POLLINATION ECOLOGY OF NATIVE POLLINATORS IN COMMERCIAL CRANBERRY FIELDS IN NEWFOUNDLAND

by © Geena Arul Jothi

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Abstract

Native bees such as bumblebees (*Bombus* spp.) and solitary bees are effective pollinators of a variety of crops. However, an understanding of the pollination services by native pollinators to commercial cranberries in Newfoundland is limited. This study assessed the diversity, abundance and effectiveness of native bees, and examined the local and landscape factors associated with high pollinator abundance and fruit yield in four commercial cranberry farms in Newfoundland (Canada). Consistent with previous research, *Bombus ternarius* was the most abundant native pollinator in the cranberry farms. Although no direct relationship between bee abundance and fruit yield was detected, it is clear that the presence of native bees is necessary for adequate fruit set in commercial cranberries as all farms studied had sufficient native bees to fully pollinate the available blossoms. It appears that other factors, which were not assessed in this study, such as crop management practices or microclimate, are more important in determining yield on these farms. Bees on these farms may respond to resources other than forage plants, e.g. nesting resources, which were not possible to assess, may be more limiting. This study contributes to the understanding of the diversity and abundance of native bees and how local and landscape factors contribute to bee abundance in the commercial cranberry fields in Newfoundland.

Keywords: cranberries, pollination, native bees, landscape ecology, Newfoundland

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Introduction

Pollinators play a crucial role in the pollination of various crops (Delaplane and Mayer 2000, Potts et al. 2010). This study explores two important aspects of the pollination of commercial cranberry in Newfoundland. The first is the effectiveness of the most abundant native bees in pollinating cranberry flowers in commercial cultivation. The second is the availability of habitats that support native bee abundance and diversity at local (within-field) and landscape (up to 2 km radius) scales around the cranberry fields; the latter reflects the known foraging distance of bumblebees (Westphal et al. 2003). A key goal of this study is to provide cranberry growers with recommendations to maximize bee populations for maximal crop yield.

Pollinators

A variety of agents such as birds, bats, insects, wind and water are involved in the transfer of pollen (Meffe 1998; Goulson 2003b; Vanbergen et al. 2014; Hanley et al. 2015). For example, insects such as honeybees (*Apis* spp. Linnaeus, Hymenoptera: Apidae), bumblebees (*Bombus* spp. Latreille, Hymenoptera: Apidae) and other wild bees pollinate alfalfa, almonds, beans, blueberries, cranberries and many other wild plants and cultivated crops (McGregor 1976). Among insects, bees are considered one of the most important pollinators of crops because of their active collection and manipulation of pollen (Steffan-Dewenter and Tscharntke 1999; Ratti et al. 2008; O'Toole 2014; Sellars and Hicks 2015). Bees play an important role in maintaining the biodiversity of natural and agricultural ecosystems (Ratti et al. 2008; Brown and Paxton 2009; Potts et al. 2010; Kennedy et al. 2013; Kleijn et al. 2015). They serve as ecologically important pollinators of the native plant community (Kennedy et al. 2013) by pollinating about 67% to 90 % of flowering plants (Droege et al. 2010). Over one third of the food we consume is dependent on the pollination services of bees (Goulson 2003a; Potts et al. 2010; Toole 2013; Vanbergen et al. 2014; Hanley et al. 2015).

As there is a decline in managed honeybee colonies throughout the world (Batra 1995; Michener 2000) due in part to diseases and parasites (Goulson et al. 2015), the demand for conservation of native bees is growing (Peters et al. 2013; Goulson et al. 2015). Declines in individual species of bumblebee in various parts of North America have also been documented (Goulson 2003b; Kosior 2007; Bartomeus et al. 2013), including *Bombus franklini* Frison (Hymenoptera: Apidae), *Bombus occidentalis* Greene (Hymenoptera: Apidae), *Bombus affinis* Cresson (Hymenoptera: Apidae) and *Bombus terricola* Kirby (Hymenoptera: Apidae) (Goulson et al. 2008, Colla and Ratti 2010, Cameron et al. 2011). With the declines of *B. affinis* and *B. terricola*, their social parasite, *Bombus ashtoni* (Hymenoptera: Apidae), is also facing a decline (Winter et al. 2006; Goulson et al. 2008). In Canada, *B. occidentalis*, *B. affinis* and *Bombus bohemicus* Seidl (Hymenoptera: Apidae) are a few bumblebee species that are currently facing a decline (Species At Risk public registry 2016). Factors that contribute to the bumblebee decline in Canada include pathogen spillover from commercially managed bumblebee colonies, intensive agricultural and other land use practices, and habitat change (Species At Risk public registry 2016). Other factors that lead to the decline of native bees are fewer floral resources in and around the fields, lack of nesting sites, use of insecticides and the effect of non-native bees on the native bee population (Mackenzie and Winston 1984; Kevan et al. 1990; Cane et al. 2001; Goulson 2003b; Goulson et al. 2003c; Goulson et al. 2008;

Hicks et al. 2011; Meeus et al. 2011; Morales et al. 2013; Hanley et al. 2015). The above-mentioned factors are the general causes of pollinator declines that may apply to varying degrees in agroecosystems in Newfoundland but have not been evaluated.

Bees require a continuous supply of floral resources from the time of emergence in early spring to their late foraging periods in early fall (Westphal et al. 2003). In commercial cranberry farms, wild flowering plants that grow on the margins of the fields and uncultivated areas around a farm (Banaszak 1992) provide important foraging resources. The use of pesticides (Meffe 1998), inorganic fertilizers, monocropping, and over-use of agricultural land limit the availability of floral resources (Cane and Tepedino 2001; Woodcock et al. 2014). The absence of floral resources during the flight period results in starvation and mortality of bees (Osborne and Corbet 1994). Preserving remaining wild areas around fields and/or restoring the natural landscapes will aid in the restoration of native pollinators and their abundance (Woodcock et al. 2014).

In addition to food sources, native bees require nesting sites (Kells and Goulson 2003). Depending on the species, native bees nest above ground or below ground. Above ground nesting bees make use of grasses or other bushes to nest and the underground nesting bees nest in small cavities below the ground. For example, *Andrena* spp. (Hymenoptera: Apidae) and *Nomada* spp. (Hymenoptera: Apidae) nest in bare soil and grasses whereas *Hylaeus* spp. (Hymenoptera: Colletidae) and *Megachile* spp. (Hymenoptera: Megachilidae) nest in dead stems. Both types of bees also make use of the empty nests of rodents (Banaszak 1992). The present day pattern of agriculture and use of farm equipment destroys the nesting sites of bees that nest above ground. Weed-free farms do not offer resources such as food to rodents and there is a minimal chance of rodents nesting in crop fields. This leads to the loss of nesting sites for above and below ground nesting bees (Goulson et al. 2008).

Use of insecticides in crops has both direct and indirect effects on bees (Meffe 1998; Kevan 1999; Goulson et al. 2008). The use of insecticides causes poor foraging memory with diminishing abilities to navigate in bumblebees (Kevan 1999). In smaller solitary bees such as *Andrena* spp., *Hylaeus* spp., *Nomada* spp. and *Lasioglossum* spp. (Hymenoptera: Halictidae), the over-use of insecticides causes direct mortality or chronic exposure effects such as reduced foraging efficiency or shorter life span (Davis et al. 1988). These effects on pollinators have consequences for crop yield such as, one well-documented example showing a reduction in blueberry yield as a result of pesticide application (Kevan 1977). Cranberry fields in Newfoundland are sprayed with various insecticides outside of the bloom period to target various pests (Agriculture and Agri-Food Canada 2015). Although these insecticides are applied when insect pollinators are not in the fields, pollinators may still come in contact with these insecticides.

Supplemental pollinators are often used in cranberry production; these include honeybees, which are not native to North America. In Newfoundland, because of the small size of the honeybee industry, honeybees are not used in the production of commercial cranberries and hence *B. impatiens* Cresson (Hymenoptera: Apidae) are sometimes used. Commercially reared, non-native *B. impatiens* are occasionally imported to pollinate commercial cranberries, although the extent of this practice is difficult to determine because this is done outside of the required permit process. Increase in acreage of cranberry farms and the perceived low population density of native pollinators in Newfoundland may explain the desire for the importation, although it appears that there is no benefit from supplementation (Hicks and Sircom 2016). The importations of non-native bees have caused a decline of the native bee communities in many parts of the world (Goulson 2003b; Cameron et al. 2011) but this has not been studied in Newfoundland. Currently, the honeybees in Newfoundland are healthy and less subject to pests and diseases because of the isolation from mainland and lower human activity e.g. less intensive agriculture (Williams et al. 2010 a; Shutler et al. 2014; Sellars and Hicks 2015). To protect the relatively disease-free status of honeybees, the importations of bumblebees (NLWild Life Regulations, Wild Life Act, Part VI, section 83) and honeybees (NL Animal Health and Protection Act, Animal Health Regulation 33/12) requires an extensive permit process (Williams et al. 2010a). It should be noted that these rules are followed to varying degrees in Newfoundland depending on the importer.

Native bees are effective pollinators (Cutler et al. 2015). In Newfoundland, about 76 species of native bees representing five families (Andrenidae, Apidae, Colletidae, Halictidae and Megachilidae) have been identified (Sellars and Hicks 2015). The native bees are adapted to foraging in adverse weather conditions (Free 1955; Corbet et al. 1993; Goulson 2003a; Cutler et al. 2015). In addition, bumblebees are hairy and thus can collect more pollen than the other native bees, which makes them more effective pollen vectors (Javorek et al. 2002; Cane and Schiffhauer 2003; Goulson 2003b; Ratti et al. 2008; Cameron et al. 2011; Eaton and Nams 2012). Studies conducted in blueberry crops in Nova Scotia showed that wild bees are capable of providing significant crop pollination services (Eaton and Nams 2012; Cutler et al. 2015). However, understanding of the pollination services by native pollinators to commercial cranberries in Newfoundland is lacking.

The study system

In Newfoundland, cranberry emerged as a commercial crop in the late 1990's and is relatively new when compared to other commercial berry crops such as blueberry (*Vaccinium angustifolium* Ait. Ericaceae), lingonberry (*Vaccinium vitis-idaea* L. Ericaceae) and strawberry (*Fragaria* spp. L. Rosaceae). Most of the commercial cranberries in Newfoundland are farmed on natural bogs that are modified. Cranberry beds are constructed by excavating to within a few centimeters of the water table and building a dyke or berm approximately 1m high around each bed. Individual beds are usually rectangular, 30-50 m wide and of various lengths as desired. They are covered 15 cm deep in sand to ensure water movement. Hardwood cuttings or rooted cuttings from mature beds are used to establish a new cranberry bed with one plant per square foot of bed (Jones 2010).

The cranberry (*Vaccinium macrocarpon* Ait. Ericaceae) is a berry crop native to North America (MacKenzie 1994, Delaplane and Mayer 2000) and is found growing wild in Newfoundland. It is a perennial trailing woody plant that is found near marshes and wetlands (Cane and Schiffhauer 2003). The morphology of cranberry flowers limits self-pollination and they must be cross-pollinated (Delaplane and Mayer 2000; Loose et al. 2005). The flowers are elongate with a single style surrounded by 5 to 8 stamens that are tightly packed. The petals roll back when the flower opens which exposes the stamens and style (MacKenzie 1994; Delaplane and Mayer 2000). The flowers are usually facing downwards with a narrow nectar-excreting organ protecting the pollen and nectar within the flower even during a downpour (Macfarlane 1995). This is important in Newfoundland, which is frequently rainy. Cranberry flowers are a good source of pollen, but do not offer high nectar rewards; nectar concentrations are relatively low, with 300–400 µg of dissolved sugar in 1.4 µl of nectar (Cane & Schiffhauer 2003). As a result, cranberry is less attractive to pollinators that are more focused on nectar collection, such as honeybees. By comparison, the closely related blueberries (e.g. *V. angustifolium*, *Vaccinium corymbosum* L. Ericaceae) can produce twice as much nectar, which can contain 30–50% sugar (Dedej 2004, Pavlis 2011). An individual cranberry flower produces about 7000 pollen tetrads, which are pollen grains arranged in a tetrahedral fashion i.e., in groups of four (Cane & Schiffhauer 1997; Cane & Schiffhauer 2003).

Cranberries, like all members of the genus *Vaccinium,* are buzz pollinated (MacKenzie 1994; Goulson 2003b; Ratti et al. 2008; Broussard et al. 2011); the bee rapidly vibrates its flight muscles without moving its wings, shaking the anthers at the frequency of middle C (~261 Hz), thus dislodging the pollen which sticks to the bee (Buchmann and Nabhan 1997; Loose et al. 2005). The bee then transports the pollen to the stigma of a flower (MacKenzie 1994). Because of their buzz pollination capability, native bees such as bumblebees are evolutionarily adapted to pollinate cranberries (Cane et al. 1993). They are also considered to be the most effective buzz pollinators (Cameron et al. 2011) of cranberries (Delaplane and Mayer 2000; Javorek et al. 2002; Roper 2006; Ratti et al. 2008, Boussard et al. 2011). Garibaldi et al. (2014) showed that the native pollinators enhance fruit set in crops throughout the world with or without supplemental pollination by non-native pollinators.

Cranberry has a short flowering period (mid-July to late July in Newfoundland) (Macfarlane 1995). Bees need access to floral resources such as pollen and nectar throughout their flight period (Westrich 1996; Goulson 2003a), which is from mid-May to late September in Newfoundland. Wild flowering plants such as *Chamaedaphne calyculata* L. Ericaceae (leather leaf), *Kalmia polifolia* Wangenh Ericaceae (bog laurel), and *Chamerion angustifolium* (L.) Scop. Onagraceae (fireweed), act as a food source for native bees when cranberry plants are not in bloom (Blaauw and Isaacs 2014). Studies have shown that the native bees respond positively to natural landscapes and the yield of crops and pollination services increases with bee abundance and diversity (Kremen et al. 2002, Ricketts et al. 2008). Cane and Schiffhauer (2003) showed that native bees are more efficient in pollinating cranberries than the non-native honeybees in New Jersey. However, agricultural practices and habitat disturbance (Westphal et al. 2003) around cranberry fields may reduce the availability of nesting locations for bumblebees (Evans and Spivak 2006) and solitary bees (e.g. Andrenidae, Halictidae, Megachilidae) that nest underground, under tree bark, or in similar natural debris (Sellars and Hicks 2015). Furthermore, habitat loss or the isolation of natural habitats, results in the reduced availability of floral resources and thus pollinators (Steffan-Dewenter and Tscharntke 1999). This study predicts that commercial cranberry fields in Newfoundland surrounded by larger quantities of natural woodlands and bogs may have higher bee abundance and yield because they provide alternative foraging and nesting habitats for native bees.

Currently, *B. impatiens* is effectively illegal to import due to stringent permit requirements, but is sometimes imported without a permit as “used” bees from blueberry fields in Nova Scotia or New Brunswick to pollinate commercial cranberries in Newfoundland. Dependence on native bees will reduce the importation costs, as well as decrease the probability of disease spread by bees imported into the province. As mentioned earlier, the pollinators in Newfoundland, both managed and wild, appear healthy and relatively free from pests and diseases (Sellars and Hicks 2015). However, imported *B. impatiens* has a higher disease load and can carry *Nosema ceranae* (Dissociodihaplophasida: Nosematidae), which had not previously been documented in Newfoundland honeybees or native bees (B. Hicks, personal communication, December 20, 2016). Conservation of natural habitats around cranberry fields could maximize the abundance of native bees and reduce the risk of illegal importation of non-native bees (Eaton and Nams 2012). This study also aims to fill the gap in understanding if native bees alone are sufficient to pollinate commercial cranberries in Newfoundland. Understanding these facets of native bee ecology will make it possible to provide recommendations on habitat management to cranberry growers.

Objectives

The main objectives of my study are to (1) assess the diversity and abundance of native bees in four commercial cranberry farms in Newfoundland (2) test the effectiveness of native and non-native bees and (3) examine the local (forage plants on the berms) and landscape (bogs) factors associated with high pollinator activity and fruit yield. I predict that the native bees will provide a yield higher than or equal to the yield by non-native bees and, the yield of cranberry fruit will be higher in the farms surrounded by larger amounts of bogs and potential forage plants because these provide alternative foraging habitat and nesting sites.

Methods

Study Area

The sampling was carried out during the 2015 growing season on four cranberry farms on the island of Newfoundland, Canada. Two farms (Farm 1, 28m above sea level, and Farm 2, 50m asl) are located in western Newfoundland, near Stephenville (48°33'N 58°34'W). The others (Farm 3, 74m asl and Farm 4, 99m asl) are located in central Newfoundland, near Grand Falls-Windsor (48°57'N 55°40'W) (Table 1). The farms in western Newfoundland are in the Southern Boreal Zone ecoregion and the central Newfoundland farms are in the Middle Boreal Zone ecoregion. The climate is similar in the two locations, with average annual temperatures of 5°C and 4.5°C, and precipitation of 1340 mm and 1099 mm, for Stephenville and Grand Falls respectively (Table 2), and similar seasonal patterns of temperature and precipitation (Figure 1A & 1B). Farm 1 was supplemented with 12 colonies of *B. impatiens*, which were present on berms in several parts of the farm from early July until mid August, whereas the other farms did not have any supplemental bees. Honeybees were not present in any of the study farms. The fields were approximately 15 years old and were planted with the cultivar Pilgrim.

Table 1. Sizes of the cranberry farms and fields in western and central Newfoundland

Farm	Area (ha)	Average field size (ha)	Average field dimensions (length × width) (m)
Farm 1	7.5	0.875	250 × 35
Farm 2	7.2	0.525	150 × 34
Farm 3	9.0	1.25	250 × 50
Farm 4	10.0	1.5	300 × 50

Table 2. Average temperature and precipitation in central and western Newfoundland in July. Canadian climate normals ,1981-2010, Environment Canada (http://climate.weather.gc.ca/climate_normals) for Grand Falls and Stephenville.

	Western Newfoundland (Stephenville)	Central Newfoundland (Grand Falls)
Daily average temperature (°C)	16.4	17.1
Daily maximum temperature (°C)	20.2	22.7
Daily minimum temperature (°C)	12.6	11.3
Precipitation (mm)	118.4	88.5

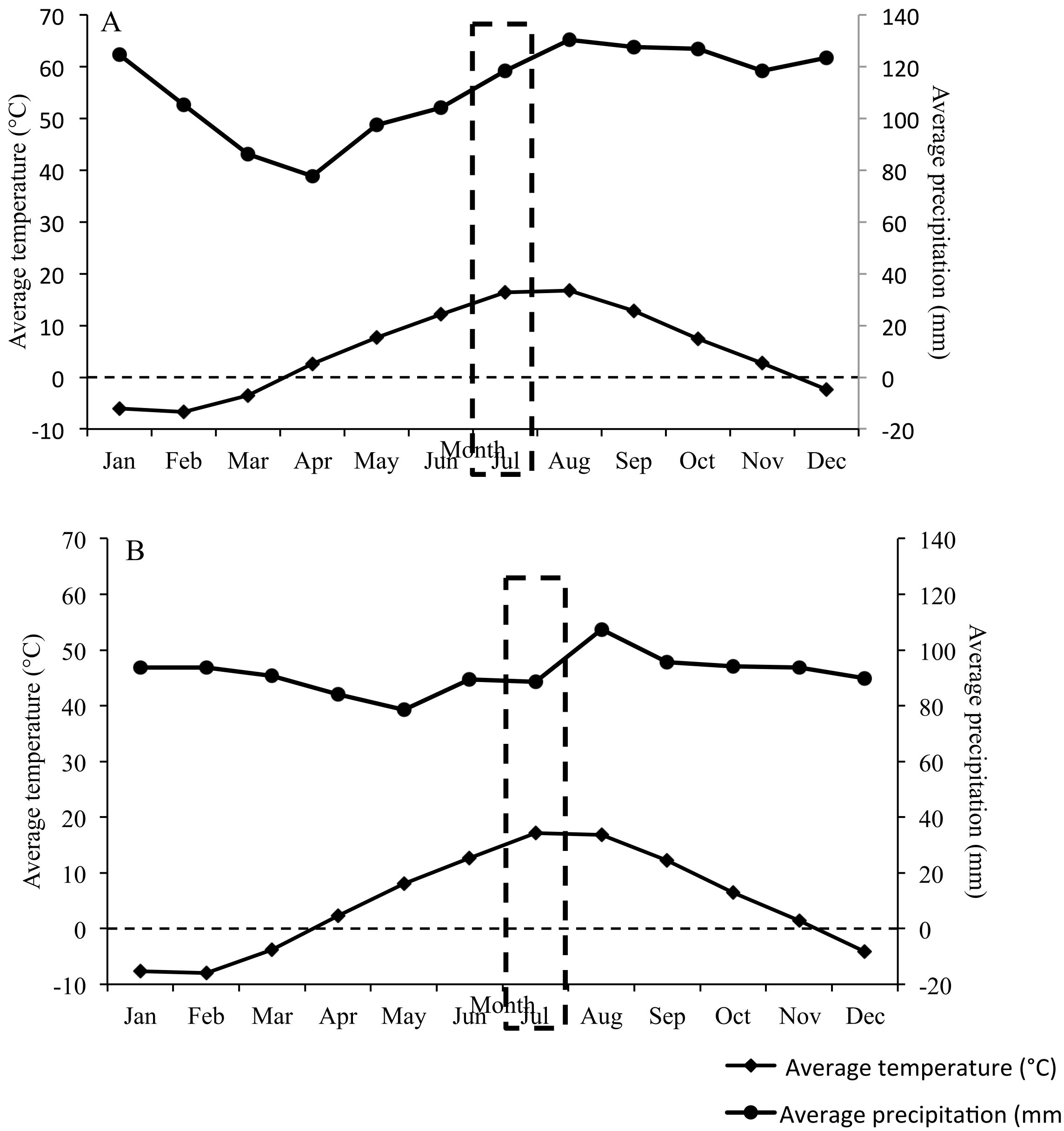


Figure 1. Climatogram showing the average temperature (diamonds) and precipitation rates (circles) during 1981 to 2010 in A) western Newfoundland (Stephenville) and B) central Newfoundland (Grand Falls) (Canadian climate normals 2016). The dashed boxes highlight the conditions in July, the key period for cranberry pollination.

Study site characteristics

At the local scale, farm 1 had largely gravel berms that were used for vehicle access with very little vegetation (Figure 2A) except along the edge of ditches. Farms 2 and 3 had denser vegetation along the berms of the fields (Figure 2B and 2C). Farm 4 had less vegetation on the berms when compared to farms 2 and 3 but more vegetation when compared to farm 1 (Figure 2D).

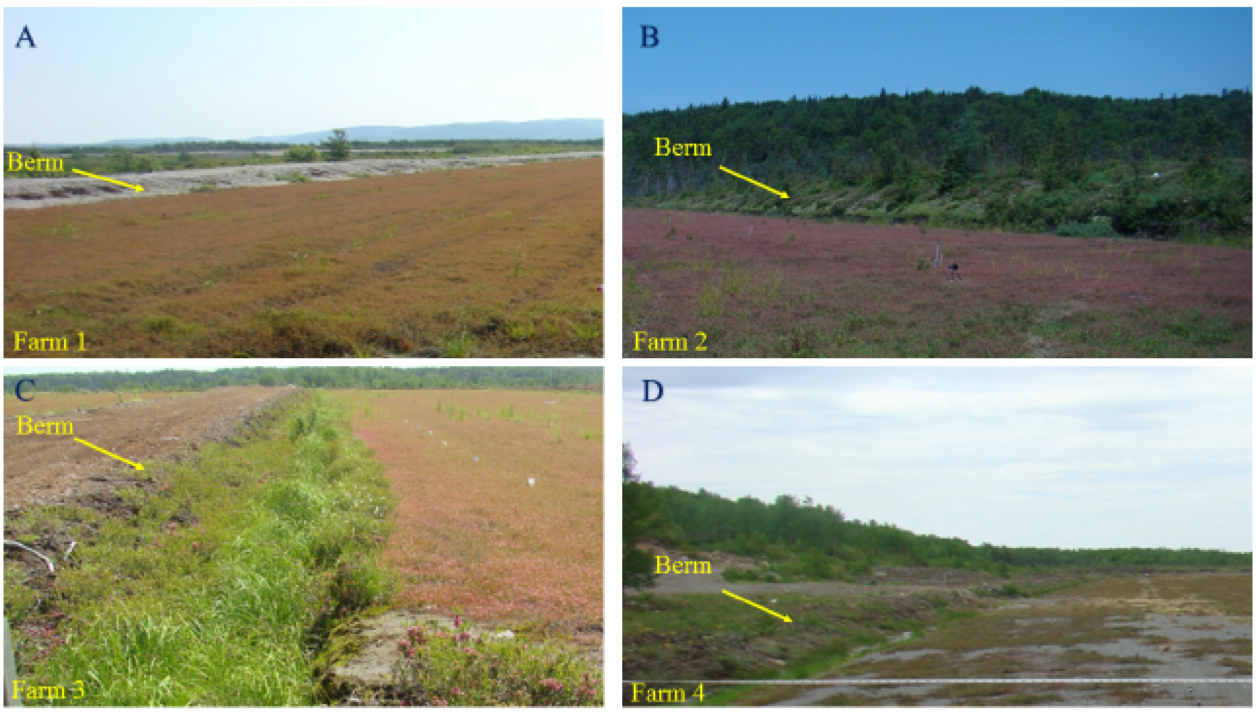


Figure 2. The cranberry farms in western Newfoundland (A – farm 1 and B – farm 2) and central Newfoundland (C – farm 3 and D – farm 4). Berms are indicated by yellow arrows.

Assessing Diversity and Abundance (Objective 1)

Cup Trapping Cup traps (455ml plastic beer cups), alternating blue, yellow and white were placed along three transects at intervals of 5 meters along the long axis of each field. Two fields were sampled on each farm, for a total of 8 fields. The transects were about 15 meters from one another, and at least 5 metres from the field margin. This spacing avoids competition among adjacent cups (Droege et al. 2010). Thus, a total of 144 cup traps were used in this study and were placed in all eight fields with 6 per transect for a total of 18 traps in each field. In my study, cups were used as traps instead of bowls for two main reasons: (i) they have a larger capacity, and thus can be left longer between visits, and (ii) they are deeper, which reduces evaporation in the very exposed, windy fields. The plastic cups initially were white; to produce the blue and yellow traps, cups were painted with rust-oleum (navy blue and sun yellow Painters Touch) paint. The traps were ~1/3 filled with propylene glycol (Droege 2008) (Prestone plumbing antifreeze decoloured with ~3 ml/l household bleach) and were mounted on holders just above the vegetation at 30 cm. As the traps were emptied weekly, propylene glycol was used as a trapping solution instead of soapy water because it acts as a short-term preservative. Propylene glycol is also not attractive to wildlife and does not dissolve paint (Droege 2008). The traps were placed in the fields on 7 and 8 July, and any bees in the traps were collected at 7-10 day intervals between trap placement and 25 August, covering the mid- and late-bloom periods (Table 3). The captured bees were preserved in 70% ethanol in the field, then brought to the laboratory where they were washed in warm soapy water and alcohol, blown dry with a dryer (Remington, chrome compact, 1875 watts) and pinned. Bumblebees were identified to species, and all other bees to genus, using available keys

(Laverty and Harder 1988; Packer et al. 2007). Multiple people identified the bees using multiple keys and no specimen identifications were ambiguous. The specimens are housed in room AS 3026 at Grenfell Campus, Memorial University of Newfoundland.

Table 3. Bloom periods during the 2015-growing season determined for fields near Stephenville and Grand Falls. Early bloom is defined as 25% of flowers open, mid bloom > 50% open flowers, and late bloom as all flowers open. The percentage of bloom was determined by the same person at all sites.

	Bloom period		
Location	Early	Mid	Late
Stephenville	7 July	14 July	18 July
Grand Falls	2 July	12 July	19 July

Sweep Netting In each cranberry field, the bees were sweep netted twice (21 July and 18 August in Stephenville fields, and 22 July and 19 August in Grand Falls fields), for half an hour (between 10:00 am and 11:00 am) during the bloom period in each field. Continuous sweep netting was carried out along the field edges only to ensure that smaller solitary native bees were not missed (Kremen et al. 2004; Ratti et al. 2008). The collected bees were transferred to a killing jar with ethyl acetate anhydrous, taken to the laboratory and pinned for identification. All the bumblebees were identified to species and the solitary bees were identified to genus using available keys (Laverty and Harder 1988; Packer et al. 2007; Colla et al. 2012). The specimens are housed at Grenfell campus, Memorial University of Newfoundland.

Pollinator Effectiveness (Objective 2)

Fruit production In each field, two groups of 7 – 10 unopened blossoms were selected at 50 cm intervals along a 10 m yield transect near the center of the field, for a total of 20 pairs in each field. Each group consisted of one to three flowering stems, most often two. At each transect point, one group of blossoms was left accessible to pollinators (open treatment), the other was covered with a 10 cm diameter, 15 cm deep cage made of window screen, secured to the ground with a metal skewer (caged treatment). These cages have previously been shown to exclude flying pollinators (J. Sircom, unpubl. data). The initial number of blossoms was recorded on 30 June and 2 July, and any resulting fruits were collected on 25 and 26 August. All the berries were full sized but not fully ripe and had not fallen to the ground. There was little evidence of insect infestation on the berries, with <2% of collected fruit showing signs such as entrance holes of cranberry fruit worm (*Acrobasis vaccinii* Riley Lepidoptera: Pyralidae).

Percent fruit set Percent fruit set is the percentage of blossoms that end up forming fruits. The berries were collected on 25 and 26 of August, 2015 from all the tagged blossoms along the yield transect in all eight fields. Percent fruit set = (the total number of berries formed / the total number of flowers tagged per transect point)* 100.

Stigma Loading Stigmas were collected during early (21 and 22 July), mid (28 and 30 July) and late bloom (4 and 5 August) periods from all eight fields along the transects used for determining bee abundance and diversity. This timing was chosen because the mid-bloom period was found to be the most effective period for cranberry pollination in Wisconsin (Evans and Spivak 2006). The weather was clear during the stigma collection period and there were no adverse weather conditions such as heavy rain the day before stigma collection. The flowers were collected at 5m, 15m and 25m along all three transects. Three to five flowers per sampling point were collected and secured in labeled centrifuge vials and the vials were gathered in zip lock bags according to their location and field and then brought to the laboratory, where they were kept in the refrigerator. Microscope slides with 3 to 5 stigmas from one point were prepared within one week from the collection date. The collected stigmas were stained by placing them on melted glycerin gel with fuchsin on a microscope slide (Parrish 2004) and were placed under a compound microscope (Nikon Eclipse *Ni*) to count the number of pollen tetrads (Hicks 2011). A minimum of 8 pollen grain tetrads on one single stigma ensures fruit set in cranberries (Evans and Spivak 2006).

Pollinator effectiveness Individual bee observations were used to assess the effectiveness of different bee species. This was done opportunistically; following whatever bees visited the observation area, and could include both native and non-native bees. Exclusion frames (0.8 m × 0.8 m × 20 cm deep) made of Coroplast^{TM} covered with window screen were placed on 23 June in the Stephenville fields and 24 June in the Grand Falls fields, and secured with metal skewers. Four frames were placed in each field in line with the yield transects (above). During the peak flowering period (28 July – 12 August) observations were made during regular site visits only if it was sunny with temperatures of 18°C – 29°C. A frame would be removed, and all visiting pollinators observed during 1 hour. Each time a bee visited a flower, the flower would be tagged with coloured elastic; if a bee visited multiple flowers they would all be marked with the same colour. Visited flowers were then covered with cages, and any resulting fruit was collected on 25 and 26 August. In both the above collections, fruit were returned to the laboratory and weighed to 0.0001 g.

Local and Landscape Features (Objective 3)

Vegetation Survey Three vegetation surveys were conducted on the berms of each field (16 and 18 June, 14 and 15 July, 12 and 14 August). Three belt transects of 1 m each (2 on the long side of the field and one on the short side of the field) were placed from center of the berm to the field. In each transect, the plants were identified, the percentage of plant cover was estimated and the presence of blossom in these plants was noted. The surveyed area was then categorized as forage plants, non-forage plants or bare ground. The forage and non-forage plants were distinguished based on published records of pollinator foraging preferences (Heinrich 1979; Kearns and Thomson 2001; Boland 2011).

Landscape Features The woodlands, water sources, bogs, crop fields and human disturbance (residential and industrial areas) around all four cranberry farms were digitized in GIS using ArcMap 10.4. The percentage of various landscape features around the cranberry farms was calculated at spatial scales 500m, 1000m and 2000m radius from the center of the two cranberry fields at each location. These spatial scales were chosen because the known foraging distance of various bumblebees is generally between 100m and 2000m (Westphal et al. 2003; Rao and Strange 2012).

Statistical Analysis

Diversity, richness and abundance of native bees The difference in total bee abundance and the abundance of the most common native bee species, *Bombus ternarius*

Say (Hymenoptera: Apidae) among the four cranberry farms was analyzed using treatment-by-subjects ANOVA (R version 3.2.3; R Core Team 2015) with the variables abundance of bees, location of farms and week of collection. The treatment-by-subjects ANOVA was used because the dependent variable bee abundance was measured in the same fields over the seven-week sampling period (King 2016). Shannon diversity indices were calculated using PAST 3 (Hammer et al. 2001) and the following formula:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where, p_i = proportion of total individuals in species *i* and *S* = total number of species (Hammer et al. 2001).

Two-way ANOVA was carried out to test bee abundance in relation to cup colour (white, blue and yellow) and site (farms 1, 2, 3 and 4) with bee abundance as the response variable and cup colour (fixed factor) and site (fixed factor) as explanatory variables. Two-way ANOVA was also carried out to understand the abundance of bees in relation to the location (edges and center) of the fields and the site with bee abundance as the response variable and the location (fixed factor) and site (fixed factor) as explanatory variables. To further understand the distribution of native bees (*Bombus* and non-*Bombus*) in the cranberry farms, a two-way ANOVA was carried out with *Bombus* abundance and non-*Bombus* abundance as the response variables and the location (fixed factor) and site (fixed factor) as explanatory variables.

Fruit production Univariate ANOVA was carried out to test fruit mass and fruit set. The dependent variables were fruit mass and proportion fruit set. The fixed factors were site and treatment (open and caged). The relationship between fruit set, total bee abundance and abundance of *B. ternarius*, were tested using a linear model (R version

3.2.3; R Core Team 2015). Residuals were plotted against fitted values and the errors are homogeneous, normal and independent. The proportion fruit set at each farm and the percentages of local and landscape features were arcsine square root transformed (Wilson et al. 2013).

Stigma loading The stigma loading efficiency was tested using treatment-by-subjects ANOVA (R version 3.2.3; R Core Team 2015) with the site and sample as explanatory variables and pollen tetrads as the response variable. Linear modelling was carried out to test the relationship between fruit mass and the proportion of stigmas that received ≥8 pollen tetrads ANOVA (R version 3.2.3; R Core Team 2015).

Local and landscape features To evaluate the relative importance of local and landscape features in determining bee abundance, generalized linear models with Poisson distribution were compared using Akaike's information. With only four farms, each variable had to be modelled separately. Variables were selected that were biologically meaningful. At the local scale, percent coverage of berms by forage plants was included. Among the landscape scale variables, coverage by woodlands at all three scales (500, 1000, and 2000m) and bogs at 500 and 1000m accounted for, on average, > 20% of land cover, and exhibited considerable variation among farms. Crop fields made up similar and low proportions of the landscape across all farms and scales, and were therefore excluded from further analysis. Water does not provide habitat for bees, and was negatively correlated with the included forest variables, so was also excluded. Human disturbed areas made up, on average, < 20% of land use at each scale; farm 2 had 21% human disturbance at 2000m and farm 3 had 22% at 1000m, thus these variables were also excluded.

Besides the analyses specified above, all analyses were performed using IBM SPSS version 23.0 (IBM Corp.2015).

Results

Because the individual fields at each farm were within the normal foraging range of native bees, they could not be considered independent. The data for the two fields on each farm was combined and analyzed at the farm level.

Diversity, richness and abundance of native bees (Objective 1)

A total of 577 bees (Appendix 1) was collected from the 144 cup traps in all the four cranberry farms. Bee abundance was significantly higher (Table 4) at farm 1 (278) than at the other three farms (farm 2 =110, farm 3 = 94, farm 4 = 95). Farm 1 had 77 individuals of the imported non-native *B. impatiens*. All the other farms had only native bees. The bee abundance in farms 2, 3 and 4 did not differ significantly from one another. There were slightly more taxa collected in the western farms (1 and 2) than the central farms (3 and 4) (Table 5). The data from the two fields in each farm was combined for analysis.

Table 4. Treatment-by-subjects ANOVA for bee abundance in the four cranberry farms at different weeks of sample collection. There is only one measurement per site per week and hence the interaction term is absent.

	DF	Sum Sq	Mean Sq	F value	Sig.
Week	6	3643	607.2	3.175	0.02643
Site	3	3430	1143.5	5.978	0.00518
Residuals	18	3443	191.3		

Table 5. Species richness, Shannon diversity index (H) and abundance of bees in the four cranberry farms located in Stephenville (farms 1 and 2) and Grand Falls (farms 3 and 4). The values include 77 individuals of *B. impatiens* at farm 1.

Location	Species richness	Diversity index (H)	Bee abundance (n)
Farm- 1	13	1.624	278
Farm- 2	14	1.805	110
Farm- 3	10	1.760	94
Farm- 4	11	1.544	95

Bombus ternarius made up > 20% of the total individual bees in each of the cranberry farms. Farms 1, 3 and 4 had fairly similar percentages of *B. ternarius* (43%, 43% and 56% respectively) while farm 2 had a lower proportion of *B. ternarius* (28%). Their abundance also significantly varied among the four cranberry farms ($F_{6, 13} = 3.175$, $p = 0.026$), with fewer *B. ternarius* at farm 2. On farm 1, 28% of collected bees were *B. impatiens*, and all other bees except *B. ternarius* made up <20% of the total. On farm 2, *Lasioglossum spp*. were abundant (32% of total bees), and *Bombus borealis* Kirby (Hymenoptera: Apidae) made up another 21% of the bee community. On farms 3 and 4, no species of bee other than *B. ternarius* made up more than 20% of the total (Figure 3).

Bees were attracted to all the traps irrespective of colour, with no significant difference in their abundance ($F_{2, 6} = 1.76$, $p = 0.250$). Likewise, there was no significant difference ($F_{1, 3} = 5.61$, $p = 0.099$) in the abundance of bees captured from the center and edges of the fields. Considering *Bombus* and non- *Bombus* species separately, there was no significant difference in the abundance of *Bombus* spp. between the center and edges of the fields ($F_{1,3} = 4.90$, $p = 0.114$), but there was a non-significant trend ($F_{1,3} = 8.40$, $p = 0.063$) towards fewer non- *Bombus* captured in the centers compared to the edges of the fields.

Seventy-seven imported *B. impatiens* individuals were collected from cup traps compared with only two individuals of this species in the sweep netting survey.

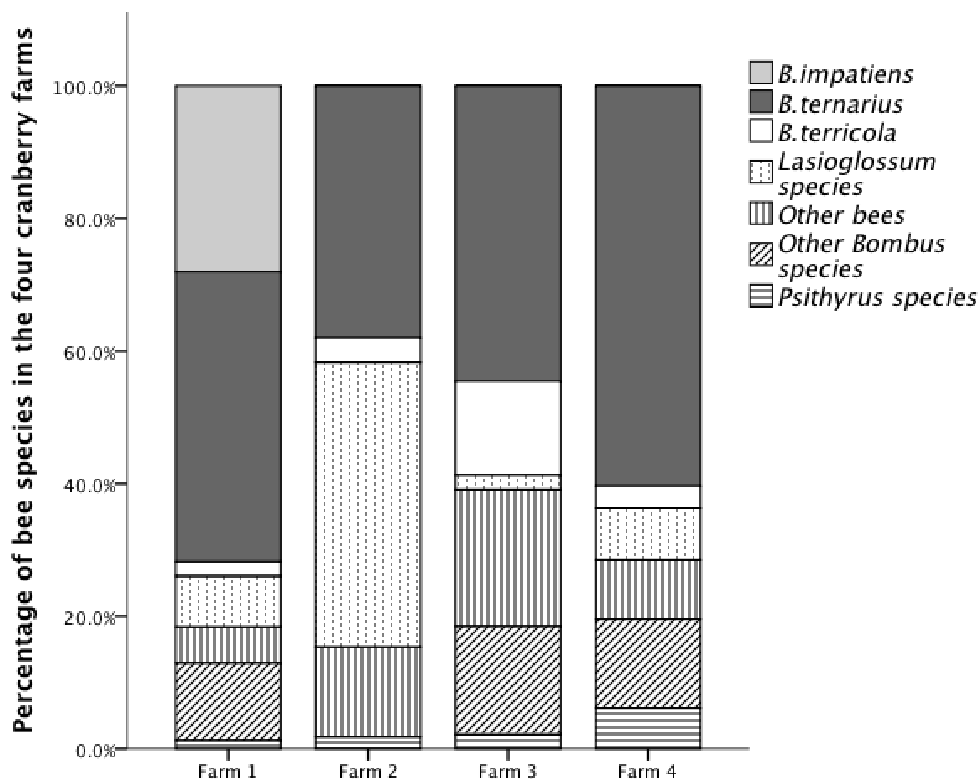


Figure 3. Community composition of bees grouped into broad categories in four cranberry farms in western (farms 1 and 2) and central (farms 3 and 4) Newfoundland based on cup trap collections.

Pollinator Effectiveness (Objective 2)

Fruit production The proportion of blossoms setting fruit was significantly greater with pollinator access (no cages: 37-61%) compared to those flowers without pollinator access (caged: 9-20%) (Table 6, Figure 4), suggesting that presence or absence of pollinators affects fruit set. Farm 1 (with imported bumblebees) had significantly higher fruit set than the other farms with pollinator access. There was no significant difference among farms in fruit set in the pollinator exclusion treatment, although farm 4 had 20% fruit set compared to 8-9% on the other cranberry farms. There was no significant relationship between fruit set and bee abundance ($F_{1,2} = 11.534$, $p = 0.0768$). Similarly, the relationship between fruit set and the abundance of *B. ternarius* was also not significant ($F_{1,2} = 4.5047$, $p = 0.1678$).

Table 6. Analysis of Variance for proportion fruit set of cranberries produced with (open) and without (cage) flying pollinator access in the four commercial cranberry farms in western and central Newfoundland.

Source	Df	Type III Sum of Squares	Mean Square	F	Sig.
Treatment	1	15.204	15.204	246.051	0.001
Site	3	1.591	0.530	8.581	0.001
Treatment*Site	3	1.474	0.491	7.952	0.001
Error	332	20.516	0.062		

Dependent variable: Proportion fruit set (arcsine square root transformed)

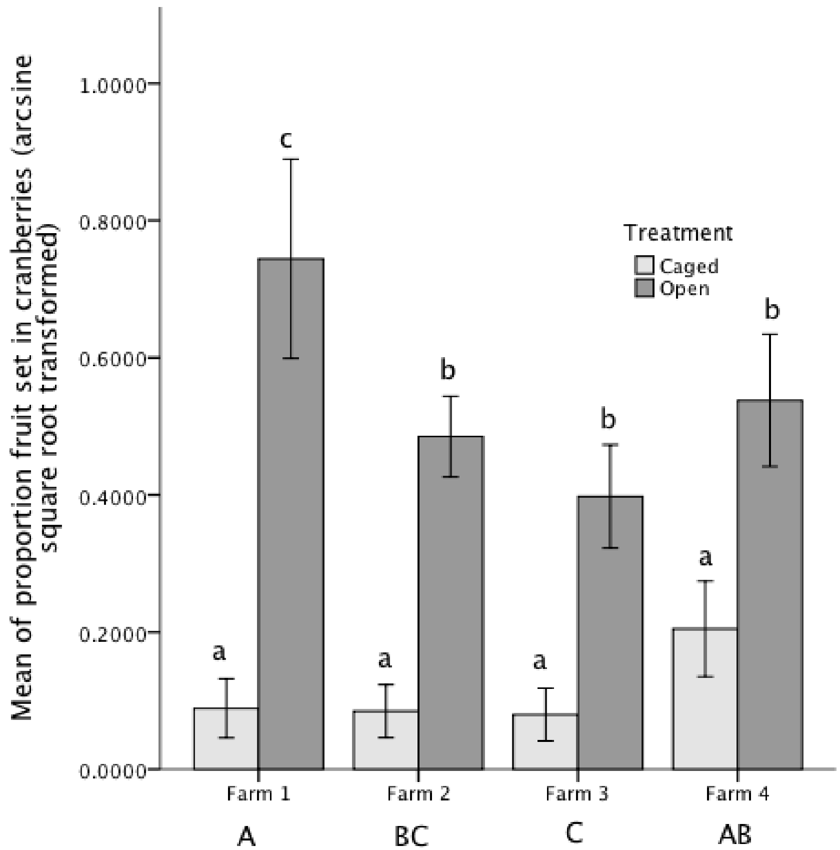


Figure 4. Mean of proportion fruit set (arcsine square root transformed) with (open) and without (caged) flying pollinator access in the four cranberry farms in western and central Newfoundland. Lower case letters indicate significant differences between farms within a treatment, upper case letters indicate significant differences in overall fruit set between farms. Error bars indicate 95% confidence intervals. Farms 1 and 2 are in western Newfoundland, farms 3 and 4 in central Newfoundland. Farm 1 had imported *B. impatiens* included.

Mean fruit mass was significantly different among farms, with higher fruit masses recorded on central than on western farms with full pollinator access (open; Figure 5, Table 7). Excluding pollinators resulted in fewer berries being produced but significantly reduced mean fruit mass only on farm 2.

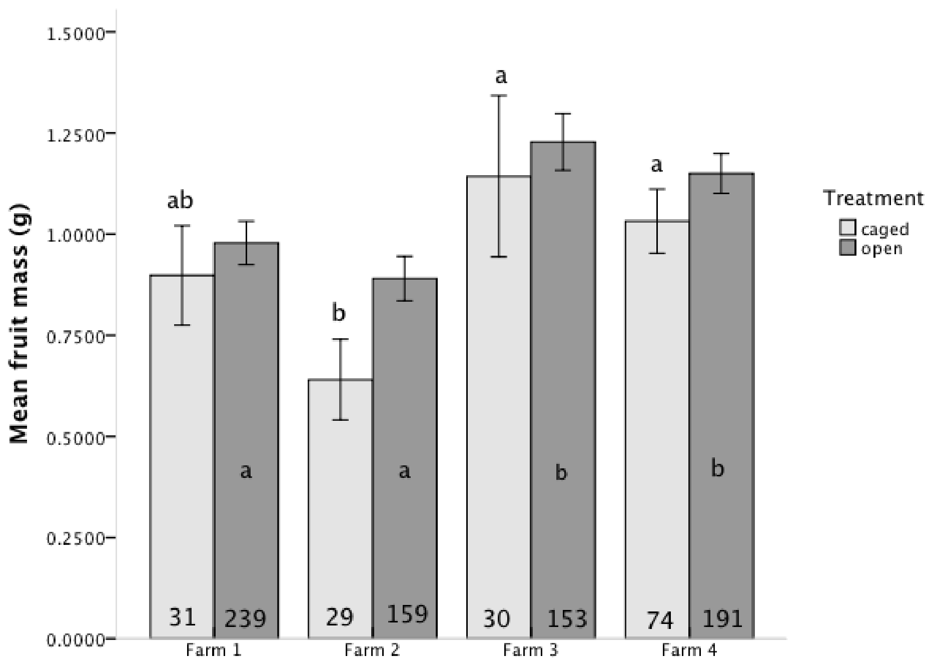


Figure 5. Mean fruit mass produced on the four commercial cranberry farms in Newfoundland with (open) and without (caged) flying pollinator access. Letters indicate within-treatment differences among farms. Numbers at the bottom of the bars indicate sample sizes (# berries). Error bars indicate 95% confidence intervals. Farms 1 and 2 are in western Newfoundland, farms 3 and 4 in central Newfoundland. Farm 1 had imported *B. impatiens* included.

Table 7. ANOVA comparing fruit mass among the four commercial cranberry farms in western and central Newfoundland (site) with and without flying pollinator access (treatment).

Source	Df	Type III Sum Sum Sq	Mean Sq	F	Sig.
Treatment	1	2.15	2.154	14.25	0.001
Site	3	15.12	5.041	33.35	0.001
Treatment * Site	3	0.481	0.160	1.060	0.365
Error	898	135.744	0.151		

Dependent Variable: Fruit mass

Stigma loading On all four farms, most of the blossoms sampled had received at least the minimum number of tetrads (8) to fully pollinate the ovules (Table 8, Table 9 and Figure 6). Farm 2 had a lower stigma loading than the other farms, which do not differ from one another ($F_{3, 534} = 12.10$, $p = 0.001$). There was no significant relationship between the fruit mass of cranberries and the proportion of stigmas that received ≥ 8 pollen tetrads ($F_{1, 2} = 0.0072$, $p = 0.9403$).

Table 8. Treatment-by-subjects ANOVA for the number of pollen tetrads in the four cranberry farms in Newfoundland at the three weeks of sample collection.

Source	Df	Sum Sq	Mean Sq	F	Sig.
Site	3	17113	5704	12.10	0.001
Sample	2	40722	20361	43.19	0.001
Residuals	534	251728	471		

Table 9. Proportion of stigmas that received ≥ 8 pollen tetrads in the four commercial cranberry farms in Newfoundland on three sampling events (21 & 22 July, 28 & 30 July and 4 & 5 August).

Sample	Farm 1	Farm 2	Farm 3	Farm 4
1	0.58	0.33	0.58	0.67
2	0.62	0.53	0.96	0.98
3	0.87	0.80	0.96	0.91

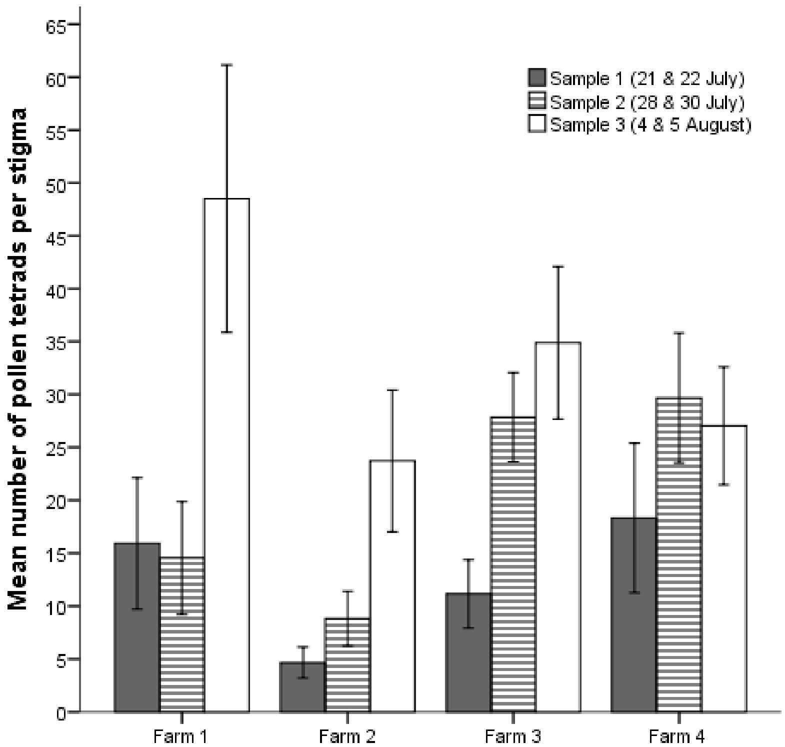


Figure 6. Mean number of pollen tetrads per stigma in the four commercial cranberry farms in Newfoundland. Samples 1, 2 and 3 indicate the stigma collection date. Error bars indicate 95% confidence intervals. Farms 1 and 2 are in western Newfoundland, farms 3 and 4 in central Newfoundland. Farm 1 had imported *B. impatiens* included.

Individual pollinator effectiveness The most abundant species collected in the cranberry fields was *B. ternarius* (Appendix 1, 2), which was also the most commonly observed bee during pollinator effectiveness trials (Table 10). Two other native *Bombus* species (*B. terricola* and *Bombus vagans bolsteri* Smith (Hymenoptera: Apidae) were also observed during these trials in smaller numbers. Only one other type of bee, *Andrena* spp.

were observed visiting >15 blossoms. The non- native *B. impatiens* was not observed during the pollinator effectiveness trials. The low number of observations precludes meaningful statistical comparison, however, it appears that *Bombus* spp. successfully pollinates a higher proportion of blossoms with a single visit than do *Andrena* spp. (30-55% vs. 12%) and result in larger fruit (0.8-1.0g vs. 0.6g). The more abundant *B. ternarius* may have lower single-visit pollination success (30%) than the other two *Bombus species* observed (39% and 55%), although as noted these results must be treated with caution due to low sample sizes.

Table 10. Bee species, number of flowers visited by the bees, percent fruit set and the mean fruit mass and fruit size of cranberries pollinated by different bees in the four cranberry farms in Newfoundland. The fruit mass of cranberries pollinated by individual bees at central and western farms is given in Appendix 3.

				Fruit mass (g)		Fruit size (mm)	
Bee type	Number of flowers visited	Number of fruits formed	% Fruit set	Mean	SE	Mean	SE
B. ternarius	58	17	29.31	0.92	0.05	13.22	0.28
B. terricola	33	18	54.55	1.00	0.06	13.81	0.49
B. vagans bolsteri	18	7	38.89	0.80	0.11	12.21	0.80
Andrena	17	2	11.76	0.61	0.37	10.56	2.91
Unidentified bees	7	4	57.14	0.68	0.05	11.74	0.45
Nomada	6	2	33.33	0.96	0.58	12.88	2.93
Megachilidae	4	0	0.00	0.00	0.00	0.00	0.00

Local and landscape features (Objective 3)

There were 26 different types of plants recorded growing on berms among the four farms during the vegetation surveys. All plants were recorded, including gymnosperms and non-vascular plants that are unlikely to provide forage, in order to reflect the availability of non-forage resources such as nesting sites. Plant diversity differed among farms, with farm 2 having the highest diversity at 18 taxa. Out of the 18 taxa, farm 2 had 14 different species of forage plants. Farms 1, 3, and 4 had 8, 10 and 12 species, respectively. Most plants were not abundant, and much of the berms were bare (Table 11). The plants were grouped according to whether or not they are typically forage plants for bees depending on the floral preferences of the bees. Important early-season forage plants that were identified on these farms include *Chamaedaphne calyculata* (leather leaf), *Kalmia polifolia* (bog laurel) and *Rhododendron groenlandicum* Oeder Ericaceae (Labrador tea) and the main late-season forage plant was *Chamerion angustifolium* (fireweed). Another important late-season forage plant, goldenrod (*Solidago* spp. L. Asteraceae), was also present near the fields, but was not observed in the vegetation survey. A complete list of forage and non-forage plants can be found in Appendix 4. Mean percent cover of forage plants among all farms was 18.2 ± 1.6 (mean ± s.e; n = 9), and ranged from 8 % (farm 1) to 25 % (farm 3). Coverage of non-forage plants (13.2 ± 2.0 %) ranged from 7 % (farm 3) to 25 % (farm 1), and bare ground (67.2 ± 2.0 %) from 45 % (farm 3) to 93 % (farm 1).

Table 11. The mean percent cover of forage plants, non-forage plants and bare ground observed at the four cranberry farms in Newfoundland. Because these are mean values, the total for each farm may not be 100%.

Site	Mean % cover of forage plants	Mean % cover of non- forage plants	Mean % cover of bare ground
Farm 1	8.33	25.00	92.50
Farm 2	21.45	13.64	54.50
Farm 3	25.36	7.00	45.42
Farm 4	12.05	14.17	69.50

The percentages of woodlands, bogs, water sources, crop fields and human disturbances were measured at scales 500 m, 1000 m and 2000 m radii from the study sites (Appendix 5; Figure 7). At 500 m radius, farms 1 and 2 had a greater percentage of woodlands and farms 3 and 4 had a greater percentage of bogs. At 1000 m radius, the percentages of woodlands and bogs were similar in farms 1, 2 and 4, but farm 3 had higher percentages of bogs and water sources. At 2000 m radius, farms 1, 2 and 4 had similar percentages of woodlands and bogs, but farm 3 had equal percentages of woodlands, bogs and water sources (Figure 8).

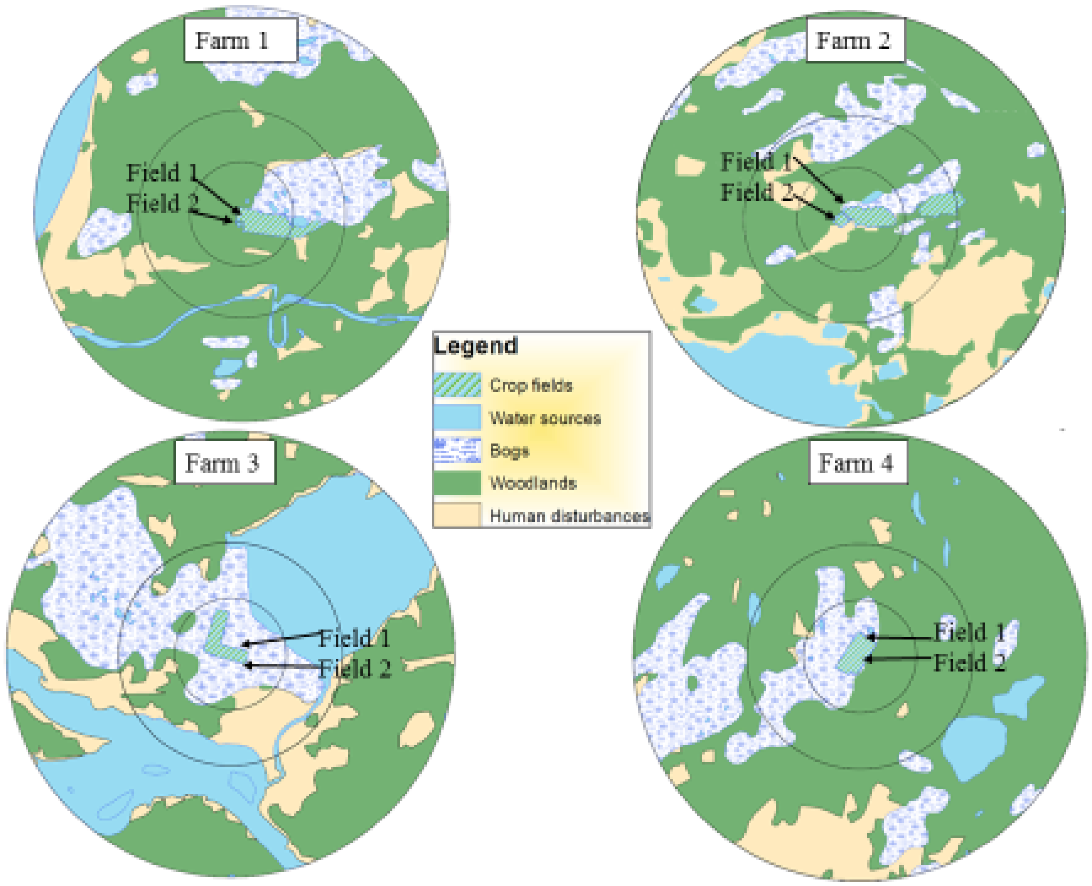
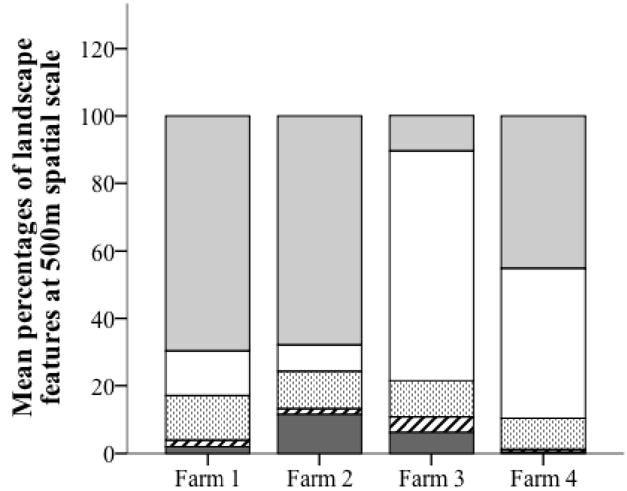
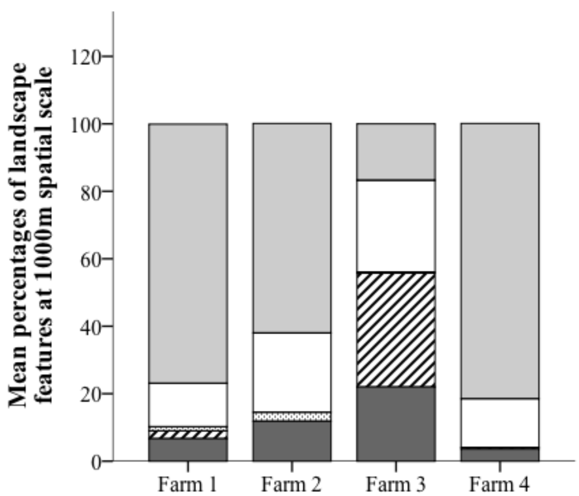


Figure 7. Landscape composition around the cranberry farms located in Stephenville (Farms 1 and 2) and Grand Falls (Farms 3 and 4), Newfoundland. The circles indicate the three spatial scales (500 m, 1000 m and 2000 m). Maps created in ArcMap 10.4 with data from Earth Observation for Sustainable Development of Forests (https://ca.nfis.org/).

A


Mean percentages of landscape features at 500m spatial scale
0
20
40
60
80
100
120
Farm 1
Farm 2
Farm 3
Farm 4

B


Mean percentages of landscape features at 1000m spatial scale
0
20
40
60
80
100
120
Farm 1
Farm 2
Farm 3
Farm 4

C

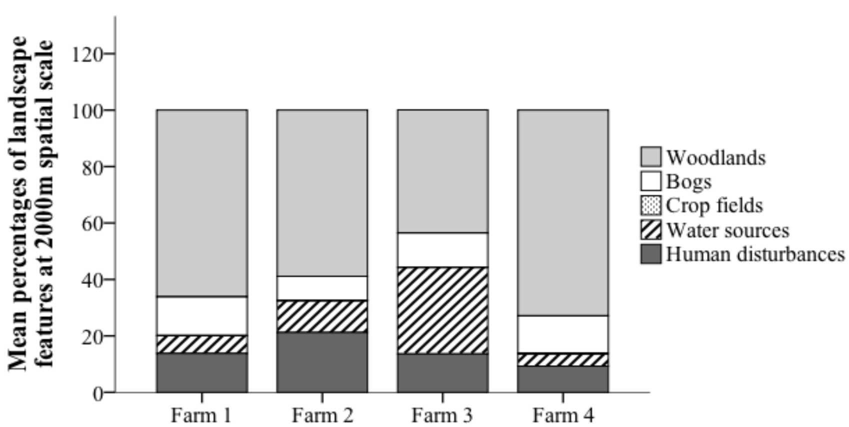

Mean percentages of landscape features at 2000m spatial scale
0
20
40
60
80
100
120
Farm 1
Farm 2
Farm 3
Farm 4
Woodlands
Bogs
Crop fields
Water sources
Human disturbances

Figure 8. (Previous page) Mean percentages of woodlands, bogs, crop fields, water sources and human disturbances at 500 m (A), 1000 m (B) and 2000 m (C) spatial scales in the four cranberry farms in Newfoundland.

The effect of local and landscape features in determining bee abundance was compared by model selection using Akaike's information criterion. Proportion of forage plants, woodlands, and bogs were used as explanatory variables with bee abundance as the response variable. Two models had nearly the same explanatory power: the proportion of the landscape made up of bogs at 1000 m, and the proportion coverage of forage plants on the berms (Table 12). All the other models had $\Delta_i > 2$. Bee abundance increased with decreasing coverage of bogs at 1000 m, and with decreasing coverage of forage plants on the berms.

Table 12. Models explaining bee abundance ranked by AICc value.

Variables	AICc	Δ_i = AICc-AICmin	Rank based on least AICc value	Direction of relationship with bee abundance
% Bogs at 1000m	0.009	0	1	Negative
% cover forage plants on berms	0.814	0.804	2	Negative
% Woodlands at 2000m	4.748	4.738	3	Negative
% Woodlands at 500m	8.876	8.866	4	Positive
% Bogs at 500m	8.926	8.916	5	Negative
% Woodlands at 1000m	9.665	9.655	6	Negative

Discussion

Native bees alone appear to be capable of providing sufficient pollination services to the commercial cranberry crops in Newfoundland. A considerable number of stigmas received more than 8 pollen tetrads (the minimum necessary for full pollination) in all four cranberry farms, regardless of the presence or absence of supplemental pollinators. When bees were excluded, some fruit was still produced. This provides further evidence that wind or non-flying insects contribute to pollination (Gaines-Day and Gratton 2015), although not at a level to be commercially viable. All farms had a diverse bee community, but no relationship between bee abundance and fruit yield was found. This provides further evidence that pollination services are sufficient, and that yield is more strongly affected by other factors, such as soil characteristics, fertilization practices, or microclimate. Bee abundance was influenced by field-scale factors, but by landscape factors only to a radius of 1000m, suggesting that most bees on these farms forage at a relatively small scale.

Pattern of Bee Abundance and Diversity

The most common species in the bee community was *Bombus ternarius*, making up > 20 percent of the total individual bees on all farms. The bee abundance in farm 1 significantly differed from the abundance at other study sites, both in total numbers and considering native bees only, i.e. excluding the imported *B. impatiens*. The most common species play a large role in maintaining the healthy functioning of an ecosystem (Winfree et al. 2015), which suggests that *B. ternarius* is particularly important in these cranberry farms. An earlier study on the two western Newfoundland farms (1 and 2) found that *B.*

ternarius was the most abundant bee species (Hicks and Sircom 2016); this study confirms its dominance in western Newfoundland and shows it also to be dominant in central Newfoundland.

The less abundant bees from the four cranberry farms include bees from the families Andrenidae, Colletidae, Halictidae and Megachilidae. These bees may or may not provide sufficient pollination services to cranberry fields. This is because endangered bees or the bees found in very small numbers in a particular ecosystem provide a small proportion of total crop pollination (Ratti et al. 2008; Kleijn et al. 2015; Winfree et al. 2015). However, the efficiency of these solitary native bees cannot be underestimated as they have been proven efficient pollinators of other berry crops such as blueberries (Isaacs and Kirk 2010; Garibaldi et al. 2014) and may provide vital pollination services when bumblebees are not present (Cutler et al. 2015).

Farm 2 (one of the western Newfoundland sites) had the most diverse population of plants growing around the berms. With such a diversity of wild plants, it was assumed that farm 2 would have a large number of bees. Interestingly, species richness (the number of different species present, not considering abundance) of bees may be less important in maintaining ecosystem services such as crop pollination, because high species richness is often due to the presence of rarely found species (Ratti et al. 2008; Winfree et al.2015). Nevertheless species richness plays an important role in ensuring pollination services to crops when the most efficient and dominant bee species fails to pollinate in the event of conditions such as pest and disease attack or weather fluctuations (Winfree et al. 2007a). For example, different species of bees have different periods of emergence. However, information is lacking on activity periods for bees in Newfoundland; this would be a valuable area of research, particularly in the context of climate change. Diverse bee population on a farm will ensure crop pollination if environmental factors such as change in temperature and rainfall have a differential effect on the timing of bloom and foraging period of bees (Ratti et al. 2008). Some studies indicate that plants and pollinators are responding similarly to climate change, but other work has shown bees to be responding more slowly (Bartomeus et al. 2011; Hegland et al. 2009; Pyke et al. 2016). These data were collected in a single year and thus do not reflect the amount of annual variation in bee abundance and species richness. Yearly differences in bee abundances and species richness must be taken into account in future studies to further understand the diversity and abundance of native bees.

As expected based on similar studies (Campbell and Hanula 2007; Droege et. al. 2010), the colour of trap did not affect capture rate. The capture rate of bumblebees was similar in the center and edges of the fields, but there was a non-significant trend for lower capture rates of smaller, solitary bees in the center of the fields than at the edges. This is consistent with patterns observed in watermelon crops in California (Kremen et al. 2004), in which bumblebees were able to forage up to 55 m into the fields, while smaller bees were restricted to the edges. The fields in this study were much smaller than those in the Kremen et al. (2004) study, with a maximum width of 50 m, i.e. 25 m from field edge to center, which appears to be within the foraging range of the smaller bees. Similarly, Ratti et al. (2008) found that the bumblebees were evenly distributed throughout cranberry fields in British Columbia whereas the majority of other small native bees species were restricted to the field edges. Despite the lack of information on field size in

Ratti et al. (2008), the uneven distribution of other native bees could be because of larger field sizes. Although the solitary bees likely provide a small fraction of pollination services, they could be important in years with unusual weather patterns or other conditions that lowers the abundance or changes the timing of peak activity of the dominant pollinators. The relatively narrow fields in this study allowed the smaller bees to reach the entire crop. Further research on field size to support maximal pollination would be valuable to provide guidelines for future farm development.

Pollinator Effectiveness

The most efficient native bees in the cranberry fields of western and central Newfoundland during 2015 were *Bombus* species. *B. ternarius* was the most abundant pollinator in all the cranberry farms in this year and sampling time and was also the most frequently observed during pollinator effectiveness surveys during both years (2015 and 2016) (Hicks and Sircom 2016). The next most commonly observed species was *B. terricola*, followed by *B. vagans bolsteri*. Even though farm 1 had imported *B. impatiens* colonies, 77 individuals were collected from cup traps, 2 individuals of this species in the sweep net survey and none from the visual observation events. Previous work suggests that single visits by *B. impatiens* result in lower fruit set than native *Bombus* species (Hicks and Sircom 2016), but this could not be confirmed in this study. Too few non-*Bombus* species were observed to allow a comparison of the efficiency of bees such as *Nomada* spp and *Andrena* spp to *Bombus* spp. Studies conducted in blueberry and cranberry fields also show that bees of the genus *Bombus* made more flower visits than any other bee species (Javorek et al. 2002; Ratti et al. 2008).

Individuals of *B. ternarius* were observed making more than 500 flower visits. However, all the flowers visited by this particular species were not able to be tracked because an individual bee might move among several flowers while one visited flower was being marked. Hence only the flowers on which the bee spent a considerable amount of time were tagged. In spite of its abundance, the mean fruit mass and the percent fruit set resulting from a single visit by *B. ternarius* to virgin blossoms was less when compared to *B. terricola* and *B. vagans bolsteri.* Floral visitation rate and pollination are two different aspects of pollinator efficiency studies and high floral visitation does not necessarily result in high pollination success (Javorek et al. 2002).

The mean number of pollen tetrads per stigma in cranberry farms 1, 3 and 4 was similar and higher than the mean number of pollen tetrads from farm 2. Even though there was no significant relationship between stigma loading and fruit mass, the mean fruit mass in farms 1, 3 and 4 was higher than the mean fruit mass in farm 2. This tends to support the fact that higher stigmatic loading results in higher fruit mass (Cane and Schiffhauer 2003; Javorek et al. 2002; Ratti et al. 2008). Furthermore, a considerable number of stigmas received more than 8 pollen tetrads in all four cranberry farms, ensuring fruit set. This shows that native bees alone are probably sufficient for pollinating cranberries in Newfoundland.

Pattern of fruit set and fruit mass Flowers that were accessible to pollinators had a higher fruit set compared to those that were caged to prevent pollinator access. Undoubtedly, bees are important in the pollination of commercial cranberries (Brown and McNeil 2006). However, the plants to which pollinators had no access did not have zero fruit set, and with exception of farm 2, produced fruit of similar mass to those with pollinator access. There was approximately 11 percent fruit set from the cranberry blossoms under the treatment cages, as compared with 24 percent in plants with full pollinator access. This shows that other agents of pollinators such as wind or terrestrial pollinators also aid in cranberry pollination (Brown and McNeil 2006; Gaines-Day and Gratton 2015). Yet, these agents of pollination alone will not be economically viable for pollinating commercial cranberries.

Although the farms had sufficient numbers of bees to pollinate the available blossoms, there was no significant relationship between fruit set and bee abundance. This suggests that environmental factors such as temperature, precipitation, soil chemistry, artificial fertilizers applied by the growers or other conditions might have a significant influence on the yield of commercial cranberries in Newfoundland. On a single flowering stem, when fruit develop in lower positions, the number of fruit set in the upper positions is reduced, indicating that there may be competition for resources among berries on individual flowering stems (Roper 2006). A related phenomenon documented in cranberry is ‘bet hedging’ (Brown and McNeil 2006), in which the fruit produced by late-pollinated blossoms at the top of a flowering stem are aborted if the early-pollinated flowers lower on the stem develop fruit. These findings suggest that there is a metabolic constraint on the number of fruit that can be produced, which may obscure the benefits of increased pollinator abundance (e.g. Bos et al. 2007).

Even though bee abundance was higher on farms 1 and 2 than on farms 3 and 4, the average fruit mass was higher in farms 3 and 4. This apparent mismatch between bee abundance and fruit mass could be because of differences in weather conditions between western and central Newfoundland. Climatic conditions such as temperature, sunshine and precipitation are important in determining the yield of cranberries (Degaetano and Shulman 1987). The daily average temperature in western and central Newfoundland in the month of July is somewhat similar but total monthly precipitation is higher in western than central Newfoundland. High precipitation rates during the pollination period can result in reduced crop yields of some crops (e.g. Lobell et al. 2007). However, this depends on the type of crop and area of cultivation. For example, in New Jersey, temperature and sunshine were the factors that influenced yield of cranberries and precipitation was of less importance (Degaetano and Shulman 1987). In Quebec, rainy days during the cranberry blooming period had a negative impact on the activity of pollinators (Brown and McNeil 2006). In addition, different species of pollinators forage at different times of the day and have different tolerance to changing weather conditions (Ratti et al. 2008). Nevertheless, high precipitation rates might still hinder the activity of bees and reduce crop yields.

Local and Landscape Features

Pollination services by native bees depend highly on the surrounding landscape (Steffan-Dewenter et al. 2002; Ricketts et al. 2004; Watson et al. 2011; Bennet and Isaacs 2014; Földesi et al. 2016; Gaines-Day and Gratton 2016) and the effect of these landscape features on the abundance of bees depends on the bees' foraging pattern (Földesi et al. 2016). Bees require floral resources, nesting sites and nesting materials to support their pollination services in a particular ecosystem (Földesi et al. 2016). All of these resources may not be available from a single landscape type. A variety of landscape habitat around a crop farm is required for the pollinators to occur in abundance (Steffan-Dewenter et al.

2002). All the cranberry farms in my study had diverse landscape features such as woodlands, bogs and water sources. The type of natural vegetation on berms differed among farms. Farm 1 had sparse vegetation on the berms. Farm 4 had slightly more vegetation, while farms 2 and 3 had greater, and similar, amounts of vegetation. A lack of floral resources may lead to low fruit mass in cranberries (Ratti et al. 2008), but this did not seem to be the case in the present study, where high bee abundance, fruit set and fairly high fruit mass were observed in farm 1 when compared to the other farms, which had very little vegetation on the berms. This may be due to differences in bee foraging behavior in response to berm vegetation, which could result in higher bee activity in crop fields with little competing forage on the berms, because of the less amount of vegetation on the berms. Alternatively, the greater amount of bare ground could provide more potential nesting sites for ground-nesting bees (Garibaldi et al. 2014).

Kremen et al. (2004) found that the pollination services by bees depend on an area of up to 2500 m from the crop fields. By contrast, in this study bee abundance was significantly influenced by landscape features at a smaller scale, with a negative association with the area of bogs at 1000 m. Bogs provide ample foraging resources, and thus would be expected to result in higher bee abundance. However, if there is little available nesting habitat, the increase in floral resources created by a large area of bog may not result in a larger bee population, if bogs do not serve as ideal nesting sites for native bees. The saturated soil and dominance of shrubs may not provide suitable nesting habitat, particularly to ground-nesting bees. With only four farms, these relationships can be driven by outliers e.g., a single farm with high or low bee abundance. Further study is necessary to determine how bogs affect native bees and how bog area interacts with other landscape features to influence native bee abundance. The findings from my study were similar to Winfree et al. (2007) with a strong negative relationship between forest cover and bee abundance found at a scale of 1600 m. The species composition tends to vary based on the type of forests (e.g. fragmented vs. extensive forests) and more species might be available in agricultural landscapes than forests (Winfree et al. 2007).

Limitations of the study

This is a single year study and thus the yearly differences in bee abundance could not be taken into account. Future research considering the yearly differences in native pollinator diversity and abundance is essential. The low number of solitary bees e.g. members of the family Halictidae limits testing their efficiency as cranberry pollinators. Soil chemistry (pH, acidity, alkalinity and the presence of nutrients) was not measured in this study. This limits the understanding of the key factors determining crop yield, and the relative importance of pollinators.

Conclusion

The assumption is often made by Newfoundland cranberry growers that pollinators are the limiting factor for cranberry production, thus the interest in using supplemental pollinators. One of my predictions was that native bees would be at least as effective pollinators as non-native bees. Although this was not possible to directly test, there were no gains in pollination rate or fruit mass associated with the non-native bees present at farm 1. I also predicted that yield would be higher on farms with more potential forage plants on the berms and more bogs within the foraging range of native bees. However, despite differences in bee abundance and species composition among farms, this study was unable to establish a consistent relationship between bee abundance and fruit set, suggesting that other, unmeasured factors were more influential on these farms. Bees are clearly necessary; without any bees, yields would be too low to be economically viable. However, after a "critical threshold" number of bees, a further increase in the quantity of bees on a farm would have little effect on yield. All four farms in this study appear to have bee abundances beyond the critical threshold. Thus, supplemental pollinators are not necessary to pollinate commercial cranberries in central and western Newfoundland.

A better understanding of how cranberry plants allocate resources is highly desirable to obtain the maximum benefit from crop pollination by native pollinators (Bos et al. 2007; Garibaldi et al. 2014). Newfoundland cranberry producers are in the enviable position of having healthy native bee populations, and appear to manage their farms in such a way that is generally beneficial to bees. Continuing to construct new fields of this scale may have considerable economic benefit and contribute to greater stability in pollination services. Supplemental pollination is expensive, and is likely to be highly restricted in future to protect local bee populations from imported diseases. Growers may obtain greater yields through crop management practices, e.g. more precise timing of fertilizer application, but using supplemental pollinators will have little effect, and runs the risk of introducing pests and diseases. Present cultivation practices support native bees, and should be continued. There may be a shortage of nesting habitat, so future research should focus on how this may be provided in or near the crop fields.

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Appendices

Appendix 1. Total bee abundance from cup traps in the commercial cranberry farms in western (farms 1 and 2) and central (farms 3 and 4) Newfoundland. ***B. impatiens*** is not native to the island of Newfoundland and was imported and used in Farm 1 only.

Bee type	Farm 1	Farm 2	Farm 3	Farm 4	Total
Andrena spp	6	1	2	1	10
B. borealis	3	23	6	5	37
B. impatiens	**77**	**0**	**0**	**0**	**77**
B. rufocinctus	1	2	1	0	4
B. ternarius	120	31	41	54	246
B. terricola	6	3	13	3	25
B. vagans bolsteri	28	2	8	7	45
Halictus spp etc for the others below	0	1	0	1	2
Hylaeus	0	2	0	0	2
Lasioglossum	21	35	2	7	65
Megachile	4	3	14	5	25
Nomada	1	1	0	1	3
Osmia	0	0	3	0	3
P. ashtoni	1	2	0	0	3
P. fernaldae	6	1	4	11	22
Sphecodes	4	3	0	0	7
Grand Total	278	110	94	95	577

Appendix 2. Bee abundance in the four cranberry farms from sweep net survey. *B. impatiens* is not native to the island of Newfoundland and was imported and used in Farm 1 only.

Bee species	Farm 1	Farm 2	Farm 3	Farm 4	Total
B. borealis	0	0	0	1	1
B. impatiens	**2**	**0**	**0**	**0**	**2**
B. ternarius	7	11	9	9	36
B. terricola	0	0	3	4	7
B. vagans bolsteri	3	2	0	1	6
Megachile spp	0	0	2	0	2
Total	12	13	14	15	54

Appendix 3. Bee species, number of flowers visited by the bees and fruit mass of individual cranberries pollinated by different bees in the four cranberry farms located in western and central Newfoundland.

Farm	Bee type	Number of flowers visited	Fruit mass (gm)
1	*B. ternarius*	1	0.000
	B. vagans bolsteri	2	0.000
	Megachilidae	1	0.000
2	*B. ternarius*	1	1.044
		1	0.778
		1	0.883
		1	0.912
	Nomada spp	4	1.551
	Unidentified bees	2	0.836
		2	0.603
3	*B. ternarius*	3	0.000
		5	0.000
		1	0.896
		9	0.865
		3	0.653
	Bombus terricola	1	0.919
	Bombus vagans bolsteri	3	0.888
	Megachilidae	3	0.000
	Nomada	1	0.385
		1	0.000
	Unidentified bee	1	0.587
	Andrena	2	0.983
4		3	0.237
		2	0.000

Farm	Bee type	Number of flowers visited	Fruit mass (gm)
		3	0.000
		3	0.000
		4	0.000
	B. ternarius	4	1.191
		2	1.317
		1	0.929
		2	1.454
		2	0.000
		4	0.000
		2	0.770
		2	0.716
		2	0.765
		3	0.752
		5	0.646
		3	1.094
	B. terricola	3	1.511
		1	1.156
		1	1.361
		1	1.065
		3	0.850
		4	0.922
		5	1.208
		1	1.543
		1	1.058
		1	0.876
		1	0.967
		1	0.782
		1	0.778

Farm	Bee type	Number of flowers visited	Fruit mass (gm)
		1	0.564
		1	0.734
		1	0.694
		5	1.133
	Bombus vagans bolsteri	3	0.000
		1	1.059
		1	0.461
		1	1.091
		1	0.924
		4	0.921
		2	0.317
	Unidentified bees	2	0.724

Appendix 4. Plant species observed during vegetation surveys on the four commercial cranberry farms in Newfoundland. * indicates forage plants. Taxa without * indicates non-forage plants.

Vascular or Non-vascular	Angiosperm or Gymnosperm	Native or Introduced	Names		Farm			
			Scientific	Common	1	2	3	4
Vascular	Angiosperm	Native	*Alnus* sp.	Alder*		✓		✓
			Aronia sp.	Chokeberry*			✓	
			Chamaedaphne calyculata	Leather Leaf*		✓	✓	✓
			Chamerion angustifolium	Fireweed*	✓			
			Eriophorum sp.	Cotton Grass			✓	✓
			Equisetum sp.	Horsetail	✓	✓		✓
			Fragaria sp.	Strawberry*		✓		✓
			Kalmia polifolia	Bog Laurel*		✓	✓	✓
			Oxyria digyna	Mountain Sorrel*	✓			
			Rhododendron groenlandicum	Labrador Tea*		✓	✓	✓
			Rubus chamaemorus	Cloudberry*	✓	✓	✓	✓
			Rubus idaeus	Raspberry*		✓		
			Vaccinium angustifolium	Blueberry*		✓		✓
			Vaccinium macrocarpon	Cranberry*	✓		✓	

Vascular or Non-vascular	Angiosperm or Gymnosperm	Native or Introduced	Names		Farm			
			Scientific	Common	1	2	3	4
		Introduced	*Hieracium sp.*	Yellow Hawkweed*				✓
			Leucanthemum vulgare	Oxeye Daisy*		✓		
			Taraxacum officinale	Dandelion*		✓		
			Trifolium pratense	Red Clover*		✓		
			Tussilago farfara	Colts Foot*		✓		
		May or may not be native	*Ranunculus* sp.	Buttercup*		✓		
			-	Grass	✓	✓	✓	✓
	Gymnosperm	Native	*Abies* sp.	Balsam fir		✓		
			Picea sp.	Spruce Tree	✓			
Non-vascular		Native	-	Lichen		✓		
			-	Moss	✓	✓	✓	✓

Appendix 5. Percentage of landscape features woodlands (WL), bogs, crop fields (CF), water sources (WS) and human disturbances (HD) at 500m, 1000m and 2000m radii from the study area in the four cranberry farms in Newfoundland

At 500m radius						
	WL	BOGS	CF	WS	HD	Total percentage
Farm 1	69.6	13.3	13.2	1.9	2	100
Farm 2	67.8	7.8	11.2	1.7	11.5	100
Farm 3	10.4	68.2	10.7	4.6	6.2	100
Farm 4	45.1	44.5	9.2	0.8	0.4	100
At 1000m radius						
	WL	BOGS	CF	WS	HD	Total percentage
Farm 1	76.8	12.9	1.2	2.3	6.7	100
Farm 2	62.1	23.5	2.7	0	11.8	100
Farm 3	16.7	27.4	0	33.9	22	100
Farm 4	81.6	14.4	0	0.5	3.6	100
At 2000m radius						
	WL	BOGS	CF	WS	HD	Total percentage
Farm 1	66.1	13.8	0	6.3	13.8	100
Farm 2	58.9	8.5	0.1	11.3	21.2	100
Farm 3	43.6	12.2	0	30.7	13.6	100
Farm 4	72.9	13.3	0	4.5	9.3	100