both managed and wild pollinators to pollination in highbush blueberry (*Vaccinium corymbosum* L.), a pollinator-dependent crop.

Wild pollinators are known to provide pollination services to many crops (Garibaldi *et al.*, 2013; Kremen *et al.*, 2002), and increases in pollinator diversity have been shown to increase crop yields (canola: Morandin & Winston, 2005; coffee: Klein, Steffan-Dewenter, & Tscharntke 2003; watermelons: Kremen, Williams & Thorp 2002). Wild

<sup>1</sup> This chapter is currently in review: Button, L. and E. Elle, *in review* at Agriculture, Ecosystems, & Environment.

pollinators can provide pollination insurance against poor honey bee performance in bad weather (Javorek, Mackenzie & Vander Kloet 2002), and some crops are almost exclusively pollinated by non-*Apis* pollinators because of specialized pollination needs. Tomatoes and peppers, for example, require their anthers to be sonicated to release pollen, so are pollinated by managed bumble bees (*Bombus* spp.) in greenhouses because bumble bees are adept at sonicating flowers (Buchmann, 1983); this sonication is termed buzz pollination. Highbush blueberry is also buzz pollinated (Free 1993), and although honey bees will visit flowers to collect nectar, they may not be the most effective pollinators because they cannot sonicate flowers (Javorek, Mackenzie & Vander Kloet 2002). In highbush blueberry, four visits by a honey bee are required to transfer the same amount of pollen as a single visit by a bumble bee (Dogterom, Winston & Mukai 2000). The greater effectiveness of bumble bees at pollen transfer may explain why the abundance of pan-trapped bumble bees is positively correlated with fruit mass in highbush blueberry in our region (Ratti *et al.* 2008). A consideration of visit rates by honeybees vs. bumble bees would therefore be informative for growers seeking to maximize yield.

Field margins can provide a refuge for wild pollinators by providing nest sites as well as alternative forage when crops are not in bloom. The presence of potential nest sites is a strong predictor of wild bee communities (Potts *et al.*, 2005), and grassy field margins have been shown to enhance the abundance of wild pollinators within agricultural fields (Marshall, West & Kleijn 2006). Wild pollinators are also more likely to visit a crop if favourable habitats exist within the vicinity of the crop (Pitts-Singer & James, 2008), but central-place foragers like bees will vary in the distance they will travel from their nests to forage. For example, solitary bees will travel <300m from their nests to forage (Zurbuchen *et al.*, 2010) whereas bumble bees will travel between 500m and 1.75km (Darvill, Knight & Goulson 2004; Osborne *et al.* 2008; Walther-Hellwig & Frankl 2000). If wild pollinators are more effective pollinators than managed honeybees, and if wild pollinators are more likely to nest in field margins than at the center of a highly managed monoculture, then we may see higher abundances of pollinators and therefore higher crop yields towards the edges of fields than at increasing distances into fields.

Pollen supplementation experiments are often used in wild plants to measure if the extent reproductive output is limited by pollen delivery (Knight *et al.* 2005; Ashman *et al.* 2004). A pollination deficit is inferred when pollen-supplemented flowers or plants have

lower fruit set, seeds per fruit, or smaller fruit than those exposed to ambient pollination conditions (Knight *et al.* 2005). Pollination deficits are well documented in wild plants, for which Knight *et al.* (2005) found 63% of 482 species examined experienced them. In contrast, less research has been performed on crop species, for which Mayfield (1998) found that 59% of only 17 examined crop species experienced deficits. In agricultural systems, high pollination deficits equate to lowered yields and substantial economic consequences for the grower.

In this study I observed and trapped potential pollinators and experimentally estimated pollination deficits to investigate the following questions: 1) what are the pollinators of highbush blueberry in our region? 2) is there a pollination deficit in highbush blueberry? and 3) is pollination deficit reduced with increasing pollinator visits? Crop cultivars vary in self- and cross-fertility (Dogterom, Winston & Mukai 2000; Ehlenfeldt 2001), blooming period (Božek 2009), and in the case of highbush blueberry, flower size and shape (Courcelles, Button & Elle 2013), all of which have the potential to influence pollinator visit patterns. To account for these differences I chose to study two widely grown cultivars of highbush blueberry, cv 'Duke', and cv 'Bluecrop'. I also consider the importance of distance from the natural field edge for pollinator visits and pollination deficits. Finally I translate deficits into economic values which are useful for stakeholders in industry.

## **Methods**

### **Field Sites and Setup**

British Columbia (BC) produces 56% of Canada's blueberries (Statistics Canada 2012) and is one of the top three blueberry producing regions in the world (British Columbia Ministry of Agriculture 2011), generating \$83 million in sales for blueberries in 2010 alone (Statistics Canada 2012). Temporally variable factors like weather have been shown to influence the pollinator community and aspects of highbush blueberry yield such as fruit weight (Tuell & Isaacs 2010), so I conducted my study across two consecutive field seasons in 2011 and 2012, and included fields across the growing region of blueberries in BC. We included 14 fields of 'Bluecrop' and 12 fields of 'Duke'. Duke has a slightly

earlier (~3 days) but mostly overlapping blooming period with 'Bluecrop', and berries take less time to ripen (Ehlenfeldt & Martin 2010). Duke flowers are also larger than Bluecrop flowers (wider and longer corollas), which increases access by relatively short-tongued honey bees to nectar, and so affects pollinator visit patterns (Courcelles, Button & Elle 2013). In general, the blueberry bloom in our study area lasts about three weeks; mid-May to mid-June. Fields were located within 16 farms in BC's lower mainland (Fig 2.1). Ten farms had fields of both cultivars. For each field we determined the most natural edge as the one apparently containing the most non-crop forage and, potentially, nesting habitat, as opposed to field edges on farm roads or abutting another cultivar. To determine the effect of the natural edge on the pollinator community and measures of crop yield, sampling was conducted along three 100m long transects parallel to and at three distances from the natural edge (0m, 50m, 100m).

## **Pollinator community composition**

### ***Visual observations***

Each 100m transect was divided into ten, 10m intervals. Pollinators were observed on one randomly selected bush within each 10m interval for one minute, meaning 10 min of observation per distance and observation date. Only insects that entered the flower legitimately (through the corolla opening) and apparently contacted the stigma were counted as pollinators. We recorded both the number of individuals (abundance) and the total number of flowers visited (visit rates). As visit rate is more relevant to crop pollination than insect abundance we only consider visit rates here.

Honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.) were identified to species on the wing. Other insects, which can only be identified to species upon close examination, were grouped into mason bees (*Osmia* spp.), flies (almost exclusively *Syrphidae*), tiny bees (mostly *Ceratina* spp., *Halictus confusus* or *H. tripartitus*, and *Lasioglossum* (*Dialictus*) spp.), "other" bees (mid-sized species, mostly *Lasioglossum* subgenera *Lasioglossum* or *Evylaeus*, *Halictus rubicundus* or *Andrena* spp.) or wasps. Observations were limited to days in which weather patterns were conducive to pollinator activity (days with full or part sun, temperatures above 13°C, and non-windy conditions) and alternated among AM, midday, and PM. The number of observation dates differed

each year, with 3-4 observation dates per field in 2011 and 2-3 observation dates in 2012, due to variation in the number of days with weather conducive to pollinator activity.

### ***Pan trapping***

I used pan traps in 2011 to assess the community of insects available to pollinate blueberry. Nine wooden stakes were placed at 10m intervals along each of the three transects per field. Stakes were placed among the bushes with the tops embedded within the canopy, and green pans were stapled to the tops. In order to control potential color bias based on pollinator acuity and preference (Vrdoljak & Samways 2011), I used three pan trap colors (“white”, “lemon yellow”, and “bright blue” from “Touch of Color” brand). Pans had .36L capacity and were filled with soapy water and placed in regular order on top of the green pans within the field to collect flying insects within the blueberry canopy. Pan trapping was conducted twice per field, with at least a week between sample collections, in fair weather conditions for a minimum of 7 hours. One pan of each color (white, yellow, and blue) was collected into a single sample, resulting in three samples per transect. Insects were stored in 75% methyl ethyl alcohol for later pinning and identification to species.

### **Pollination Deficit Experiments**

In order to determine if fruit production was limited by pollination, I conducted hand pollination experiments at all fields in both years. Bushes were randomly selected within the ten intervals in each transect described earlier. Two canes with similar phenology, flower number, and length were selected and designated as either control (open to ambient pollination) or treatment (open to ambient pollination and supplemented by hand with pollen of the same cultivar). As a single cane on a blueberry bush often contains between 125 and 700 flowers, experiments were restricted to the terminal 10-20 flowers on a cane, henceforth referred to as floral or fruit “clusters”. Pollen was collected using a battery-operated toothbrush to sonicate flowers, and applied to stigmas of treatment flowers with paintbrushes once every 4-8 days to a maximum of 5 times during bloom. Pollination deficits were calculated as the difference in proportion fruit set and average fruit weight between treatment and control clusters. Pollinators were additionally excluded from a third, matched cluster in a subset of fields of each cultivar (three ‘Bluecrop’ and

three 'Duke') in 2012 only. The exclusion treatment was applied to clusters on 5 bushes per transect, randomly located in every other interval, to assess fruit production in the absence of pollinators. I used mesh bags of bridal veil netting to exclude pollinators, placed over wire frames to reduce contact between the netting and the flowers.

### ***Fruit Collection***

To prevent fruit loss from birds, over ripening, and picking, mesh bags were placed on all experimental fruit clusters between the end of bloom and harvest. Fruit was collected when at least 50% of the berries in a cluster were fully ripe. This collection method provides similar fruit weight data when compared to harvesting each berry as it ripens (Tuell & Isaacs 2010) but is substantially less logistically challenging when studying a large number of fields as I do here. Berries were refrigerated (maximum 2 days) until the number of fruit per cluster could be counted and the fruit collectively weighed. One berry from each cluster was selected in a haphazard fashion to be individually weighed and for seed counts (next section). These berries were frozen until processing.

### ***Seed Counts***

In order to establish fruit weight as an appropriate proxy for successful pollen delivery and fertilization, seeds were counted for at least 100 berries of each cultivar. Frozen berries were thawed, outer skin removed, and the berry contents were squeezed between the bottom and the inverted lid of a petri dish so that seeds were in a single dimension. The dish was then placed under a dissecting microscope and seeds were counted. Seeds were divided into three categories; true seeds, pseudo seeds, and ovules as per Desjardins and De Oliveira (2006).

## **Statistical Analyses**

### ***Pollinator community composition***

All analyses were conducted using SAS (9.3) statistical software (SAS Institute Inc. 2002) unless otherwise stated. I tested the effect of cultivar, distance from the natural edge, and year on honey bee visit rates using mixed linear models (Proc MIXED, SAS 9.3) with field included as a random effect. Honey bee visits were summed across the 10, 1-min observation periods within each transect to reduce zero inflation and give us a value



for total visits observed/10 min. This model was then run on log transformed honey bee visit data to eliminate heteroscedasticity.

Bumble bee visit rates had high levels of heteroscedasticity and zero inflation, and so were analyzed differently. Bumble bee visits were converted into a binary response of either present (1) or absent (0) at each distance for each field. To test the effect of cultivar, distance from the natural edge, and year on bumble bee presence/absence, I ran a generalized mixed linear model with a logit link function and binomial error, implemented by the GLIMMIX procedure in SAS (9.3). Again, field was included as a random effect. Other pollinators made up less than 3% of the total pollinator visits observed so visits were not analyzed.

I used mixed linear models to test the effect of cultivar and distance from the natural edge on pan trapped wild insect abundance and richness. Samples were summed across each transect to give a measure of the total abundance and richness of insects caught in each of the three 100m transects per field. Wasps and non-syrphid flies were removed from analyses as they were rarely seen on blueberry flowers (see results).

### ***Pollination deficits***

I calculated Pearson correlation coefficients between seed number and fruit weight to establish fruit weight as a proxy for pollination. I then tested the effect of treatment, cultivar, distance from the natural edge, and year on logistically transformed proportion fruit set (Warton & Hui 2011) and square root transformed average fruit weight using mixed linear models with field included as a random effect. This model was used twice; first on all paired control and pollen supplemented treatments, and secondly on only the subset of bushes from 2012 that also included exclusion treatments. I used a Tukey-Kramer post hoc test to examine the differences between fruit set and fruit weight for clusters exposed to ambient pollination conditions at increasing distance from the natural edge.

### ***Visit rates and pollination deficits***

I ran four separate model sets to determine if pollination deficits were reduced by honey bee, bumble bee, or total pollinator (honey bee + bumble bee) visits. Pollination deficits were calculated as the difference in fruit set or fruit weight between control and supplemented clusters on a single bush. Mixed effects regression models were performed

using the nlme package (Pinheiro *et al.* 2013) in R (R Core Team 2013). Each field was included as a separate point, using average pollination deficit for the field (averaging across bushes and distances) and the sum of all pollinator visits observed in each transect (averaged across field and corrected for sampling effort). This eliminated the zero inflation found in bumble bee visit rates in previous analyses. Model sets were run separately for each deficit estimate (fruit set, fruit weight) by cultivar and were ranked by Akaike's Information Criteria (AIC) using the MuMIn package (Barton 2013) in R (R Core Team 2013). Year was included in each model as a random effect.

## Economic analysis

In order to assess the total profit lost due to insufficient pollination, I performed an economic analysis on pollination deficit data. I estimated total fruit production per hectare under ambient pollination conditions (*c*) for each field (Eq. 2.1). Bushes/100m row was an average across the three 100m transects, canes/bush was averaged across 10 bushes/row stratified by 10m intervals as before, and fruit clusters/cane was averaged across one haphazardly selected cane per each of the 10 bushes/row. Fruit/cluster was an average of 2 clusters on each of 5 bushes per row.

$$\left(\frac{fruit}{ha}\right) = \left(\frac{rows}{100m}\right) * \left(\frac{bushes}{100m\ row}\right) * \left(\frac{canes}{bush}\right) * \left(\frac{clusters}{cane}\right) * \left(\frac{fruit}{cluster}\right) \quad (Eq. 2.1)$$

I then determined yield (*Y*) as fruit production in kg/ha under ambient pollination conditions (*c*), maximum pollination conditions (*s*), and total pollinator exclusion (*e*) for each field (Equations 2.2, 2.3, and 2.4 respectively) using the fruit/ha value from Eq. 2.1, and measurements of fruit weight (*FW*) and fruit set (*FS*) averaged across all clusters within treatment and field. Each of these yield values was then averaged across fields to attain an average yield value for each cultivar.

$$Y_c = \left[\left(\frac{fruit}{ha}\right) * FW_c\right] \quad (Eq. 2.2)$$

$$Y_s = \left[\left(\frac{fruit}{ha}\right) + \left[\left(\frac{fruit}{ha}\right) * (FS_{supplement-control})\right]\right] * FW_s \quad (Eq. 2.3)$$

$$Y_e = \left[\left(\frac{fruit}{ha}\right) - \left[\left(\frac{fruit}{ha}\right) * (FS_{control-exclusion})\right]\right] * FW_e \quad (Eq. 2.3)$$

Farm gate values (the price of blueberries sold directly from the farm) of \$1.58/lb from 2011 were used to calculate the dollar value that farmers could expect to earn for the yields calculated for each field under the three pollination conditions (ambient, supplemented, excluded). These values were then averaged across fields in order to attain an average dollar value for both cultivars and all treatments. These values do not take production costs into account but I assumed these were similar among fields.

## **Results**

### **Pollinator community composition**

#### ***Observations***

Across two years, we conducted 5300 minutes of pollinator observations, and counted 9591 insect visits to highbush blueberry flowers. Honey bees were the most frequent visitor (6818 visits observed, 71.1% of the total) and bumble bees were also common (2596 visits observed, 27.1% of the total). Other pollinators made up 1.8% of the total observed visits (43 by tiny bees, 11 by *Osmia*, 38 by other bees, 78 by flies, 6 by wasps, and one butterfly visit). Although observations were not categorized as to the type of fly for this study, subsequent research has found that syrphids make up 89% of fly visits to highbush blueberry in our region (Elle unpublished data). There were significantly more honey bees observed visiting Duke than Bluecrop, and no effect of distance from the natural edge on number of honey bee visits observed for either cultivar (Table 2.1, Fig 2.2). Bumble bees visited Bluecrop more often than Duke, and were observed more frequently closer to the natural field edge than at either 50m or 100m into the field (Table 2.1, Fig 2.2). There were significantly more visits overall to Duke than Bluecrop (Table 2.1, Fig 2.2), and there was no effect of year on either honey bee visits or bumble bee presence (Table 2.2).

#### ***Pan traps***

In 2011 we collected a total of 1,279 specimens in pan traps (species list provided in Appendix A). The total catch was comprised primarily of honey bees (51.1% of total catch) with only 3.8% of the catch comprised of *Bombus* spp. (primarily *Bombus flavifrons*

and *Bombus mixtus*). Other bees collected included *Andrena* spp. (19.5%; primarily *A. hemileuca*), Halictidae (8.4%; primarily *Lasioglossum (Dialictus)* spp.), *Osmia* spp. (1.7%), and *Ceratina* spp. (1.3%). Syrphid flies made up 0.7% of the total catch and were included in the analyses as we observed them visiting blueberry flowers. Wasps and other (non-syrphid) flies comprised 13.2% of the total catch, but were removed from analyses as they were rarely ever seen visiting blueberry flowers. There was a significant effect of cultivar on both wild (non-*Apis*) insect abundance and species richness (Table 2.2, Fig 2.3), with higher abundance and richness of wild insects in Bluecrop than Duke. The effect of distance on wild species abundance and richness was non-significant, though there was a general trend towards declining abundance and richness at increasing distances into the field (notably for Bluecrop; Fig 3).

## **Pollen limitation**

Fruit weight was strongly correlated with, and therefore an appropriate proxy for, seed set (Duke:  $n=100$ ,  $r = 0.36$ ,  $P = 0.0002$ ; Bluecrop:  $n=100$ ,  $r = 0.58$ ,  $P < 0.0001$ ). Duke had significantly higher fruit set and average fruit weight than Bluecrop when open to ambient pollination, and fruit weight was significantly higher in 2012 than in 2011 for Duke, but not Bluecrop (Tables 2.3 and 2.4, Fig 2.4). Generally, ambient pollinated clusters closest to the natural edge had higher fruit set and fruit weight than those 100m into the field, though Tukey-Kramer post hoc analyses showed that this trend was only significant in 2012 (fruit set 2012; Bluecrop  $P = 0.04$ , Duke  $P = 0.3$ ; fruit weight 2012; Bluecrop  $P = 0.004$ , Duke  $P = 0.025$ ). Pollen-supplemented flowers had significantly higher fruit set and heavier fruit than flowers pollinated by insects alone, though this difference was greater for Bluecrop than Duke (Tables 2.3 and 2.4, Fig 2.4). Flowers from which pollinators were excluded had significantly lower fruit set and average fruit weight than either control or pollen supplemented treatments (Fig 2.4).

## ***Visit rates and pollination deficits***

Declines in fruit set deficits were most supported by models that included both honey bee and bumble bee visits for both cultivars. Though support was only slightly less strong for models that contained bumble bees alone or honey bees alone ( $\Delta AIC < 2$  (Burnham & Anderson 2002); Table 2.4; Fig 2.5), model weights for Duke in particular

were much higher for total visits than either bumble bees or honey bees alone (Table 2.4). Declines in fruit weight deficit were most supported by bumble bee visits alone for both cultivars, though  $\Delta AIC$  values between this model and models including both honey bees and bumble bees were less than 2 suggesting that they hold similar levels of support (Burnham & Anderson 2002), the weights of subsequent models were substantially smaller suggesting that bumble bees are indeed the strongest predictor of fruit weight deficit (Table 2.4; Fig. 2.5). Of note is that honey bee visit rates alone were almost always the least supported model (Table 2.4; Fig. 2.5), suggesting that honey bee visits are not enough to result in a reduction in pollination deficits in our study system.

## **Economic estimates**

Under ambient (control) pollination conditions, there are approximately 14.7 million fruit/ha in Bluecrop (approximately 18,200 kg/ha) and 11 million fruit/ha in Duke (approximately 17,100 kg/ha). If bushes received maximum pollination (estimated with hand-supplementation) these yields would increase to approximately 23,500 kg/ha in Bluecrop and 19,300 kg/ha for Duke. In the absence of pollinators, yields would decline to 6,000 kg/ha for Bluecrop, and to 5,700 kg/ha for Duke.

At a farm gate value of \$1.58/lb I estimate an income of approximately \$63,400/ha for Bluecrop growers, and \$59,400/ha for Duke growers, under current pollination conditions. Duke growers could be making an additional \$7,800/ha whereas Bluecrop growers could be making an additional \$18,400/ha if all flowers achieved maximum possible pollination. In the absence of pollinators, growers would lose \$32,214/ha for Bluecrop and \$51,834/ha for Duke compared to current levels of pollination.

## **Discussion**

British Columbia's highbush blueberry crop is a multimillion dollar industry that is experiencing sub-optimal pollination conditions. I have shown that yields would decline an average of 50-80% from current yield estimates in the absence of pollinators, and have the potential to increase by up to 30% with maximum pollination. Previous research in other crops suggests the combination of wild pollinators and managed honey bees can

maximize yield (Garibaldi *et al.* 2013; Holzschuh *et al.* 2012). My study similarly illustrates that a combination of both managed and wild pollinators results in the lowest pollination deficits. Honey bees, despite providing the majority of observed visits, did not reduce pollination deficits in this crop in BC.

### **Pollinator community composition: observations vs. pan traps**

The majority of my observed visits were made by honey bees (71%) and bumble bees (27%), with only 2% by “other” insects. In contrast, pan trapping collected a substantially different insect community, with 45% of the catch being comprised of these “other” insects (primarily *Andrena* spp. and *Halictidae*). The catch of a previous study in our region consisted of 6% other (non-*Bombus* or *Apis*) bees (Ratti 2006), and in Oregon, Halictids (specifically *Lasioglossum* spp.) were the most common pan trapped wild pollinator in blueberry fields (Rao, Stephen & White 2009). My study shows that while pan traps are useful in identifying the community as a whole, active pollinators that are potentially providing services to the crop itself can only be accurately assessed through observations. When communities are more diverse than what I found in this study, netting insects off of crop flowers would be the best method of assessment.

Although nineteen percent of pan trapped specimens were of the genus *Andrena* I rarely saw species within this genus visiting blueberry flowers. In Michigan, the most prevalent wild pollinators observed visiting blueberry flowers were from the genus *Andrena* (Tuell, Ascher & Isaacs 2009), primarily *A. carolina* Viereck, a *Vaccinium* specialist (LaBerge 1980; cited as *A. longifacies*). However, BC is well outside of the native range of this eastern *Vaccinium* specialist. As *Andrena* are ground-nesting excavators (Michener 2007) their prevalence in pan trap samples may indicate that they nest in the open soil between the rows of bushes within fields in our region and are foraging outside of fields.

### **Cultivar differences in pollinator community**

Although there are several studies that have examined the pollinator community composition in highbush blueberry (Mackenzie & Winston, 1984; Rao, Stephen & White 2009; Ratti 2006; Tuell, Ascher & Isaacs 2009), none have addressed whether the community differs between different cultivars. My observations revealed a significant difference in the pollinator community between cultivars, with relatively more honey bees

visiting Duke than Bluecrop and relatively more bumble bees visiting Bluecrop than Duke. This cultivar difference is likely due to morphological differences in floral shape between the two cultivars that make it more difficult for honey bees to access nectar rewards from Bluecrop compared to Duke (Courcelles, Button & Elle 2013). Because honey bees accounted for so many of the total visits, there were also significantly more visits overall to Duke than Bluecrop. This effect of cultivar was also reflected in yield (fruit set and fruit weight were higher in Duke than Bluecrop), and pollination deficits, though present in both cultivars, were significantly lower in Duke than Bluecrop. Cultivar must be considered both when comparing results among studies and regions, and when interpreting results within studies, some of which use multiple unspecified cultivars (e.g. Ratti *et al.* 2008). This caveat is likely true for any pollinator-dependent crop where cultivars differ in floral morphology (Courcelles, Button & Elle 2013).

### **The effect of field edges**

In general, field edges and natural landscapes surrounding fields are expected to provide nesting habitat for wild pollinators (Kennedy *et al.* 2013). Field margins may also provide forage when the crop is not in bloom. Extensive work in Europe has shown that field margins sown with pollen- and nectar-producing plants have the potential to supplement available forage and increase wild pollinator abundance and diversity in agricultural landscapes (Carvell *et al.* 2011, 2007; Haaland, Naisbit & Bersier 2011; Korpela *et al.* 2013; Pywell *et al.* 2006).

Wild bumble bees will forage 500m on average from their nest in search of food (Walther-Hellwig & Frankl, 2000) while smaller bees will travel shorter distances (Greenleaf *et al.* 2007). I found abundance of wild bees declined with increasing distance from the natural edge for both my pan trap data (Fig 2.3; non-significant trend) and my observations of flower-visiting bees (Fig 2.2). It is likely that many wild bees (bumble bees in particular) are foraging on blueberry closer to field edges, and thus closer to potential nesting sites. This foraging pattern may explain the generally higher fruit set and fruit weight I observed closer to natural edges. In BC's lower mainland, highbush blueberry field edges are often unmanaged strips of weeds and grasses or woody debris (Button personal observation). These edges range in size from a single strip a few meters wide to an entire adjacent forest or meadow. Further studies should examine these broad

differences in surrounding landscape, and consider whether enhancing field edges could benefit wild pollinators and thus impact crop yield.

### **Deficits in relation to pollinator visits: honey bees vs. bumble bees**

Wild pollinators have been shown to provide insurance against consistent losses in managed honey bee populations (Winfree *et al.* 2007) and many crops have shown increased yields when wild pollinators are in high abundance regardless of honey bee visit rates (Garibaldi *et al.* 2013). Available evidence therefore suggests that honey bees may supplement, but cannot replace agricultural pollination by wild insects (Garibaldi *et al.* 2013; Holzschuh *et al.* 2012). In this study, I demonstrated that both cultivars examined experienced lower pollination deficits when either bumble bee visits or total pollinator visits were high. In contrast, neither cultivar had a strong relationship between pollination deficit and honey bee visit rates alone. This could be due to the greater efficacy of bumble bees at pollinating blueberry (Dogterom, Winston & Mukai 2000; Javorek, Mackenzie & Vander Kloet 2002), but there may also be an interaction between bumble bees and honey bees in which the presence of bumble bees increases the efficacy of honey bee pollination by encouraging greater movement among plants (Brittain *et al.* 2013; Greenleaf & Kremen, 2006).

Bumble bees also have a lower temperature threshold for activity than honey bees, so are expected to forage earlier and later in the day when temperatures are cooler (Corbet *et al.* 1993), and even under weather conditions such as light rain that are less conducive to honey bee activity (Javorek, MacKenzie, and Vander Kloet 2002) . As my pollinator observations were conducted under generally fair conditions, it may be that bumble bee visit rates have been underestimated. The relationship between bumble bee visit patterns and blueberry yield may indeed be stronger than what I have shown here if weather conditions adequate for bumble bees but not honey bees had been included in my sample design.

### **Economic implications and conclusions**

I have calculated that Bluecrop growers could be earning an additional \$18,400/ha, and Duke growers would earn an additional \$7,800 if pollinator activity were increased.



This is an increase of up to one third over current income. Consideration of pollinators in an economic sense is therefore essential for not only sustaining, but improving current yields and profits.

Pollination services have been valued at over €153 billion worldwide (Gallai *et al.* 2009). Previous studies have demonstrated that deficits in crops can be substantial (coffee: Ricketts *et al.* 2004; canola: Morandin & Winston, 2006). Such studies have led to various agro-environment schemes to conserve and/or improve the surrounding land for pollinators (Carvell *et al.* 2011, 2007; Morandin & Winston, 2006; Ricketts *et al.* 2004), and when implemented in Michigan blueberry resulted in an increase in yield three years later (Blaauw & Issacs 2014). The use of pollinator enhancements to reduce the economic costs of suboptimal pollination could also be considered for BC. In that case, a more detailed economic analysis than what I have provided in this thesis would also include costs associated with enhancements including site preparation, planting, and maintenance, as well as potential negative impacts of enhancements such as whether they are a source of unwanted pests. Habitat enhancements were not the focus of my research, but should they occur in BC, future research should work towards understanding their costs as well as their benefits for pollination.

My work shows that pollination deficits are related to visits provided by both honey bees and wild bumble bees, meaning a mixed pollinator strategy is required to achieve the highest yields in our region. This strategy must both maintain current honey bee populations, while enhancing bumble bee populations and field attractiveness to bumble bees.

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## Tables

**Table 2.1** Mixed linear models testing the effect of cultivar, distance from the natural edge, and year on log transformed honey bee visit rates with field included as random effect (Proc MIXED, SAS 9.3). Bumblebee visits were converted into a binary response of either visited (1) or not visited (0) and analysed for the same predictor variables using a generalized mixed linear model (Proc GLIMMIX, SAS 9.3). DF is given as (num, denom). Mean values are shown in Figure 2.2.

Response	Predictor variables	DF	F value	<i>P</i>
log(honeybee visits + 1)	cultivar	1, 501	73.53	<b>&lt;0.0001</b>
	distance	2, 501	0.01	0.99
	year	1, 501	0.35	0.55
	cultivar*distance	2, 501	0.60	0.55
	cultivar*year	1, 501	1.03	0.31
	distance*year	2, 501	0.11	0.90
	cultivar*distance*year	2, 501	0.28	0.76
bumblebee presence (binary)	cultivar	1, 501	14.69	<b>0.0001</b>
	distance	2, 501	3.53	<b>0.030</b>
	year	1, 501	3.33	0.069
	cultivar*distance	2, 501	0.37	0.69
	cultivar*year	1, 501	1.40	0.24
	distance*year	2, 501	0.96	0.38
	cultivar*distance*year	2,501	0.05	0.95



**Table 2.2** Mixed linear models of 2011 pan trap data, testing the effect of cultivar and distance on log transformed wild insect abundance and log transformed wild species richness (Proc MIXED, SAS 9.3). Field was included as a random effect. DF is given as (num, denom). Mean values are shown in Figure 2.3.

Response	Predictor variables	DF	F	<i>P</i>
log (abundance + 1)	cultivar	1,57	7.89	<b>0.007</b>
	distance	2,57	0.6	0.55
	cultivar*distance	2,57	1.22	0.30
log (richness + 1)	cultivar	1,57	7.2	<b>0.009</b>
	distance	2,57	0.46	0.63
	cultivar*distance	2,57	1.42	0.25

**Table 2.3** Mixed linear models testing the effect of treatment, cultivar, distance and year on logistically transformed proportion fruit set (# fruit/# flowers). Treatments included controls open to ambient pollination (c), flowers supplemented by hand (s), and flowers for which pollinators were excluded (e). All variables were included in a single model for fruit set and a second model for fruit weight. Analyses comparing treatments c, and s for both years, and treatments e, c and s for a single year, were conducted separately as exclusions were only implemented in 2012 in a subset of fields. DF is given as (num, denom). Mean values are presented in Figure 2.4.

Predictor variables	cs: total branches = 3003			ecs: total branches = 270		
	DF	F value	<i>P</i>	DF	F value	<i>P</i>
treatment	1,2850	85.02	<b>&lt;0.0001</b>	2,240	121.12	<b>&lt;0.0001</b>
cultivar	1,2850	64.56	<b>&lt;0.0001</b>	1,240	14.18	<b>0.0002</b>
cultivar*treatment	1,2850	24.37	<b>&lt;0.0001</b>	2,240	6.01	<b>0.0028</b>
distance	2,2850	6.70	<b>0.0013</b>	2,240	4.10	<b>0.018</b>
treatment*distance	2,2850	1.15	0.32	4,240	1.21	0.31
cultivar*distance	2,2850	0.72	0.49	2,240	1.18	0.31
cultivar*treatment*distance	2,2850	0.13	0.88	4,240	0.17	0.95
year	1,2850	9.71	<b>0.0019</b>			
year*treatment	1,2850	0.77	0.38			
year*cultivar	1,2850	1.64	0.20			
year*cultivar*treatment	1,2850	0.55	0.46			
year*distance	2,2850	1.65	0.19			
year*treatment*distance	2,2850	1.53	0.22			
year*cultivar*distance	2,2850	0.57	0.57			
year*cultivar*treatment*distance	2,2850	0.01	0.99			

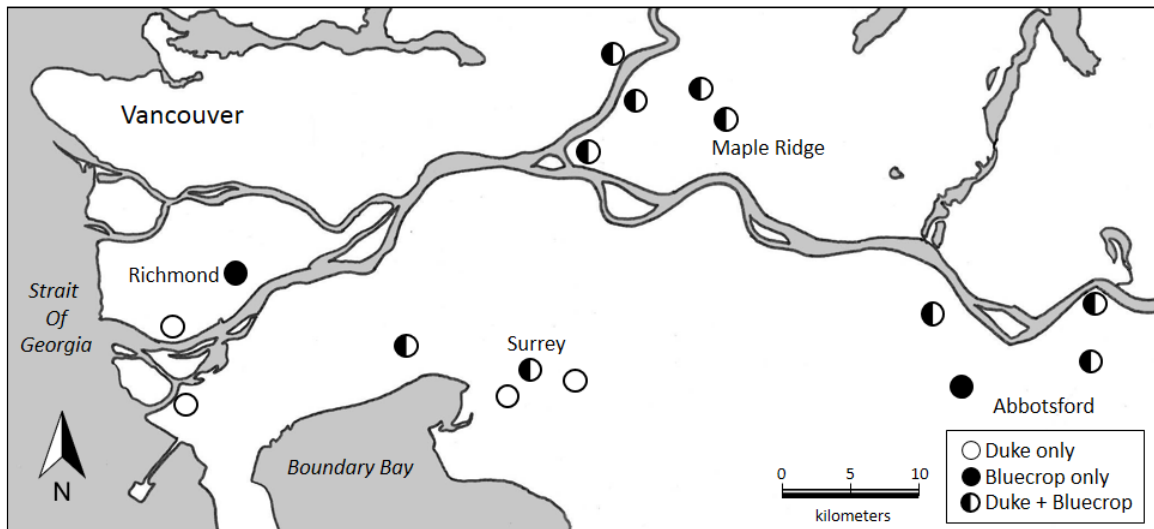
**Table 2.4 Mixed linear models testing the effect of treatment, cultivar, distance and year square root transformed average fruit weight. Treatments included controls open to ambient pollination (c), flowers supplemented by hand (s), and flowers for which pollinators were excluded (e). All variables were included in a single model for fruit set and a second model for fruit weight. Analyses comparing treatments c, and s for both years, and treatments e, c and s for a single year, were conducted separately as exclusions were only implemented in 2012 in a subset of fields. DF is given as (num, denom). Mean values are presented in Figure 2.4.**

Predictor variables	cs: total branches = 3003			ecs: total branches = 270		
	DF	F value	<i>P</i>	DF	F value	<i>P</i>
treatment	1,2843	169.96	<b>&lt;0.0001</b>	2,226	73.37	<b>&lt;0.0001</b>
cultivar	1,2843	177.69	<b>&lt;0.0001</b>	1,226	2.55	0.11
cultivar*treatment	1,2843	20.32	<b>&lt;0.0001</b>	2,226	6.93	<b>0.0012</b>
distance	2,2843	4.59	<b>0.010</b>	2,226	1.82	0.16
treatment*distance	2,2843	0.10	0.91	4,226	0.40	0.81
cultivar*distance	2,2843	0.13	0.88	2,226	6.13	<b>0.0026</b>
cultivar*treatment*distance	2,2843	0.33	0.72	4,226	0.70	0.59
year	1,2843	22.58	<b>&lt;0.0001</b>			
year*treatment	1,2843	0.11	0.74			
year*cultivar	1,2843	30.29	<b>&lt;0.0001</b>			
year*cultivar*treatment	1,2843	2.70	0.10			
year*distance	2,2843	2.89	0.056			
year*treatment*distance	2,2843	0.31	0.74			
year*cultivar*distance	2,2843	1.11	0.33			
year*cultivar*treatment*distance	2,2843	0.42	0.66			

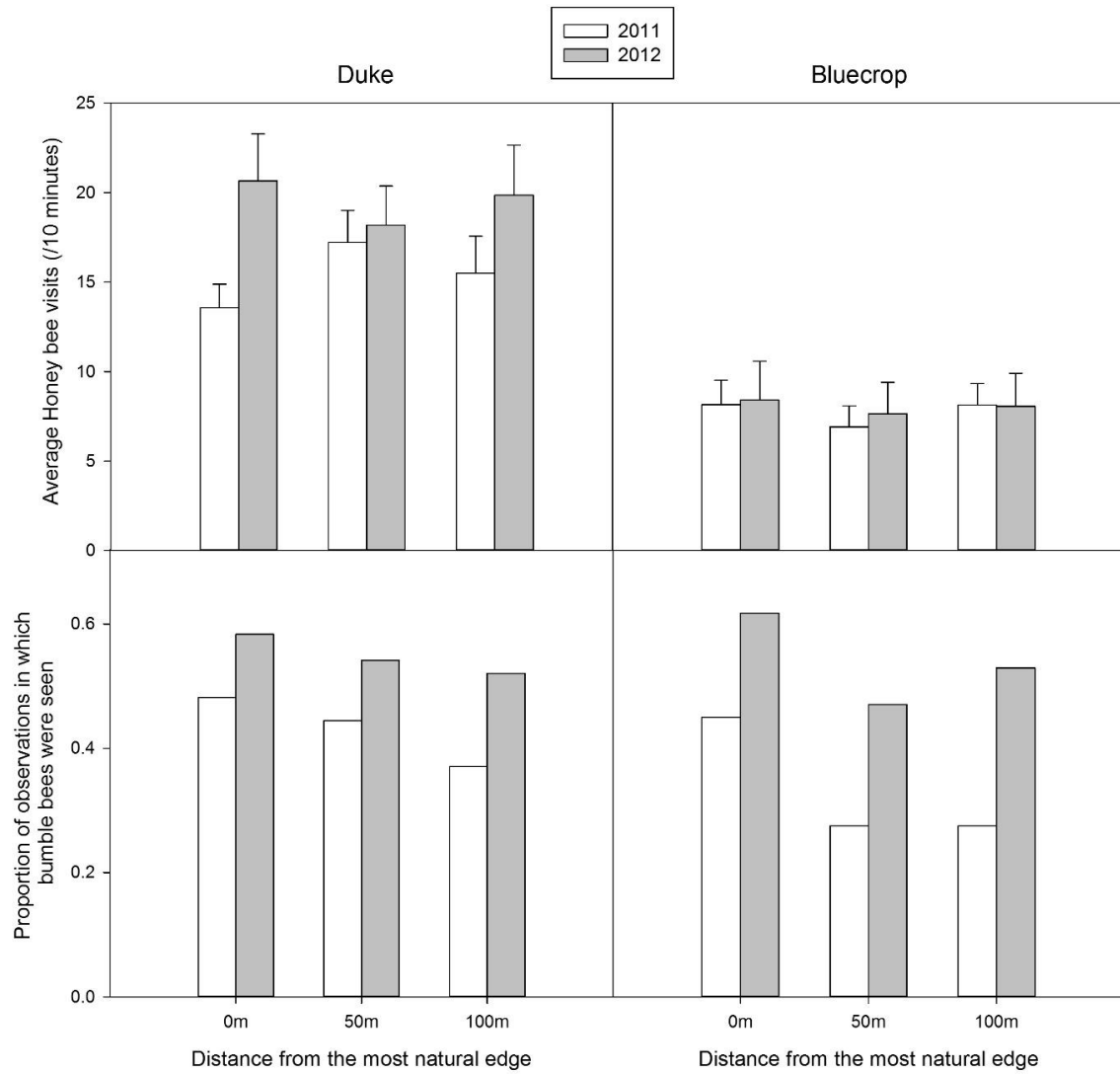
**Table 2.5 Model selection components for 1) fruit set (# fruit / # flowers) and 2) fruit weight (g) deficits (supplement – control) as explained by pollinator visits. Visits were grouped as honey bees alone, bumble bees alone, or honey bees and bumble bees combined. Because cultivars differed for both deficit values and pollinator visit rates, separate models were constructed for each cultivar for each yield metric. Predictive models are presented in the order of most to least supported within each response variable. Models that fall within  $\Delta AIC < 2$  and have higher weights are said to have substantial support, whereas those with  $\Delta AIC > 2$  and lower weights are said to be much less supported (Burnham and Anderson, 2002).**

Response variable	Cultivar	Predictor variables	df	Log <sub>e</sub> ( $\xi$ )	AIC	$\Delta AIC$	w
1) Fruit set deficit	Duke	Total visits	5	28.73	-79.20	0.00	0.50
		Bumble bees	4	33.38	-77.30	1.90	0.19
		(Null)	3	38.29	-76.89	2.31	0.16
		Honey bees	4	32.85	-76.86	2.34	0.15
	Bluecrop	Total visits	5	13.38	-46.69	0.00	0.37
		Bumble bees	4	17.82	-46.03	0.66	0.27
		Honey bees	4	18.35	-45.36	1.34	0.19
		(Null)	3	23.00	-45.14	1.56	0.17
2) Fruit weight deficit	Duke	Bumble bees	4	9.13	-25.03	0.00	0.49
		Total visits	5	3.19	-23.45	1.58	0.22
		(Null)	3	12.68	-23.35	1.68	0.21
		Honey bees	4	7.08	-21.23	3.80	0.07
	Bluecrop	Bumble bees	4	3.80	-15.43	0.00	0.62
		Total visits	5	-0.87	-14.13	1.31	0.32
		(Null)	3	6.10	-9.86	5.57	0.04
		Honey bees	4	1.42	-8.42	7.01	0.02

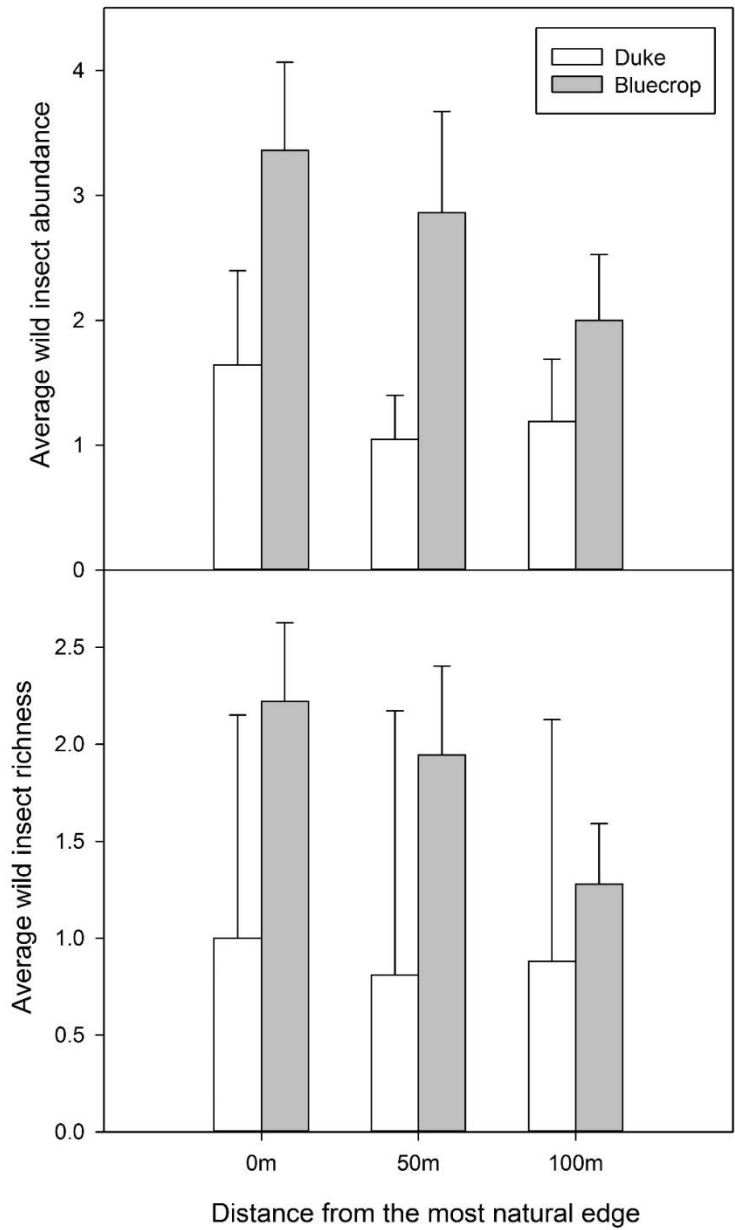
## Figures



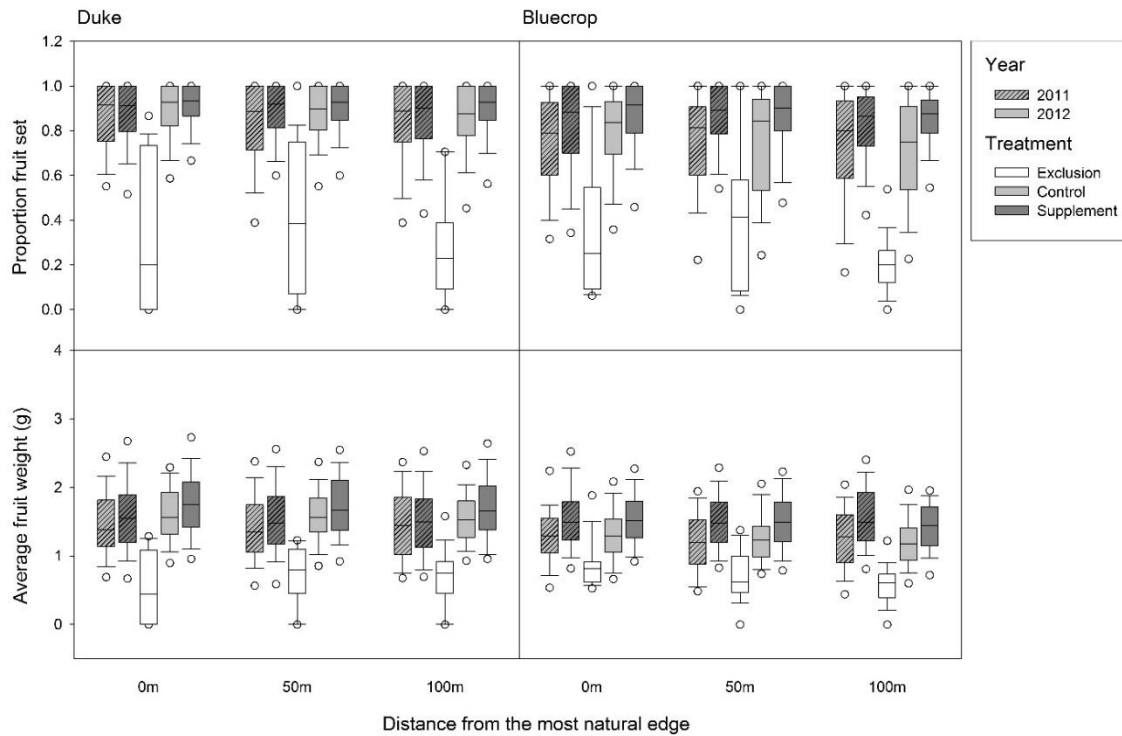
**Figure 2.1** Map of blueberry fields. Open circles indicate a cv. Duke field, filled a cv. Bluecrop field. Circles with both colors indicate a farm where both cultivars were present and one field of each was included in the study.



**Figure 2.2** Average visits by honey bees and the proportion of observations in which bumble bees were seen in Duke (left side) and Bluecrop (right side) cultivars by distance from the natural edge and year. Whiskers denote standard errors. Statistical analyses are shown in Table 2.1.

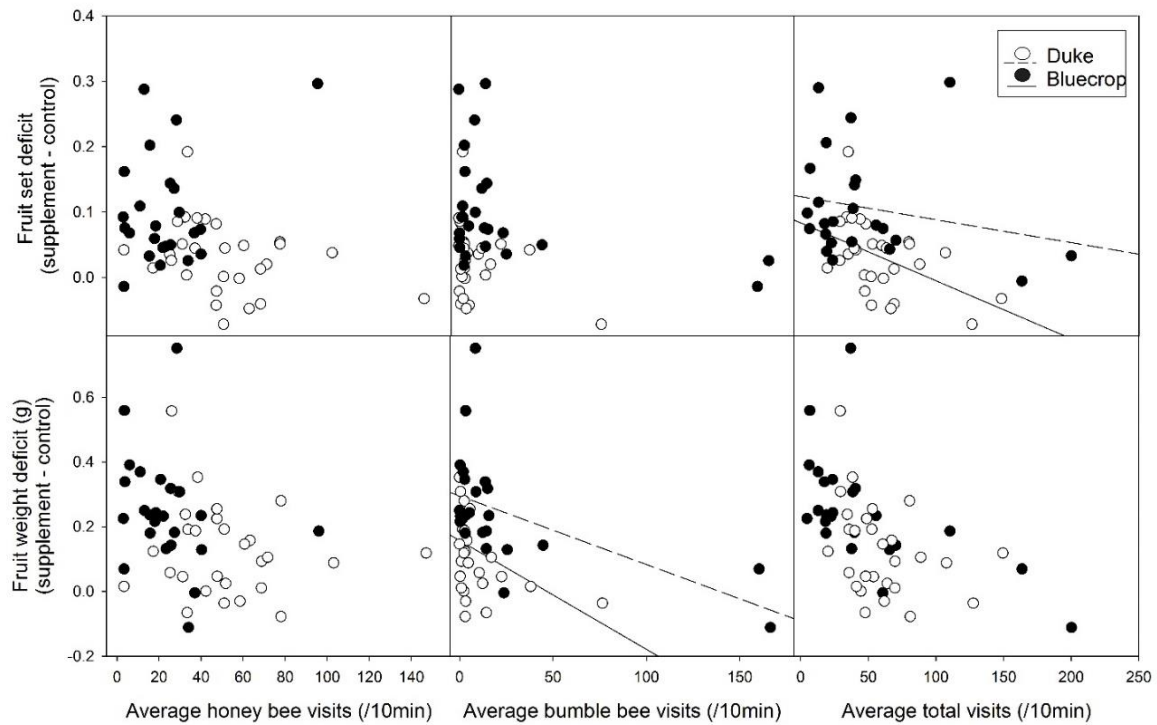


**Figure 2.3** Average abundance and average richness of wild insects caught in pan traps across years, cultivars, and distance from the natural edge. Wild insects included all bees or syrphid flies caught except *Apis mellifera* (as honey bees are managed and not considered “wild”), and were comprised primarily of species from the genera *Andrena* (19.5% of total catch), and *Lasioglossum* (6.6% of total catch; see Appendix A). Whiskers denote standard errors.



**Figure 2.4** Proportional fruit set (# fruit / # flowers) and average fruit weight (g) for both Duke and Bluecrop cultivars across treatment, distance from the natural edge, and year. Exclusions were only conducted in 2012 and included a total of 270 clusters across 5 fields. Control and supplement treatments were conducted in both 2011 and 2012 and included a total of 3003 clusters across 12 fields. Median values are shown by the lines across the middle of the boxes. Box boundaries represent the 25th and 75th percentile, with points outside of the boxes showing the 5 and 95th percentiles and whiskers denoting standard errors. Statistical analyses were conducted on transformed data and are shown in Table 2.3.





**Figure 2.5** Fruit weight and fruit set deficits (pollen supplemented – control) plotted as a function of honey bee, bumble bee, or total (honey bee + bumble bee) visits. Each symbol represents one field from one year, with open symbols representing Duke fields and closed symbols representing Bluecrop fields. Regression lines are only shown for the top models for each deficit type within each cultivar. Model components are shown in Table 2.4.

## **Chapter 3.**

# **Local management and landscape influences on bumble bee abundance in highbush blueberry fields**

### **Introduction**

Over one third of the world's crops rely on animal pollinators for some aspect of yield (Klein *et al.* 2007), and pollinator abundances are likely influenced by both local and landscape factors (Kennedy *et al.* 2013). Pollination of global agriculture has been estimated to value \$210 billion (€153 billion; Gallai *et al.* 2009) and although managed honey bees are the most commonly used pollinators in agroecosystems (National Research Council 2007) recent research has emphasized the importance of wild pollinators in terms of pollination deficits and subsequent crop yields (Holzschuh, Dudenhöffer & Tscharntke 2012; Garibaldi *et al.* 2013).

Wild pollinators can be more efficient than honey bees at pollen transfer (eg. blueberry: Javorek, Mackenzie & Vander Kloet 2002; apple: Vicens & Bosch 2000), and provide insurance against potential losses in managed pollinator colonies (Winfree *et al.* 2007) and poor honey bee performance in bad weather (Javorek, Mackenzie & Vander Kloet 2002). High diversity and abundance of native pollinators can improve crop yield (Kremen, Williams & Thorp 2002; Klein, Steffan-Dewenter & Tscharntke 2003; Morandin & Winston 2005) and strategies that incorporate both managed and wild pollinators can result in higher yields than managed honey bees alone (Chapter 2, Garibaldi *et al.* 2013). It is therefore important to understand factors that affect wild pollinator abundance in anthropogenically modified landscapes.

Both local management practices and landscape composition are known to affect pollinator abundances in agroecosystems (Kennedy *et al.* 2013). Local management practices such as planting pollen- and nectar-producing flowers along field margins or

within fields may affect non-crop foraging resource availability, which could increase honey bee colony growth by increasing pollen resource diversity (Sagili & Breece 2010). Pollinator plantings have been shown to increase pollinator abundance in agricultural fields (Fussell & Corbet 1992; Pontin *et al.* 2006; Pywell *et al.* 2006; Hannon & Sisk 2009; Haaland, Naisbit & Bersier 2011; Carvell *et al.* 2011; Korpela *et al.* 2013). Fields with a high proportion of weeds could also be expected to have greater pollinator abundance (Morandin & Winston 2005).

In contrast, other agricultural management practices, particularly pesticides, herbicides, and fungicides, create problems for pollinators in agroecosystems. Insecticides, specifically neonicotinoids, have been associated with reductions in pollinator colony growth (Whitehorn *et al.* 2012), reduced learning and memory in honey bees (Cresswell 2011; Belzunces, Tchamitchian & Brunet 2012), and lowered pollen collecting efficiency (Belzunces, Tchamitchian & Brunet 2012; Gill, Ramos-Rodriguez & Raine 2012). Fungicides exposure is linked to longer navigation times, most likely due to olfactory contamination (Sprayberry, Ritter & Riffell 2013). Herbicides are often less toxic to bees than other agrochemicals (Kovach *et al.* 1992), but can have indirect impacts through the reduction of weedy species that provide alternative forage for bees as noted previously (Morandin & Winston 2005). Even spray adjuvants, often assumed to be biologically inert (Cox & Surgan 2006), can impede honey bee learning capabilities (Ciarlo *et al.* 2012). Although honey bees have been studied extensively in this regard, the negative impacts of sprays likely affect other (wild) pollinators as well.

At the landscape scale, agricultural intensification has been linked to reductions in pollination services provided to crops by wild bees (Kearns, Inouye & Waser 1998; Kremen *et al.* 2002; Goulson 2003). Agricultural intensification destroys natural habitat and replaces it with an intensely managed monoculture, removing foraging resources that are available within more diversified landscapes (Kremen *et al.* 2002). Some natural areas also provide nesting habitat that may be unavailable within an intensive crop system (Watson, Wolf & Ascher 2011; Kennedy *et al.* 2013).

In this study I investigated the effects of both local management practices and surrounding landscape composition on the abundance of wild pollinators in a pollinator-dependent crop, highbush blueberry (*Vaccinium corymbosum* L.). I have previously shown

that bumble bees (*Bombus* spp.) are the most common and important non-managed pollinator in this crop in British Columbia, Canada (Chapter 2). Here I explore how i) non-crop forage, ii) spray regimes, and iii) landscape elements (e.g. semi-natural land and agricultural crops) influence the abundance of bumble bee visitors to highbush blueberry. I expect that fields using highly toxic sprays at high frequencies are likely to have fewer bumble bees than those using less toxic alternatives or spraying less frequently, and that fields with more locally available bee forage (weeds) will have a higher abundance of bumble bees. I also expect fields surrounded by landscape elements that are likely to include pollen-and nectar-producing plants (wild or managed) and nesting resources will have higher abundances of wild bees than other fields.

## **Methods**

### **Field sites**

British Columbia produces 95% of Canada's cultivated blueberries and is one of the top three blueberry producing regions in the world (British Columbia Ministry of Agriculture 2013). As of 2010, 98% of blueberry acreage in British Columbia can be found in the Lower Mainland-Southwest region of the province, where blueberries account for 32% of British Columbia's total fruit farm sales (Statistics Canada 2012). For this study, I included 19 fields of the highbush blueberry cultivar 'Bluecrop' (Figure 3.1) that were separated by at least 2 km.

### **Bumble bee abundance**

In British Columbia's lower mainland, bumble bees make up almost half of the total visits to cv. 'Bluecrop' (managed honey bees perform 51.3% of visits and other wild bees make up 2.3%) and play a large role in reducing pollen limitation (Chapter 2). My observations therefore focused on bumble bees as the relevant wild pollinator for blueberry in this region. Bushes bloom for about three weeks, mid-May to mid-June. To quantify bumble bee abundance, visual observations were conducted during this time period along three, 100m long transects (2 fields had transects of approximately 30m due to field size restrictions) located at three increasing distances from the most natural field

edge (0m, 50m, 100m). Each 100m transect was divided into 10m intervals. Bumble bees observed visiting blueberry flowers were counted for one minute on randomly selected bushes within these 10 intervals per transect. Only insects that apparently contacted the stigma by entering the flower legitimately (through the corolla opening) were counted. Bumble bees were identified to species on the wing. Observations were limited to days with full or part sun, temperatures above 13°C, and non-windy conditions (conditions conducive to pollinator activity) and alternated between AM, midday, and PM for each field. Observations were conducted 2-3 times during bloom for each field.

## **Local Management**

### ***Toxicity scores***

Spray records were attained from growers for 16 of the 19 fields. Records were restricted to pesticides, fungicides, and herbicides and contained the product name, dates of application and concentration of application. Where concentration was missing from the records, spray label rates as per the MSDS sheet for that spray were assumed. Sprays were then matched with their relative bee toxicity scores taken directly from Kovach et. al. (1992), and multiplied by the total times applied over the course of the full season of activity for bumble bees in our region (mid-March to the end of August).

### ***Non-crop forage (“Weediness”)***

The presence of non-crop flowering plants (alternative forage for bees) within blueberry fields was assessed at each of the three 100m transects, plus a fourth 100m transect along the most natural field edge. As the between-row distance was 3m (10ft) in my fields, I ran 10, 3m line transects perpendicular to the rows at stratified random intervals along each 100m transect. Each line transect was divided into 10 even intervals and presence/absence of flowering plants within each interval was recorded by species. Sampling was performed once during bloom, and twice after blueberry bloom had finished for each field.

The abundance of each plant species was summed across each field (maximum presence would therefore be 4 distances x 10 line transects x 10 intervals = 400) and multiplied by a “bee friendliness” score from 1 to 4 based on their hypothesized

attractiveness to bumble bees. For example, clover (*Trifolium* spp.) and dandelion (*Taraxacum officinale*) were given a value of 4, whereas little mouse-ear (*Cerastium semidecandrum*) was given a value of 1. Values were then summed across all plant species to attain a single index of ‘weediness’ for each field.

## **Surrounding Landscape**

Bumble bees travel between 100m and 1750m from the nest in search of forage, though when resources are readily available they will often remain within 500m of the nest (Walther-Hellwig & Frankl 2000; Darvill, Knight & Goulson 2004; Osborne *et al.* 2008). Morandin and Winston (2006) have estimated the maximum foraging range of bumble bees in agriculture to be between 450m and 758m, and other studies have found 1km to be the most supported distance when examining the relationship between bumble bee abundance and surrounding landscape (Watson *et al.* 2011; Williams & Winfree 2013). I therefore examined the surrounding landscape up to 1km from the center of each blueberry field.

Land use maps were produced for radii of 1km around each field in ArcGIS (ESRI 2011) using a combination of road maps and aerial photographs taken in 2010 from GeoBC (2010) and verified via ground truthing. Aerial photos were accessed using the BingMaps base layer provided by ArcGIS. Once ground truthed, land use parcels were drawn by hand over aerial photographs, and I extracted the proportion of the landscape comprised of each land use category from these maps. My categories included semi-natural land (forest and scrubland, meadows, pastures), ‘bee-friendly’ agriculture (flowering crops like blueberry, raspberry, potato), other (‘non-bee-friendly’) agriculture (crops such as corn, hay), developed land (residential, commercial, roads, greenhouses), and water (rivers, bogs, wetlands). Water was not included in any analyses (see Appendix B for a full list of observed land uses).

## **Statistical Analyses**

I used Akaike’s information criteria (AIC) to investigate the influence of both local management and surrounding landscape on bumble bee abundance. AIC model selection identifies the optimal set of parameters that explain the variation in a given response

variable (Zuur, Ieno & Smith 2007), which in this case is bumble bee abundance. As 6 parameters in all possible combinations result in a total of over 700 models, I chose to only consider models that fell within the top 95% confidence sets in model averaging procedures (R package 'MuMIn': Barton 2013).

My first set of linear models incorporated both local management (toxicity and weediness) and surrounding landscape (semi-natural, 'bee-friendly' agriculture, other agriculture, and developed land), a total of six parameters, to test their relative influence on bumble bee abundance. For this analysis, I only included the 16 fields with spray records (toxicity scores) available. Parameters were considered important predictors of bumble bee abundance if they appeared in the top models ( $\Delta AICc < 2$ ; Burnham & Anderson 2002), had a relatively high summed Akaike weight, and parameter estimates for which the 95% confidence interval did not cross zero.

I then examined 'bee-friendly' agriculture in more detail to determine if bumble bee abundance predicted by 'bee-friendly' agriculture was primarily due to blueberry (the most common crop in the region), other types of agriculture, or a combination of the two. This candidate set included 3 possible models (bumble bee abundance as predicted by blueberry alone, other 'bee-friendly' agriculture alone, or blueberry + 'other-bee-friendly' agriculture) and all 19 fields for which landscape composition data was measured.

Spatial autocorrelation in bumble bee abundance was tested using SAM (Rangel, Diniz-Filho & Bini 2010). All other analyses were run in R (R Core Team 2013). For all models, bumble bee abundance was log transformed to meet assumptions of normality. Proportional values for land covers were logistically transformed as per Warton and Hui (2011). Local and landscape parameter data was collected along two separate scales; local variables were calculated as an index, whereas landscape data was a proportion of the surrounding landscape. In order to facilitate comparisons between parameter estimates all parameters were therefore centered and scaled using the scale function provided in the base package in R, which subtracts the mean of the parameter and divides it by 2 standard deviations. To ensure that my models were not influenced by collinearity between parameters, I calculated the variance inflation factors for each parameter within the global model. There was minor correlation between semi-natural land and 'bee-friendly' agriculture, however the variance inflation factors on these parameters were  $< 10$

(4.68 and 4.32 respectively) suggesting the analysis is robust to this level of correlation (Quinn & Keough 2002).

## Results

Of the total observed wild (non-*Apis*) pollinators, 98% of individuals were comprised of bumble bees (*Bombus* spp.). Bumble bee abundance varied from 0 to 120 animals observed per field in 30 minutes (mean = 6.4). Common species included, in order of decreasing abundance, *Bombus mixtus*, *B. flavifrons*, *B. melanopygus*, and *B. vosnesenskii*. Bumble bee abundance was not spatially auto-correlated between fields.

When examining the relative effects of local and landscape factors on bumble bee abundance, the most strongly supported models ( $\Delta AIC_c < 2$ ; Burnham & Anderson 2002) contained both local and landscape parameters (Table 3.1). The top model included all parameters except semi-natural land and had an  $R^2$  value of 0.76. Of the over 700 possible models, 95% of the total Akaike weight was contained within a subset of 33 models which were then included in the model averaging procedure. Local parameters (weediness and toxicity) had the highest relative importance values (toxicity: 0.78; weediness: 0.74), with weediness having a negative influence on bumble bee abundance and toxicity having a positive influence on bumble bee abundance (Figure 3.2). 'Bee-friendly' agriculture, other agriculture, and developed land were negatively related to bumble bee abundance whereas semi-natural land was positively related to bumble bee abundance (Figures 3.2 and 3.3).

Regarding 'bee-friendly' agriculture, bumble bee abundance declines most strongly in fields with a high proportion of surrounding blueberry ( $\Delta AIC_c = 0.00$ ,  $w = 0.56$ ) or a combination of blueberry and other types of 'bee-friendly' agriculture ( $\Delta AIC_c = 0.53$ ,  $w = 0.43$ ). The model containing other 'bee-friendly' agriculture on its own received substantially less support ( $\Delta AIC_c = 12.16$ ,  $w = 0.00$ ). The top model of this set had an  $R^2$  value of 0.76.



## Discussion

A recent meta-analysis by Kennedy *et al.* (2013) found both local and landscape factors to be important in predicting wild pollinator abundance in agroecosystems. Both local and landscape factors appear in the top models of the current study as well, however, weediness has a negative influence while toxicity has a positive influence on bumble bee abundance. The directions of local influence were unexpected as local habitat quality is expected to positively influence wild pollinator abundance (Carré *et al.* 2009; Williams & Winfree 2013) and intensive agricultural spray regimes negatively influence them (Kennedy *et al.* 2013). It may be that in the present study landscape simply has much stronger influence on wild bumble bee abundance, confounding the effects of local management, or that the local parameters I measured are correlated with other unmeasured metrics of local habitat quality.

### Local management

Research comparing organic to conventional fields has shown that bumble bees are in higher abundance in organic (or no-spray) fields than conventionally-managed fields (Kremen, Williams & Thorp 2002; Holzschuh, Steffan-Dewenter & Tscharntke 2008; Otieno *et al.* 2011; Kennedy *et al.* 2013). In this study, all growers practiced conventional management strategies so I was not able to investigate the same extremes as would be found when comparing between conventional and organic farming. For example, all but two fields had neonicotinoids sprayed at least once (5 fields sprayed twice) between April and August, and the high toxicity level of neonicotinoids is known to have a strong negative impact on bumble bee foraging efficiency and colony strength (Whitehorn *et al.* 2012; Gill *et al.* 2012). Although fields were similar in the amount of neonicotinoids used, they did vary in other aspects of spray regime (ie. fungicides and herbicides, both of which can have negative impacts on bumble bees), and so the finding that higher toxicity scores were positively associated with bumble bee abundance was surprising. It may be that growers who are spraying more intensively could also be engaging in other management strategies that might make fields attractive to bumble bees. For example, large local floral patch size can increase pollinator visit rates in other systems (Williams & Winfree 2013). The overall floral display of the field itself may affect its attractiveness to bumble bees,

and may be affected by unmeasured management efforts like pruning, watering regime, and fertilizer applications. If toxicity is an indicator of a highly managed field, it may be that highly managed fields are better for bumble bees when considered within a spectrum of conventional management. A more in-depth examination of other aspects of grower practices may be able to shed some light on local management influences on bumble bee abundance.

Weediness had a strongly negative influence on bumble bee abundance. This result was unexpected, as on-field weed cover has been previously shown to positively influence wild bee abundance and richness in canola fields (Morandin 2005), though Morandin (2005) focused on proportional cover of weeds rather than on abundance and attractiveness as I do here. When I modified my weediness index by removing the attractiveness factor, a strongly negative influence on bumble bees remained. One possible, but unlikely, explanation is that high levels of weediness within fields may distract wild bees from blueberry flowers, thus resulting in a negative influence on the abundance of bumble bees observed foraging on blueberry flowers. If this were the case, I would expect a strongly negative influence of during-bloom weediness on bumble bee abundance and a positive influence of post-bloom weediness, as post-bloom forage should enhance bumble bee populations. However, when I compared during-bloom and post-bloom weediness, there was no effect at all on bumble bee abundance, and global models that included post-bloom weediness rather than full season weediness yielded similar results (analysis not shown). As weediness only appeared to have a strong influence when included in models with landscape and other factors, it is likely that weediness is correlated with other, unmeasured characteristics of the fields I studied. I also cannot say quantitatively if bumble bees actually utilize weeds within fields as a source of pollen and nectar, as I did not include observations on weeds in this study. Future studies should determine if bumble bees are actually foraging on weedy species between rows and whether such flowers actually do provide alternative forage for bees in this crop and region.

## **Surrounding Landscape**

Fields in landscapes with higher proportions of 'bee-friendly' agriculture had a lower abundance of bumble bees. This result is contrary to research from Europe, which

demonstrated that mass-flowering of crops (in this case, oilseed rape) can actually increase bumble bee abundances (Westphal, Steffan-Dewenter & Tschardtke 2003). When I compared blueberry to other 'bee-friendly' crops, the most strongly supported models both included blueberry. Other "bee-friendly" agriculture had substantially less support on its own, making blueberry the driving land use category in my analysis. In my study region, the most common 'bee-friendly' crop in the landscape is blueberry. When blueberry makes up a substantial proportion of the overall landscape, there may be a dilution effect in which bumble bees spread throughout the landscape and visit multiple blueberry farms during bloom, thereby appearing to be less abundant at any one farm. However, dilution effects are often believed to be temporary results of increased landscape homogenization (Holzschuh *et al.* 2011), and the majority of the fields in my study were at least five years old. In some cases (when crops have nectar and pollen-producing flowers) landscape homogenization can benefit pollinator populations in the long term by providing ample resources and attracting solitary bees to nest around fields (Westphal *et al.* 2003). It is not clear that such findings would apply to social bumble bees, which require forage for an extended period of time that is longer than the bloom period of any single mass-flowering crop. In my system, it is likely that there is simply not enough food to sustain bumble bees that forage throughout the season in a landscape dominated by a single mass-flowering crop that only blooms for three weeks in spring.

Semi-natural land is known to support wild bee abundance in agroecosystems (Morandin & Winston 2006; Ricketts *et al.* 2008; Carré *et al.* 2009; Holzschuh, Dudenhöffer & Tschardtke 2012). Semi-natural land in our area consisted primarily of meadows and pasture (cattle, sheep, and llamas). Grassy meadows can have foraging resources for bees that extend beyond the bloom time of the crop itself, though more importantly, these areas can also provide nesting habitat (Öckinger & Smith 2006). If no suitable nesting habitat exists within foraging distance of a blueberry field, it is safe to assume that there will be very few bumble bees foraging within that field. Unfortunately bumble bee nests themselves are extremely difficult to locate and monitor, limiting our ability to examine nesting requirements in more detail. However, bumble bees are expected to nest in abandoned rodent holes (Kearns & Thomson 2001) and have been shown to be in higher abundance when such holes are readily available (McFrederick & LeBuhn 2006). Rodent holes are presumed to be in high abundance in grassy meadows

(Kearns & Thomson 2001) such as those comprising our semi-natural areas, which may explain the positive relationship seen in this study. Although cattle grazing (and associated vegetation trampling) can have a negative impact on pollinators (Xie, Williams & Tang 2008), several studies have shown no impact (Elwell 2012) or a positive impact (Carvell 2002; Vulliamy, Potts & Willmer 2006; Morandin *et al.* 2007) on pollinator abundance. It is possible, then, that meadows and pastures provide similarly high levels of resources for pollinators in terms of nest sites, resulting in an increase in the abundance of bumble bees foraging on blueberry.

## **Conclusions**

Extensive homogenization of the landscape has resulted in an area primarily composed of blueberry fields in British Columbia's lower mainland. Recent work has demonstrated that bumble bee numbers can be enhanced when the surrounding landscape includes a mix of semi-natural land and multiple crops that bloom at varying times across the season (Riedinger *et al.* 2014). Diversifying the landscape both with multiple cropping systems, but more importantly with non-crop areas similar to meadows and pastures, may be the most effective way to increase bumble bee abundance. Growers should therefore strive to retain or - if possible - restore semi-natural areas around their fields. Enhancing field margins can increase both wild pollinator abundance and crop yields (Blaauw & Isaacs 2014). As weediness within fields did not result in a strong increase in bumble bee abundance in this study, field edge enhancements, implemented on a large scale with much greater densities of floral resources than would be found as weeds within the field itself, may be most effective at providing non-crop forage. Edge enhancements may also have the greatest impact when implemented in fields that have extant semi-natural land in their surrounding landscape to provide nesting habitat for bumble bees.

Wild bumble bees provide essential yield-enhancing services to agriculture. In light of increasing concerns regarding the sustainability of managed pollinators, efforts must be made to conserve wild bumble bee populations. Conserving natural areas and enhancing on-crop management strategies with bumble bees in mind will help growers maximize current yields and sustain them into the future.

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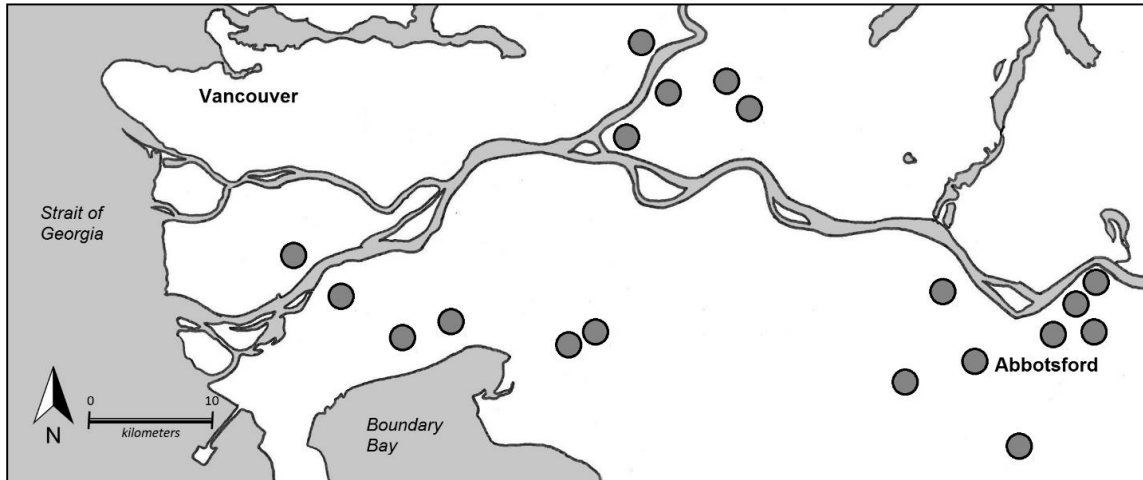
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## Tables

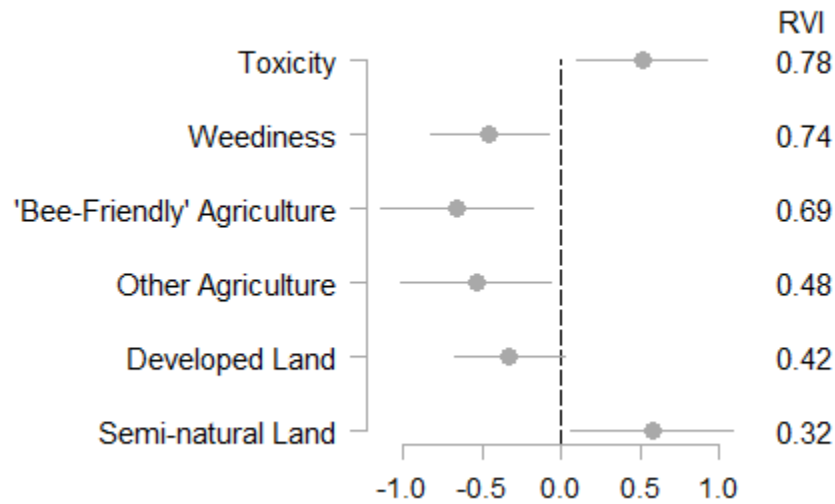
**Table 3.1** Linear models including both local and landscape parameters as predictors of bumble bee abundance and their model averaged coefficients. The 95% confidence set contained a total of 33 models, but only the top ten models (those with the lowest  $\Delta AIC_c$  and highest weight) are shown here. Models are presented in order of increasing  $\Delta AIC_c$ . Bumble bee abundance was represented by the 16 fields for which I was able to collect spray records.

Model	df	Log <sub>e</sub> (£)	AIC <sub>c</sub>	$\Delta AIC_c$	w
'Bee-friendly' agriculture + Developed land + Other agriculture + Toxicity + Weediness	7	-7.19	42.37	0.00	0.28
Semi-natural land + Toxicity + Weediness	5	-13.96	43.92	1.55	0.13
'Bee-friendly' agriculture + Other agriculture + Semi-natural land + Toxicity + Weediness	6	-11.31	43.96	1.59	0.13
Semi-natural land + Toxicity	4	-17.07	45.77	3.40	0.05
'Bee-friendly' agriculture	3	-19.07	46.14	3.77	0.04
'Bee-friendly' agriculture + Weediness	4	-17.34	46.31	3.94	0.04
Developed land + Semi-natural land + Toxicity + Weediness	6	-12.53	46.40	4.02	0.04
'Bee-friendly' agriculture + Developed land	4	-17.75	47.13	4.76	0.03
'Bee-friendly' agriculture + Toxicity + Weediness	5	-15.69	47.39	5.02	0.02

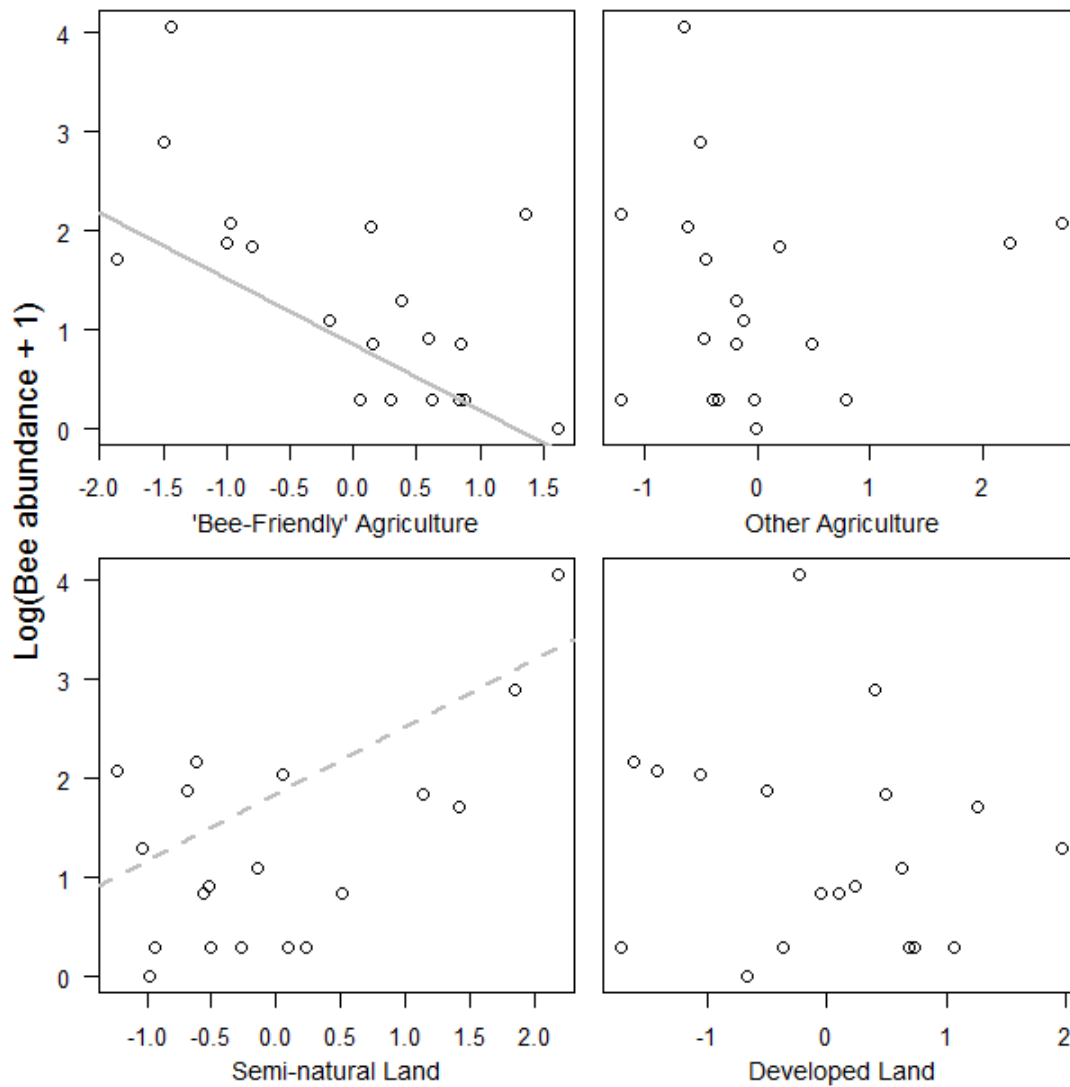
## Figures



**Figure 3.1** Map of highbush blueberry (cv. 'Bluecrop') fields in British Columbia's lower mainland from 2012.



**Figure 3.2** Scaled model parameter estimates (circles) with 95% confidence intervals (lines) from averaged linear models of landscape (Semi-natural land, 'bee-friendly' agriculture, other agriculture, and developed land) and local (weediness, and toxicity) parameters on bumble bee abundance. Confidence intervals that overlap the zero line are unlikely have a directional influence on bumble bee abundance, where as those on the negative side have a negative influence and those on the positive side have a positive influence. Parameters are labeled on the left axis and ranked in accordance to relative variable importance (RVI) as determined by model averaging and shown on the right axis.



**Figure 3.3** Scatterplots of log transformed bumble bee abundance against each scaled land cover category. Each circle denotes a field. A solid line is shown for the land cover category with the highest relative importance value. The dashed line represents the only land cover that was positively related to bumble bee abundance.

## Chapter 4.

# General Conclusions

Pollination deficits are prevalent in wild plants (Knight *et al.* 2005), but are less commonly investigated in agricultural crops (Mayfield 1998) though they can be responsible for a loss of potential yields. I found deficits up to 30% in highbush blueberry in BC's lower mainland. These deficits differed by cultivar, and will likely only be reduced by increasing bumble bee abundance. My results indicate that higher honey bee abundances alone do not affect deficit levels in this crop in BC, despite honey bees providing the majority of flower visits.

Managed European honey bees are the most common and widely used agricultural pollinator (National Research Council 2007). Beekeepers can move hives among crops as needed over the course of a summer to facilitate the pollination needs of multiple crops with varying bloom times. A single honey bee hive contains thousands of individuals in comparison to the hundreds of individuals found in a bumble bee colony; other wild bee species are largely solitary. This aspect of natural history, coupled with the ease of moving honey bee hives from place to place, makes honey bees ideal for providing pollination services in intensely managed mono-cropped areas in which wild bees are scarce (Kremen, Williams & Thorp 2002). All fields in this study were supplemented by growers with honey bees, and, not surprisingly, honey bees accounted for over 90% of the total visits to cv. 'Duke', and 50% of the visits to cv. 'Bluecrop'.

However, blueberry is buzz pollinated (Free 1993), a behaviour limited to bumble bees (though some bees will 'drum' anthers to release pollen; Buchmann 1983), making bumble bees more efficient pollinators of this crop than honey bees (Buchmann 1983; Dogterom, Winston & Mukai 2000). Bumble bees were the second most common pollinator after honey bees in blueberry fields, comprising about half the total visits to cv. 'Bluecrop'. Although honey bees are not capable of buzz pollinating, they will dislodge some pollen grains while foraging among blueberry flowers for nectar and are therefore still capable pollinators of blueberry (Javorek, Mackenzie & Vander Kloet 2002). However,

deficits for both cultivars declined most strongly with increasing bumble bee visits or total visits, not with honey bee visits alone. It is unlikely then that increasing honey bee stocking rates will reduce deficits in highbush blueberry. My results add to the growing body of literature that suggests it is wild pollinators, and not honey bees, that are most important for achieving maximum pollination in agriculture (Holzschuh, Dudenhöffer & Tscharnke 2012; Garibaldi *et al.* 2013). The importance of bumble bees to highbush blueberry in British Columbia emphasizes the importance of understanding the factors that influence bumble bee abundance in agricultural landscapes, including implementing management strategies that provide habitat for wild bumble bees.

Providing habitat by increasing diversity and temporal availability of forage can have strong positive influences on wild bee abundance (Kremen *et al.* 2007; Korpela *et al.* 2013). When a landscape is homogenized with a crop that only blooms for a fraction of the season in which bumble bees are active, bee populations may not be sustained throughout the season (Kremen *et al.* 2007). My research showed that fields that were surrounded by a high proportion of 'bee-friendly' agriculture had a lower abundance of bumble bees foraging within focal blueberry fields. In this region, 'bee-friendly' agriculture primarily consisted of other blueberry fields, which may not provide nesting habitat and would not provide temporally complementary resources to those available in focal fields. Although wild bees may disperse throughout the landscape among multiple fields when blueberry is in bloom, thus reducing their apparent abundance within focal blueberry fields, it is more likely that lower abundances of bumble bees in this case was due to the lack of available non-crop forage and nesting habitat, resulting in an overall decline in population size and the number of colonies in the landscape.

Wild bumble bees were more abundant in fields surrounded by semi-natural land and more likely to be found closer to field edges. Semi-natural land can provide non-crop forage for pollinators in areas such as meadows and pastures in the form of wild flowers or so-called weedy species. In addition to forage, semi-natural land can also provide nesting habitat that may be otherwise unavailable within an intensely farmed area (Watson, Wolf & Ascher 2011; Kennedy *et al.* 2013). When such resource-rich areas abut field edges, bumble bees foraging or nesting within them may additionally travel into the crop to forage, thus pollinating the crop itself (Pitts-Singer & James 2008).



Bumble bee abundance was also negatively influenced by on-field abundance and/or quality of non-crop flowers, suggesting local availability of alternative forage may not be the best explanation of bumblebee abundance patterns. However, when the effect of landscape was removed from the global model, weediness lost its effect on bumble bee abundance, and there was no change in directionality when full season weediness was replaced with post blueberry bloom weediness (when weeds would provide important complementary forage to bumble bees). The negative influence of weediness in bumble bee abundance is most likely because the surrounding landscape has such a strong influence on bee abundance that I was unable to separate the influence of local- scale habitat quality from that of landscape-scale habitat quality. Bumble bees were likely found in higher abundance closer to field edges due to proximity to nesting habitat as opposed to locally available alternative forage in these edges.

Wild bees are in global decline (Potts *et al.* 2010). A key driver of this decline is increased agricultural intensification (Kremen, Williams & Thorp 2002). Recent work suggests that agricultural pollination is performed by only a small subset of wild pollinators (Klein *et al.* submitted), but by recognising the contributions made by wild bees to the economic viability of agriculture, conservation efforts may be able to not only protect the pollinators that provide this essential service to agriculture, but by proxy protect other less common pollinators which may be important in natural systems.

## **Final Thoughts and Recommendations**

I have shown here that wild bumble bees are essential players in the reduction of pollination deficits, and respond positively to landscapes containing semi-natural areas. Although honey bee visits alone do not reduce deficits, fruit set deficits are most strongly reduced by combined visits from both wild bumble bees and managed honey bees. Growers should therefore continue to hire honey bees at the currently recommended rate of 2.5 hives per acre (BC Ministry of Agriculture 2012). More importantly, growers should consider ways to encourage wild bumble bees in blueberry by maintaining and conserving semi-natural areas. Managing for wild pollinators may be most important for cultivars like Bluecrop, which has a flower shape that discourages visits by honeybees (Courcelles, Button & Elle 2013) and so benefits more from visits by bumble bees. Habitat conservation

as an agricultural practice may not be feasible for fields already surrounded by agricultural land, but it is possible that the cultivation of bee friendly plants into currently un-used field margins may be a workable substitute.

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## Appendix A

### Pan trap species list

Insects caught in pan traps in 2011. Bees and syrphid flies were retained in the analysis. Wasps and individuals from the superfamily Muscoidea were removed from analyses as they were rarely seen visiting blueberry flowers. Analyses concerned wild insects only, so honey bees (*Apis mellifera*) were also removed from analyses. Non-visitors captured in pan traps were not always identified to species. The total number of individuals caught in each cultivar is provided along with the total number of individuals for each species across both cultivars.

	Species	Bluecrop	Duke	Total
Included in analyses	<i>Agapostemon texanus</i>	0	0	0
	<i>Andrena angustitarsata</i>	20	2	22
	<i>Andrena barbilabris</i>	1	1	2
	<i>Andrena caerulea</i>	5	1	6
	<i>Andrena cressonii</i>	0	1	1
	<i>Andrena cupreotincta</i>	0	3	3
	<i>Andrena hemileuca</i>	77	41	118
	<i>Andrena miserabilis</i>	10	0	10
	<i>Andrena nigrocaerulea</i>	4	4	8
	<i>Andrena nivalis</i>	3	8	11
	<i>Andrena prunorum</i>	1	0	1
	<i>Andrena salicifloris</i>	33	16	49
	<i>Andrena suavis</i>	1	0	1
	<i>Andrena transnigra</i>	6	3	9
	<i>Andrena trevoris</i>	2	1	3
	<i>Andrena vicinoides</i>	1	0	1
	<i>Andrena w-scripta</i>	0	1	1
	<i>Andrena sp. 5</i>	2	1	3
	<i>Andrena sp. 9</i>	1	0	1
	<i>Bombus californicus</i>	0	2	2
	<i>Bombus flavifrons</i>	7	11	18
<i>Bombus melanopygus</i>	6	3	9	
<i>Bombus mixtus</i>	6	10	16	

	<i>Bombus vosnesenskii</i>	3	1	4
	<i>Ceratina acantha</i>	8	9	17
	<i>Cheilosia</i> spp.	2	0	2
	<i>Eristalis arbustorum</i>	3	1	4
	<i>Eristalis bardus</i>	1	0	1
	<i>Halictus rubicundus</i>	9	8	17
	<i>Heliophilus latifrons</i>	2	3	5
	<i>Heringia</i> sp.	1	0	1
	<i>Lasioglossum (Dialictus) brunneiventre</i>	0	2	2
	<i>Lasioglossum (Dialictus) cressonii</i>	5	4	9
	<i>Lasioglossum (Dialictus) laevissimum</i>	6	2	8
	<i>Lasioglossum (Dialictus) macroprosopum</i>	16	1	17
	<i>Lasioglossum (Dialictus) nevadense</i>	1	0	1
	<i>Lasioglossum (Dialictus) pacatum</i>	7	2	9
	<i>Lasioglossum (Dialictus) pruinatum</i>	1	1	2
	<i>Lasioglossum (Dialictus) sagax</i>	11	4	15
	<i>Lasioglossum (Evylaeus) sp. 1</i>	2	5	7
	<i>Lasioglossum (Evylaeus) sp. 2</i>	1	1	2
	<i>Lasioglossum (Evylaeus) sp. 3</i>	0	1	1
	<i>Lasioglossum (Evylaeus) sp. 4</i>	3	2	5
	<i>Lasioglossum (Evylaeus) sp. 5</i>	1	0	1
	<i>Lasioglossum (Evylaeus) sp. 10</i>	2	0	2
	<i>Lasioglossum (Lasioglossum) zonulum</i>	2	2	4
	<i>Osmia dolerosa</i>	9	1	10
	<i>Osmia lignaria</i>	8	2	10
	<i>Osmia pusilla</i>	1	1	2
	<i>Panurginus atriceps</i>	1	0	1
	<i>Scaeva pyrastris</i>	1	0	1
	<i>Sphecodes</i> spp.	1	1	2
	<i>Temnostoma vespiformis</i>	1	0	1
	<i>Toxomerus occidentalis</i>	0	0	0
Excluded from analyses	Anthomyiidae	0	1	1
	<i>Apis mellifera</i>	328	325	653

Bibionidae	1	3	4
<i>Calliphora genarum</i>	0	1	1
<i>Calliphora latifrons</i>	0	1	1
<i>Calliphora vomitoria</i>	1	0	1
Cimbicidae	4	2	6
Coleoptera	1	3	4
<i>Cyanus elongata</i>	2	0	2
Diptera	3	2	5
Ichneumonidae	0	1	1
<i>Lucilia elongata</i>	1	1	2
<i>Lucilia illustris</i>	3	0	3
<i>Lucilia thatuna</i>	0	1	1
<i>Melanodexia spp.</i>	1	1	2
<i>Muscidae spp.</i>	10	3	13
Muscoidea	29	41	70
Odonata	1	0	1
<i>Odontomyia sp. 4</i>	1	0	1
<i>Polistes spp.</i>	1	2	3
<i>Protophormia terraenovae</i>	0	1	1
Rhagionidae	1	0	1
Sarcophagidae	24	6	30
<i>Scathophagidae spp.</i>	1	1	2
Tachinidae	8	0	8
Therevidae	3	0	3
<i>Tryptocalliphora braueri</i>	1	0	1

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## Appendix B

### Landcover Classes and Land Uses

Detailed land uses for each landcover class included in linear models of local and landscape influence on bumble bee abundance. Land uses were recorded during ground truthing and then grouped into landcover classes. 'Bee-friendly' agriculture included bee pollinated crops, whereas all "non-bee-friendly" crops were included in 'other' agriculture. All landcover classes except water were included in model averaging. A second set of models examined land uses within the bee-friendly agriculture class.

Categories	Land uses
'Bee-friendly' agriculture	Blueberry
	Cranberry
	Raspberry
	Buckwheat
	Potatoes
	Nursery
Other (non 'bee-friendly') agriculture	Hay
	Corn
	Turf (lawn / maintained grass)
	Nursery
	Unknown crop
Seminatural areas	Forest
	Scrub
	Meadow
	Pasture
Water	Open water
	Wetland
	Bog
	River
Developed	Residential
	Industrial / Commercial
	Highway
	Construction Zone
	Greenhouse
	Golf Course