International Journal of Fruit Science

ISSN: 1553-8362 (Print) 1553-8621 (Online) Journal homepage: www.tandfonline.com/journals/wsfr20

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To cite this article: Ana María Quiroga-Arcila, Frédéric McCune, Valérie Fournier & Pierre Giovenazzo (2025) Bee-ing a Pollinator: Constraints, Concerns, and Challenges of Lowbush Blueberry Pollination, International Journal of Fruit Science, 25:1, 28-63, DOI: 10.1080/15538362.2025.2534352

To link to this article: https://doi.org/10.1080/15538362.2025.2534352

INTERNATIONAL JOURNAL OF FRUIT SCIENCE
2025, VOL. 25, NO. 1, 28–63
https://doi.org/10.1080/15538362.2025.2534352

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Bee-ing a Pollinator: Constraints, Concerns, and Challenges of Lowbush Blueberry Pollination

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ABSTRACT

Lowbush blueberry (*Vaccinium angustifolium* Ait.) represents the most economically significant fruit crop in Canada. The primary production areas are in the provinces of Quebec, the Maritime provinces of Canada, and the state of Maine, USA. Effective entomophilous pollination is indispensable for achieving optimal fruit sets; however, significant challenges persist due to gaps in knowledge regarding the crop's biology, factors influencing pollination and yield variability, optimal densities of commercial pollinators, and limitations associated with commercial pollination practices. This review systematically explores the critical components underpinning the pollination of lowbush blueberry fields in North America. The article is organized into six sections, addressing the crop's commercial importance, its biological and pollination requirements, factors affecting pollination and yield, the efficacy and constraints of wild and commercial pollinators, and the risks inherent in commercial pollination systems. The findings identify monoculture dependence, the decline of wild pollinator populations, the increasing use of commercial pollinators, and the risks associated with managed bumble bee introduction as the primary challenges for sustainable pollination. This review underscores the indispensable role of wild pollinators in lowbush blueberry production and suggests that future research should prioritize the development of conservation strategies at the landscape level to ensure sustainability and long-term productivity.

KEYWORDS

Wild bee; managed pollinators; pollination effectiveness; yield variation; diversity

Introduction

In 2022, lowbush blueberry *Vaccinium angustifolium* Ait. was the most important fruit crop by value (USD $270 million) in Canada (Agriculture and Agri-Food Canada, 2023). Lowbush blueberry is native to North America and is managed as a crop mostly in eastern Canada and the state of Maine in the USA (Jensen and Yarborough, 2004). Canada is the world's leading producer, ahead of the USA, with 70% of the world's wild blueberry production (IBO, 2023; MAPAQ, 2022). The lowbush blueberry industry has experienced rapid growth in value, volume, and cultivation area due to positive blueberry markets, increased overall blueberry consumption, nutraceutical properties, and beneficial compounds (Strik and Yarborough, 2005; USHBC, 2023).

Bees (Hymenoptera: Apoidea), represented by at least 20,000 species worldwide (Michener, 2007), are the most important pollinators supporting terrestrial ecosystems and crop production such as the lowbush blueberry. An estimated 133 different wild bee species visit lowbush blueberry flowers in northeastern USA blueberry fields (Bushmann and Drummond, 2015). Lowbush blueberry mainly

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reproduces through cross-pollination, with entomophilous pollination being essential to achieve a good fruit set (Drummond, 2019b; Gagnon et al., 2011). Wild pollinators are known to be effective blueberry pollinators, being 2.6 to 10 times more effective than honey bees based on the percentage of fruit set per bee (Asare et al., 2017; Bushmann and Drummond, 2020; Drummond and Hoshide, 2024). The study by Bushmann and Drummond (2020) stated that a disruption in honey bee supplies could reduce the crop yield by approximately 30%. This low reduction is due to the compensatory effect of wild bee pollination. However, due to landscape characteristics and annual variations, wild bee abundance can be lower than what is required to achieve the desired fruit set and maintain economic viability, which increases the pressure to add commercial pollinators (Bushmann and Drummond, 2020; Hanes et al., 2013). Despite being necessary, introducing commercial pollinators poses economic limitations and ecological risks. These risks include pathogen spillover, competition for floral resources, spread of exotic weeds, and decline of native plants (Goulson, 2003; Mallinger et al., 2017).

Optimizing crop pollination for maximum fruit set is challenging for lowbush blueberry growers and beekeepers (Fulton et al., 2015). In Quebec, for example, these stakeholders have access to limited information for making practical decisions on the most effective and efficient strategies to maximize crop pollination needs. As outlined by Isaacs et al. (2016) in highbush blueberries, these decisions must be made within the context of the local or regional farm pollination system, pest management intensity, economic resources, and the available bee species (wild or managed), that can promote an integrated pollination strategy. In the sections that follow, we examine the various components involved specifically in the pollination of North American lowbush blueberry fields, *Vaccinium angustifolium* Ait. The first section discusses the commercial importance of lowbush blueberry production in the USA and Canada. The second section examines the relationship between inflorescence, pollination requirements, pollinating agents, and current pollination practices. The third section assesses inherent and environmental factors that affect pollination, such as flower characteristics, weather, fertility of soil, and various cultural practices. Section four analyses the importance of the diversity of pollinators that visit lowbush blueberry flowers, their effectiveness, and their limitations and decline in lowbush blueberry landscapes. The fifth section examines the management and efficacy of commercial pollinators used for lowbush blueberry pollination. It covers their impact on blueberry pollination, the densities used, and their effectiveness. The last section analyses the limitations and risks of commercial pollination. We anticipate that this review will function as a comprehensive technical reference for lowbush blueberry producers and enhance the understanding of the complexities involved in blueberry pollination dynamics.

Lowbush Blueberry Production and Consumption

Lowbush blueberry, also known as wild blueberry, encompasses several species of *Vaccinium* spp. section *Cyanococcus* A. Gray (Ericaceae) (Crowl et al., 2022; IBO, 2023). The most prevalent species, *Vaccinium angustifolium* Ait. and *Vaccinium myrtilloides* Michx., are native to North America, spanning from Newfoundland and Labrador to Manitoba and Minnesota, and extending south-east to Virginia (Jensen and Yarborough, 2004). Other species, though less commercially significant, exist, adding to the global diversity of these berries. Some species related to *V. angustifolium* and *V. myrtilloides*, such as *V. boreale* Hall and Aalders and *V. pallidum* Ait., can also be found in North America. *Vaccinium boreale* is found in northern Quebec, the Maritimes, northern New England, and northern New York, while *V. pallidum* ranges from Minnesota and southern Ontario to Maine, reaching as far south as the upland regions of Georgia, Alabama, and Arkansas (Crowl et al., 2022). For instance, Eurasian species include *V. myrtillus* L., or bilberry, a European species primarily harvested in Scandinavian countries, particularly in the forests of Norway, Finland, and Sweden, and species like *V. uliginosum* L. and *V. vitis-ideae* L. that are more commonly found in Eurasia and China (Gailīte et al., 2020; IBO, 2023).

Specific characteristics can be used to differentiate between the most common lowbush blueberry species. *Vaccinium angustifolium* is an acidophilic species usually found in sandy soils with a pH between 4.2 and 5.2 (Agriculture, Aquaculture and Fisheries, 2010). It can grow with *V. myrtilloides* (velvet leaf blueberry) in the same field. *Vaccinium angustifolium* accounts for 95% of the crops in

North America, while *V. myrtilloides* accounts for the remaining 5% (IBO, 2023). *Vaccinium angustifolium* is distinguished from *V. myrtilloides* by its height (7 to 38 cm), the absence of hairs on its bushes, and the presence of a grayish waxy layer (pruine) on the skin of its fruits (Agriculture, Aquaculture and Fisheries, 2010; Madrid and Beaudry, 2020Native Plant Trust, 2022). Both *V. angustifolium* and *V. myrtilloides* are differentiated from highbush blueberries (*Vaccinium corymbosum* L.) by having naturally occurring clones (conglomerate of stems coming from the rhizomes of a single mother plant, which leads to the absence of breeding or cultivar selection), smaller fruits and bushes, a variation of plant and fruit characteristics within the same field, and a high variability of yields over time (Forney et al., 2022).

Lowbush Blueberry Production

The Canadian lowbush blueberry industry is rapidly growing in value, production, and cultivation area. In 2022, blueberries were the most important fruit crop by value (USD $270 million) in Canada (Table 1) (Agriculture and Agri-Food Canada, 2023). For the same year, lowbush blueberry (*V. angustifolium* Ait.) constituted 55.2% of the total value of blueberries and 61.1% of the total volume in Canada. Between 2018 and 2022, the lowbush blueberry export value increased by 53.32% (Agriculture and Agri-Food Canada, 2023).

In 2023, lowbush blueberry production in metric tonnes was mainly found in Quebec (42%), New Brunswick (26%), Nova Scotia (21%), and Prince Edward Island (11%). In terms of cultivated area, lowbush blueberry covered a total of 68,577 hectares in Canada, with Quebec reporting 31,306 hectares and the Maritime provinces collectively accounting for 31,386 hectares – comprising 11,136 ha in New Brunswick 15,153 ha in Nova Scotia, and 5,097 ha in Prince Edward Island (Agriculture and Agri-Food Canada, 2025).

In 2022, 50.2% of the total Canadian area used for fruit production was destined for lowbush blueberry. Between the years 2018 and 2022, the Canadian lowbush blueberry area increased by 4.48%, but the production volume soared by 34.42%, representing 11.5% of the total fruit volume in Canada (Table 1). The USA production is essentially in the state of Maine, with about 8,000 hectares harvested per year and yields of 4.4 t/ha in 2022 (Bushmann and Drummond, 2020; Calderwood and Yarborough, 2023).

Although most of the production in Canada is concentrated in Quebec, the province's overall yields remain suboptimal compared to the rest of the country. The average yield in Quebec for 2019 was 2.21 t/ha, 26% lower than the Canadian average (2.98 t/ha), while Nova Scotia and New Brunswick reached yields of 3.08 and 4.40 t/ha respectively (MAPAQ, 2022). According to the report of Province du

Table 1. Canadian lowbush blueberry production. Source (Agriculture and Agri-Food Canada, 2023).

Variable	2018	2019	2020	2021	2022	2022 % (share with total Canadian fruit production)	Position in 2022 compared to Canadian fruits
Lowbush blueberry total area (hectares)	65,642	65,159	65,341	68,625	68,577	50.2%	First position, followed by apples (13.1%), grapes (9.8%) and highbush blueberry (8.8%)
Lowbush blueberry production volume (metric tons)	81,932	87,950	71,290	73,773	110,132	11.5%	Third position after apples (39.8%) and cranberries (21.9%)
Lowbush blueberry export value (USD million)	176.73	218.17	232.54	224.91	270.97	32.6%	First position followed by highbush blueberry (26.5%) and sweet cherries (11.6%)
Lowbush blueberry export volume (metric tons)	89,684	103,263	94,516	72,296	76,826	23.3%	First position followed by apples (20.6%) and highbush blueberry (16.5%)
Blueberries available for consumption in Canada (kg per person)	1.19	1.45	1.37	1.86	1.39	1.9%	14th position

Nouveau-Brunswick (2018), the higher yields found in New Brunswick can be explained by the geographic distribution of blueberries in the province, which reduces the risks related to bad weather conditions or pest problems. Moreover, this province employs more intensive management practices than Quebec, particularly in pesticide use and land leveling, and it implemented pollination supplementation and mechanical harvesting earlier than in Quebec (Yarborough, 2004). Mechanical harvesting allows for rapid, large-scale harvesting at peak ripeness, helping to offset moderate fruit losses while also addressing labor shortages in both lowbush and highbush blueberry production systems (Hall et al., 1983; Takeda et al., 2017).

Lowbush Blueberry Consumption

The nutraceutical properties and beneficial compounds in blueberries offer benefits in preventing diseases such as cardiovascular diseases, cancer, prediabetes, and obesity (USHBC, 2023). The consumption of blueberries is also related to improving gut microbiota, neuroprotection, and visual function (Dunford, 2022; Kalt et al., 2020). Some studies show higher levels of phenolics, chlorogenic acid, and anthocyanins in lowbush blueberries than in highbush blueberries (Dunford, 2022; Kalt et al., 2020; Rodriguez-Mateos et al., 2012).

Even though lowbush blueberries contain higher levels of beneficial compounds than highbush blueberries, the Canadian consumption of lowbush blueberries has declined in recent years. Lowbush blueberry fruits are mostly commercialized in the frozen fruit market. Between 2015 and 2019, there was a 45% reduction in Canadian consumption of frozen blueberries, while fresh blueberries doubled during the same period (MAPAQ, 2022). Statistics Canada (2024) revealed a 32.8% reduction in lowbush blueberry sales from 2022 to 2023. This is due to the loss of popularity of frozen food consumption and the growing preference for fresh products (MAPAQ, 2022; USHBC, 2023). The same trend has been observed in the USA in the last ten years (MAPAQ, 2022).

Lowbush Blueberry Biology and Pollination

Unlike other commercial crops, lowbush blueberry fields are not planted and do not follow a predetermined genetic pattern (Drummond, 2019b). Their onset is initiated by forest clearing and flail mowing, with blueberry being one of the first plants in the successional stage (Eaton et al., 2004; Jensen and Yarborough, 2004). Lowbush blueberries are propagated mainly from the rhizomes of a mother plant. All the stems coming from the rhizomes of a single mother plant will form a conglomerate called a clone (Figure 1), which can measure between 7 and 23 m^2 and can be visually differentiated by the formation of patches of different colors, particularly during flowering (Bell et al., 2009, 2010; moisan-De Serres, 2013).

The presence of clones results in great variability in terms of genetics, morphology, phenology, and yields within a field (Bell et al., 2010). This variability can be explained by spatial genetic structure (Bell et al., 2009). Generally, each stem of the same clone has the same genetic characteristics and flower simultaneously (Barai et al., 2022; Chiasson and Argall, 1996). However, Bell et al. (2009) showed variability in the same patch or clone, finding 1.6 genets (a unique genetic entity) per patch. This variability is observed especially at the edges between one clone and another. The same study revealed that lowbush blueberry fields have a random spatial genetic structure, and that most clones are not direct offspring of their neighbors (78.3%).

The inbreeding depression and self-auto incompatibility reported in lowbush blueberry can cause this random spatial genetic structure (Beers et al., 2019; Bell et al., 2010; Bushmann and Drummond, 2020). Inbreeding depression occurs when closely related individuals mate, leading to the expression of deleterious alleles during seed development and resulting in the abortion of embryos (Hokanson and Hancock, 2000). Indeed, a hypothetical high genetic similarity between neighbors would lead to low reproductive success and yields, forcing blueberries to outcross (Bell et al., 2009, 2012). Therefore, gene dispersion depends on the possibility of distributing pollen and seeds. This long-distance distribution is

Figure 1. Color variation in a lowbush blueberry field in Saguenay-Lac-Saint-Jean region, QC, Canada. Each colored patch represents a different clone. a) Spring season before the pollination period. b) Lowbush blueberry field during the production stage. Photos Ana María Quiroga-Arcila.

normally carried out by birds or bears, even more than bees, which pollinate near neighbors. Thus, genes are isolated over long distances, which explains greater genetic differentiation as distance increases (Barai et al., 2022; Bell et al., 2009).

Growth of commercial lowbush blueberry commonly occurs over a two-year cycle: the first year is characterized by vegetative growth, while the second year involves fruiting. Vegetative growth is characterized by foliage development until late summer. In the fall, plants will produce flowers and leaf buds that will develop during the second year of growth, after the winter dormant period (Chiasson and Argall, 1996). The dormant period is essential for growth, and a good snow cover avoids bud freezing and death, especially those located at the top of the stem, as they are the most susceptible to winds. The minimum temperature tolerated by dormant flower buds is −30°C (Agriculture, Aquaculture and Fisheries, 2010). During the second year of growth, in the fruiting stage, the bud clusters swell and produce clusters of flowers. On average, a stem bears four to six buds depending on its length, which will depend on genetics (Chiasson and Argall, 1996). Each bud contains five to six flowers that will bear fruits in late summer if they are pollinated and if the plant grows optimally (Figure 2a).

After the harvest in fall, the blueberry fields will be pruned to begin a new growing cycle (Agriculture, Aquaculture and Fisheries, 2010). Regular pruning of lowbush blueberry fields sustains production over time. This practice has traditionally been done by burning but has progressively changed toward mowing because of the lower costs of this practice (Morvan et al., 2022). However, when not correctly adjusted, mowing can damage rhizomes and remove soil, especially in fields that have not been properly leveled (Eaton et al., 2004).

The development of lowbush blueberry flowers and fruits is divided into different stages. After the development of bud clusters, there is an individual development of the flowers (Figure 2b). The pollination period is marked by the opening of the flowers (Figure 2c). The lowbush blueberry flower is viable eight to ten days, the style is receptive one to four days after opening, and the chances of

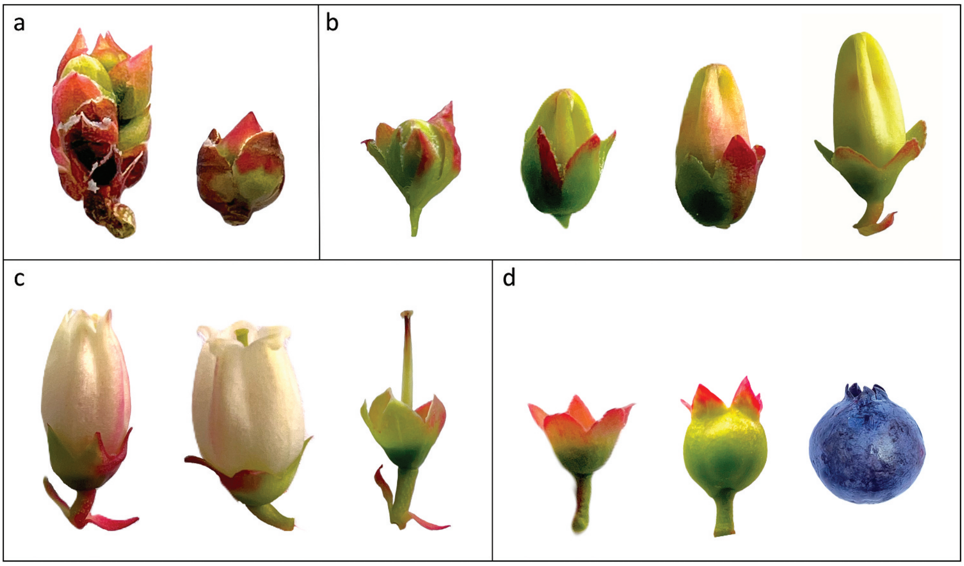

Figure 2. Flower and fruit development in lowbush blueberry (*Vaccinium angustifolium* Aiton.). a) cluster of flowers and beginning of flower bud. b) Development of flower bud to become a flower. c) flower opening and falling petals after pollination. d) Fruit development. Photos Ana María Quiroga-Arcila.

producing a berry decrease after three days (Bourgeois, 2006; Bushmann and Drummond, 2020; Chiasson and Argall, 1996). Once the flower is pollinated, the corolla falls after two days, exposing the pistil completely (McGregor, 1976). Blueberry flowers have inferior ovaries, causing the fruit to develop at the bottom of the flower (Figure 2d). Once the fruit development begins, the flower will lose the pistil and the fruit development will be observed within a few days after pollination. Most of the fruit weight will be gained three to four weeks before harvest, gaining 10 to 15% weight per week (Chiasson and Argall, 1996).

Lowbush blueberries have limited self-pollinating ability due to their flower characteristics, and they mostly rely on cross-pollination by insects (Bell et al., 2009). Lowbush blueberry flowers are hermaphroditic and comprise eight to ten stamens inserted at the base of the corolla. The style is longer than the stamens (McGregor, 1976). This strong separation of the male and female reproductive organs restrains self-pollination (Bell et al., 2009). In addition, blueberry pollen is heavy and large and can hardly be transported by the wind. Blueberry anthers are poricidal, where the pollen is released through small pores rather than through longitudinal slits (Buchmann, 1983; Proctor et al., 1973). This pollen dispensing mechanism requires specific pollination techniques, such as buzz pollination. Therefore, lowbush blueberry reproduces mainly by cross-pollination. Entomophilous pollination is thus essential to obtain a good fruit set (Drummond, 2019b). Insects are indeed responsible for 91% of blueberry pollination (Gagnon et al., 2011). In highbush blueberries (*V. corymbosum*), pollen remains in the anthers until bees visit the flower, where vibrations cause the pollen to be released through these pores (Isaacs et al., 2016). Bumble bees, for example, take the base of the anthers between their jaws and use the flight muscles of their wings to vibrate the anthers (Jesson et al., 2014). In the case of honey bees in highbush blueberries, they unintentionally deposit pollen onto stigmas through contact with different parts of their bodies while foraging for nectar (Hoffman et al., 2018).

Maximizing ovule fertilization and seed production at the right time guarantees fruit set gains (Arrington and DeVetter, 2018). The fruit set rate represents the proportion of flowers that give fruit after fertilization and it is correlated with the average number of viable seeds (Desjardins and de Oliveira, 2006; Drummond, 2019b; Gagnon et al., 2011). In highbush blueberries, fruit size depends on the number of viable seeds releasing hormones that stimulate berry growth (Arrington and DeVetter,

Figure 3. Lowbush blueberry seed classification (*Vaccinium angustifolium* Aiton.). a and b) mature filled seeds > 0.75 mm. c) irregular and constricted pseudo-seeds > 0.75 mm. D and E) ovules < 0.75 mm. Photos Ana María Quiroga-Arcila.

2018; Isaacs et al., 2016; WSU, 2021), which is probably similar to lowbush blueberries. The total number of seeds (mature seeds + aborted seeds + unfertilized ovules, Figure 3) represents the yield potential of a clone (Bell et al., 2010). The increase in total seed numbers (yield potential) is positively correlated with yield, and the increase in the number of mature seeds (decrease in aborted seeds) per fruit is correlated with fruit size (Bell et al., 2010). Bell et al. (2012) dissected newly opened lowbush blueberry flowers, finding an average of 63 ± 8 ovules per flower and 1,788 ± 994 pollen tetrads, without a correlation between the two variables. The ovule fertilization with pollen produces heavier berries (Bushmann and Drummond, 2020). Drummond (2019b) discovered that the positioning of pollen on receptive stigmas influences fruit set, with even just one pollen tetrad being sufficient, while 12 tetrads could increase fruit set to an average of 50%.

The success of pollination can be determined a few days after the pollination and can be measured with the fruit set. Fruit set is variable, ranging from 10% to 50% in fields without commercial pollinators, and up to 80% when commercial pollinators are present (Drummond, 2020b). A high number of "pinheads" indicates a poor fruit set (Eaton et al., 2004). Pinheads are described as the flower ovaries that do not enlarge and remain on the stem. The final fruit set also depends on fruit drop, ranging from 23.3% to 49.4% of the fruits (Drummond, 2020b).

Factors Affecting Lowbush Blueberry Pollination and Yields

Lowbush blueberry fruit set is influenced by multiple factors that have a significant impact on berry yields (Fulton et al., 2015). Drummond (2019a) reports that pollination could explain between 20% and 60% of variation affecting lowbush blueberry yields (between 300 and 17,000 kg/ha). Other studies show that fruit set, yields, and pollination efficiency are affected by intrinsic and environmental factors such as clone genetics, floral morphology, flower density, pollinating insect density, spring weather conditions, water and nutrient supply, and landscape characteristics (Chiasson and Argall, 1996; Eaton et al., 2004).

Inherent Characteristics of Lowbush Blueberry

Some inherent characteristics of lowbush blueberry plants can limit pollination, thus affecting fruit set and yields (Figure 4). Aalders and Hall (1961) reported that almost 45% of plants produce little or no pollen in Nova Scotia, Canada, while Myra et al. (2004) reported an average of 1,373 tetrads/flower (ranging from 2 to 3,242). Other authors report that 68% of the clones evaluated in Maine have at least 1,000 tetrads per flower, with an average of 1,788 tetrads/flower (ranging from 320 to 4,615) (Bell et al.,

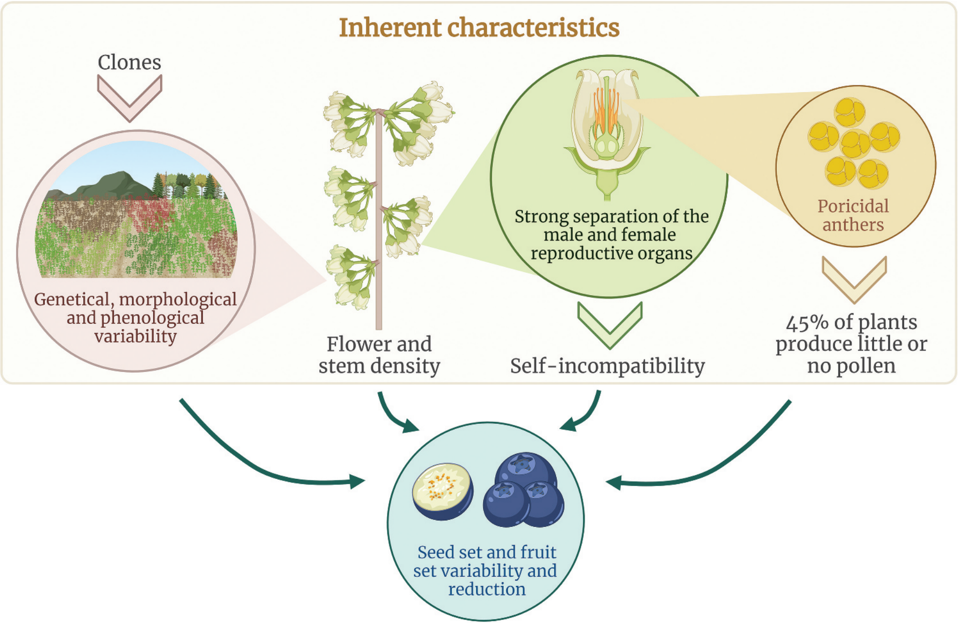

Figure 4. Inherent characteristics of lowbush blueberry *(Vaccinium angustifolium* Aiton.) affecting fruit set and yield. Created in BioRender by Ana María Quiroga-Arcila. https://BioRender.com/i83i322.

2012). Additionally, the rate of sterile male plants is 5% (Aalders and Hall, 1961; Bell et al., 2009). These conditions can directly affect pollen transfer. On the other hand, there is reproductive isolation between *V. angustifolium* species and *V. myrtilloides*. They are often found in the same fields, and their crossing can result in small fruits or abortions (Gagnon et al., 2011; Jesson et al., 2014).

Stem density and the number of flowers per stem can also affect fruit set and yields (Drummond, 2019b). Sometimes, lowbush blueberry plants produce many small flowers, varying between four and 127 flowers per stem (Bajcz and Drummond, 2017). A higher number of flowers per stem can decrease fruit set and lead to the production of smaller fruits (Drummond, 2019b, 2020b). Flower densities also have an impact on pollinators. Pollinators with shorter foraging territories (e.g., *Megachile* spp.) will travel on flowers closer to each other, thus increasing the probability of self-fertilization between flowers of the same clone (Fulton et al., 2015). In this case, an increase in the density of these “short distance” pollinators will not significantly increase yields (Jesson et al., 2014). In addition, the increase in the size of a clone in the field reduces the yields and the fruit set, due to the increased probability of self-pollination generated during the foraging activity (Bell et al., 2010; Bushmann and Drummond, 2020).

Self-incompatibility was described well in Section 2, however, Drummond (2019a) reports that around 20% of genotypes have a high level of self-compatibility. That means that clones with high self-compatibility levels have a high potential yield, with both self-pollination and outcrossed pollination. This also means they can accept pollen from a high diversity of clones, maintaining a high fruit set (also known as universal mother genotypes). Contrary, a non-reciprocal genetic compatibility between clones has also been reported by Drummond (2019a). Then, a low level of pollen deposited in a receptive stigma from a genotype X to Y can result in a high fruit set, but a high level of pollen deposited from genotype Y to X can result in a low fruit set.

Crop Management

Weed, diseases, and pest management can indirectly and directly impact yields (Figure 5). Some defoliator insects or leaf-spot pathogens can reduce the number of flower buds and their development,

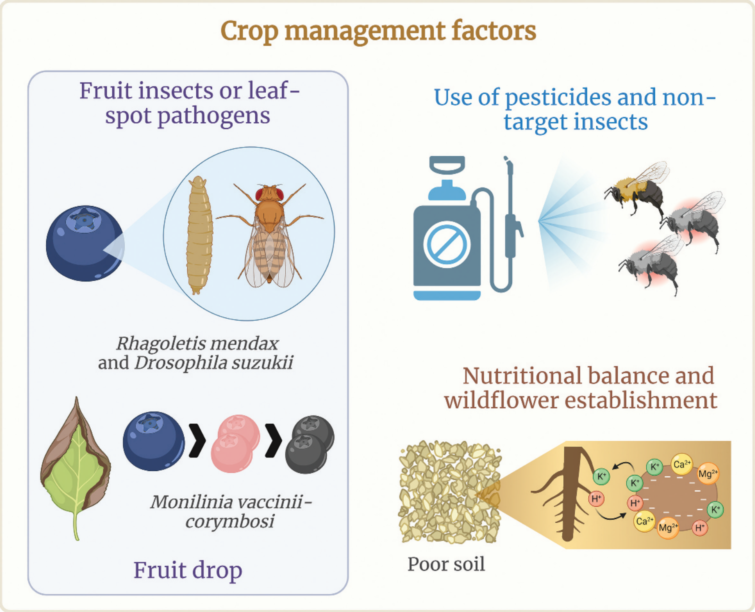

Figure 5. Factors in the management of lowbush blueberry crops (*Vaccinium angustifolium* Aiton.) affecting fruit set and yield. Created in BioRender by Ana María Quiroga-Arcila. https://BioRender.com/i83i322.

and other pests and pathogens of the fruit can reduce fruit number (Drummond, 2019a). For example, Drummond (2020b) reported that the blueberry maggot fly (*Rhagoletis mendax* Curran), spotted wing drosophila (*Drosophila suzukii* Matsumura), and mummy berry disease (*Monilinia vaccinii-corymbosi* Reade) cause lowbush blueberry fruit drop. Additionally, mummy berry was also reported to cause the death of flowers prior to pollination (Gagnon et al., 2011).

Pesticides represent a risk to wild and commercial bees before and during the blooming of lowbush blueberries (Averill et al., 2024; Drummond et al., 2024). However, few studies have been found during this review that analyzes their direct impact on wild bee populations in the context of lowbush blueberry. Bushmann and Drummond (2015) indirectly evaluated the impact of pesticide use, finding a higher bumble bee species richness in organic fields compared to conventional fields. Among the insecticides most used in blueberry fields in Saguenay-Lac-Saint-Jean (Quebec) are acetamiprid, spinosad, and phosmet (personal communication with Pierre-Olivier Martel, adviser at MAPAQ in Alma, May 4, 2022). Although insecticides are used to a lesser extent, there is also widespread use of herbicides and fungicides such as hexazinone, glyphosate, fluazifop -P-buty, rimsulfuron, mesotrion, prothioconazole, and propiconazole (personal communication with Pierre-Olivier Martel, adviser at MAPAQ in Alma, May 4, 2022). A study by our research team in the same region found that, despite the presence of pesticides (mainly insecticides) in lowbush blueberry fields, pesticide concentrations in bee bread and nectar remain well below the LD_{50} for each active ingredient (unpublished data, manuscript in preparation). Using the methodology of Drummond et al. (2021), we calculated Contact Hazard Quotients (HQ) for all detected active ingredients in a same field. While Drummond et al. (2021) reported an HQ of 0.02 during bloom in Maine, our findings were lower (0.002), indicating that pesticide use in Quebec is likely less intensive. In Maine, the use of phosmet, imidacloprid, acetamiprid, spinosad, methoxyfenozide, and propiconazole prevail (Choate and Drummond, 2013; Drummond, 2022).

Some studies, however, have analyzed the impact of specific pesticides normally used in lowbush blueberry on commercial pollinators. An experiment conducted by Drummond (2012b) showed a reduction in the strength of *Bombus impatiens* (Cresson) colonies foraging lowbush blueberry fields exposed to imidacloprid. The same author demonstrated that honey bee worker longevity can be reduced by 17.3% in colonies exposed to lowbush blueberry fields treated with the fungicide propiconazole prior to bloom. Exposed colonies also presented an 8.3% hypopharyngeal acini hypertrophy in five-day old nurse bees (Drummond, 2022). Other studies assessed the impact of commonly used insecticides in controlling pests in lowbush blueberry on *B. impatiens* and *Megachile rotundata* (Fab) through direct contact bioassays (Gradish et al., 2012; Gradish et al., 2012). Research results indicate that phosmet, spinosad, spinetoram, and deltamethrin at recommended application rates are hazardous to adults of both bee species.

Lowbush blueberry fields are normally implemented in acidic and poor soils, impacting wildflower establishment and plant nutritional balance (Bushmann and Drummond, 2020). The implementation of wildflowers is essential for the maintenance and attractiveness of wild bee populations. Some studies have shown the preference of wild pollinators for native flora and the increase of blueberry fruit set when these plants are well established on the edges of fields (Drummond et al., 2017; Venturini et al., 2017). Poor soils also represent a challenge for the good nutritional balance of the plant. Some studies report an interaction between low-fertility soils and fruit drop due to excessive fruit production (Drummond, 2020b). On the contrary, an excess of nitrogen can cause an increase in vegetative growth, generating competition between fruits and vegetative organs for the plant photosynthates (Bajcz and Drummond, 2017).

Meteorological Factors

Meteorological factors can affect lowbush blueberry production by influencing the development of buds and fruits, and by affecting pollination efficiency (Figure 6). Lowbush blueberry fields are in northern, cold regions. Winter, during the dormant period, can lead to bud and stem injuries if snow cover is insufficient. Frost events during spring bloom are also a big problem because a single frost can damage or kill buds and blossoms, significantly reducing the crop potential (Eaton et al., 2004). Frost can also cause fruit drop, resulting in the death of embryos (Drummond, 2020b). On the contrary, extreme heat and drought can also negatively impact yields by affecting the production of

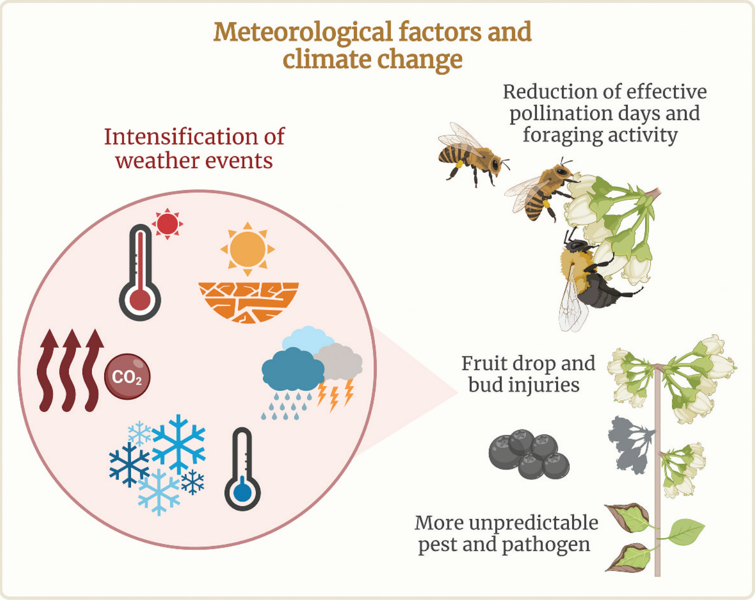

Figure 6. Meteorological factors affecting fruit set and yield in lowbush blueberry crops (*Vaccinium angustifolium* Aiton.). Created in BioRender by Ana María Quiroga-Arcila. https://BioRender.com/i83i322.

photosynthates, thus reducing fruit size or inducing fruit drop (Drummond, 2020b). Droughts can generate changes in the growth habits of the plant, changing the reproductive state to vegetative (Glass et al., 2005). Higher temperatures during spring can also reduce bee foraging activity and increase the development rate of lowbush blueberries, making the flowering period shorter (Drummond et al., 2017). On the other hand, the pollination period coincides with spring, which usually has low temperatures and high wind speeds and precipitation (Arrington and DeVetter, 2018). Heavy precipitation and cold temperatures reduce bee foraging activity, affect bee abundance, cause nectar dilution, pollen degradation, and volatile removal Drummond et al. (2017); Glass et al. (2005). Even if water availability during fruit maturation is essential, heavy precipitations have also been related with the increase of flower death and the incidence of plant fungal diseases (Hall et al., 1982).

Several studies have shown that climate change will intensify events of droughts, frost, and precipitation (Drummond et al., 2017; Gumbrewicz and Calderwood, 2022). These conditions not only reduce the number of effective days of pollination in lowbush blueberry fields, as described before, but they also change the plant physiology and pollinator phenology (Chen et al., 2022; Tasnim et al., 2021). However, Bartomeus et al. (2011) suggested that pollinators can adapt to climate change. Their study on 10 bee species in northeastern North America, including key blueberry pollinators (*Osmia* spp. and *Bombus impatiens*), found a 10.4 ± 1.3 day advance in emergence due to warming, aligning with plant phenology and indicating no significant mismatch. However, they did not assess the direct impacts on lowbush blueberries. Other studies suggest climate warming may benefit pollinators at higher latitudes by increasing species diversity through migration (Vasiliev and Greenwood, 2021), though some considerations of the ecological consequences remain essential. We found a critical data gap on both the positive and negative effects of climate change on lowbush blueberry pollinators.

Furthermore, predictions show that climate change will make pests and pathogens more unpredictable (Chen et al., 2022). There is still limited research on how these changes will affect lowbush blueberry production. However, pests like *Drosophila suzukii* could emerge earlier under hotter temperatures (Drummond et al., 2019) and survive the harsh Canadian winter if temperatures remain above 0°C (Cloutier et al., 2021). On the contrary, Chen et al. (2022) found that, under controlled conditions, temperature rise did not change the prevalence of red leaf disease (*Exobasidium vaccinii* Wor), blueberry gall midge (*Dasineura oxycoccana* Johnson), red-striped fireworm (*Aroga trialbamaculella* Chambers), or any weed species in six different genotypes of lowbush blueberry. Other pathogens such as Sphaerulina leaf spot (*Sphaerulina* vaccinii Ali, Hildebrand and Abbasi), powdery mildew (*Microsphaera vaccinii* Schweinitz), and other leaf spot diseases presented a lower incidence.

Wild Pollinators

Pollinator Diversity in Lowbush Blueberry Crops

Bees (Hymenoptera: Apoidea), estimated to number more than 20,000 species worldwide (Michener, 2007), are the most important pollinators for supporting terrestrial ecosystems and crop production. Bees are also the primary pollinators of lowbush blueberries (Figure 7). Wild bees can contribute from 30 to 55% of fruit set in lowbush blueberry without commercial pollinator supplementation (Bushmann and Drummond, 2020; Desjardins and de Oliveira, 2006; Drummond, 2012b; Stubbs and Drummond, 1997a). Even if commercial supplementation can enhance fruit sets, pollination by wild bees cannot be interchangeable due to the complementarity that it provides to crops like highbush blueberries (Garibaldi et al., 2013). Bushmann and Drummond (2020) show that growers would lose close to 1.76 tons/ha of berries without wild pollinators, regardless of the increasing honey bee colony density.

Several studies have been conducted to inventory the diversity and abundance of insects in the lowbush blueberry agroecosystem in Maine and eastern Canada (Table 2). These studies indicate that bees from the Andrenidae and Halictidae families are the predominant

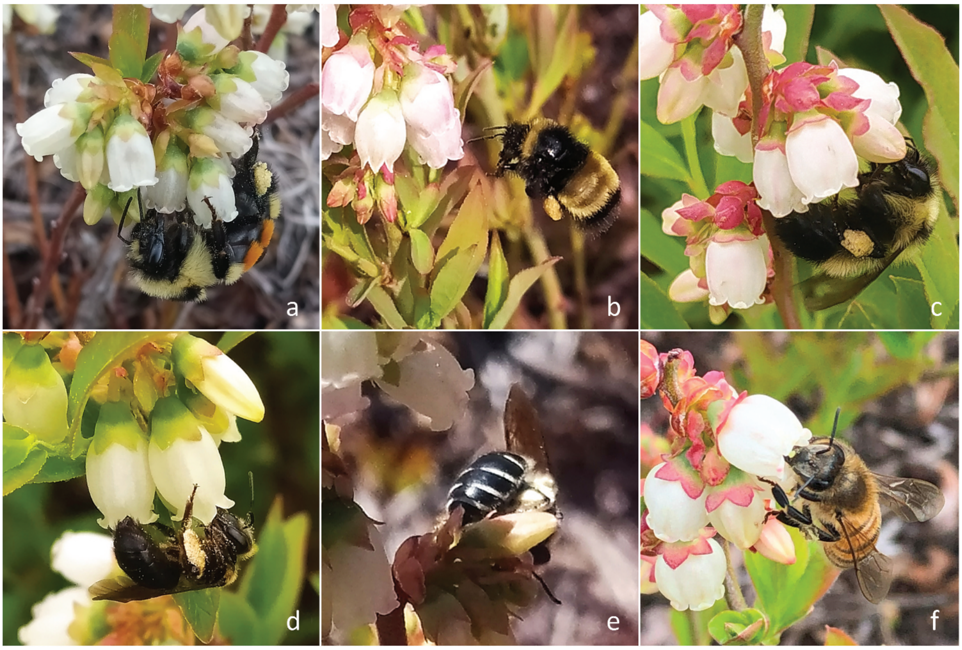

Figure 7. Wild (A, B, D, E) and commercial bees (C, F) foraging in lowbush blueberry (*Vaccinium angustifolium*) flowers. A) *Bombus ternarius* Say. B) *Bombus terricola* Kirby. C) *Bombus impatiens*. D) *Andrena* spp. E) *Colletes validus* Cresson. F) *Apis mellifera* L. Photos Ana María Quiroga-Arcila.

pollinators. While bees are the most significant pollinators, other studies have also documented vespid wasps, flies, beetles, and butterflies visiting lowbush blueberry flowers (Table 2). Even though other non-Apoidea insects may visit these flowers, they are considered secondary pollinators due to their low pollen loads. moisan-De Serres et al. (2014) found that the primary non-Apoidea carriers of *Vaccinium* pollen were flies of the families Syrphidae (mostly of the genus *Sericomyia*, *Volucella*, *Syrphus* and *Parasyrphus*) and Bombyliidae (*Bombylius* spp.). Among these carriers, *Sericomyia transversa* (Osburn) was the most significant. However, this species was considered a poor pollen carrier in the study because it carries only 4.3% of the average load carried by *Bombus impatiens*, which carried the highest number of pollen grains on its body.

Nocturnal pollinator insects can also contribute to lowbush blueberry fruit set. This fruit set can reach between 30% and 64% in plants exclusively exposed to night pollination, depending on field localization (Cutler et al., 2012; Noone et al., 2022). In some cases, fruit set in blossoms with strictly nocturnal pollination is not different than those with diurnal pollination (Noone et al., 2022). However, species that carry out nocturnal pollination remain unknown. Likewise, it is hypothesized that white flowers have a greater attractiveness toward nocturnal pollinators, which could explain the diversity of pollinators found during the night (Noone et al., 2022).

Efficacity of Wild Pollinators and Foraging Behaviors

The pollination efficacy of bee species depends on the quantity and quality of the pollen deposited, the synchronization of the flowering period with the flight of the pollinator, the number of visits per minute, the length of the tongue, the ability to produce vibratile pollination (also called sonication), the crop fidelity, and the foraging preferences (Gagnon et al., 2011). Furthermore, pollination efficacy also depends on the diversity of pollinators visiting the flowers. Pollen deposition on the

Table 2. Pollinator insects related to lowbush blueberry agroecosystems in Maine and Eastern Canada.

Richness reported	Orders	Principal families	Principal species	Region	Observations	References
Reported bees						
89	Hymenoptera	Andrenidae and Halictidae	*Andrena regularis* and *Lasioglossum quebecense*	Maine and eastern Canada	Species related to lowbush blueberry agroecosystem during bloom, of which 59 species were collected directly on blueberry flowers	(Boulanger et al., 1967)
46	Hymenoptera	Halictidae and Apidae	*Lasioglossum pilosum*, *L. quebecense*, and *Bombus ternarius*	Lac-Saint-Jean	Species reported visiting lowbush blueberry flowers	(Morrissette et al., 1985)
62	Hymenoptera	Halictidae	*L. pilosum* and *L. quebecense*	Lac-Saint-Jean	Species related to lowbush blueberry agroecosystem	(moisan-De Serres et al., 2014)
133	Hymenoptera	Halictidae for solitary bees	*Lasioglossum cressonii* and *Augochlorella aurata* for solitary bees and *B. ternarius* for bumble bees	Downeast Maine	Species related to lowbush blueberry agroecosystem during and after bloom, of which 124 species were solitary bees and 9 were bumble bees	(Bushmann and Drummond, 2015)
95	Hymenoptera	Halictidae	*L. cressonii* and *Lasioglossum acuminatum*	Nova Scotia	Species related to lowbush blueberry agroecosystem during bloom	(Cutler et al., 2015)
-	Hymenoptera	Apidae	*Bombus vagans/ sandersoni*	Kent Island, New Brunswick	Species reported visiting lowbush blueberry flowers	(Noone et al., 2022)
Other common pollinator insects						
-	Diptera	Syrphidae Coelopidae	*Toxomerus marginatus*	Lac-Saint-Jean and Kent Island	Species related to lowbush blueberry agroecosystem during bloom and visiting lowbush blueberry flowers	(moisan-De Serres et al., 2014; Noone et al., 2022)
-	Other Hymenoptera	Vespidae	*Vespula consobrina* and *Dolichovespula arenaria*			
-	Lepidoptera	Sphingidae Nymphalidae	*Hemaris thysbe* and *Vanessa atalanta*			
Potential nocturnal pollinators						
-	Coleoptera	Elateridae and Curculionidae	-	Kent Island and Nova Scotia	Species related to lowbush blueberry agroecosystem during bloom	(Manning and Cutler, 2013; Noone et al., 2022)
-	Diptera	Lauxaniidae and Tachinidae	-			
-	Lepidoptera	Geometridae and Noctuidae	-			

stigma increases with the number of visits from different species rather than consecutive visits from individuals of the same species (Blüthgen and Klein, 2011). Thus, specific genera of wild bees (e.g., *Andrena, Bombus, Osmia, Halictus, Agapostomon, Augochlora, Augochlorella, Megachile, Lasioglossum*) easily deposit pollen on blueberry stigmas and are well adapted to pollinating lowbush blueberries (Drummond, 2019a; Fulton et al., 2015). Depending on the size of the pollinators, they will have different contact areas with the reproductive organs of the flowers (Chagnon et al., 1993; Hoehn et al., 2008). Some studies carried out on strawberry and pumpkin flowers have shown that smaller bees, such as the Halictidae or Andrenidae, show preferences for the pollen of basal stigmas of the

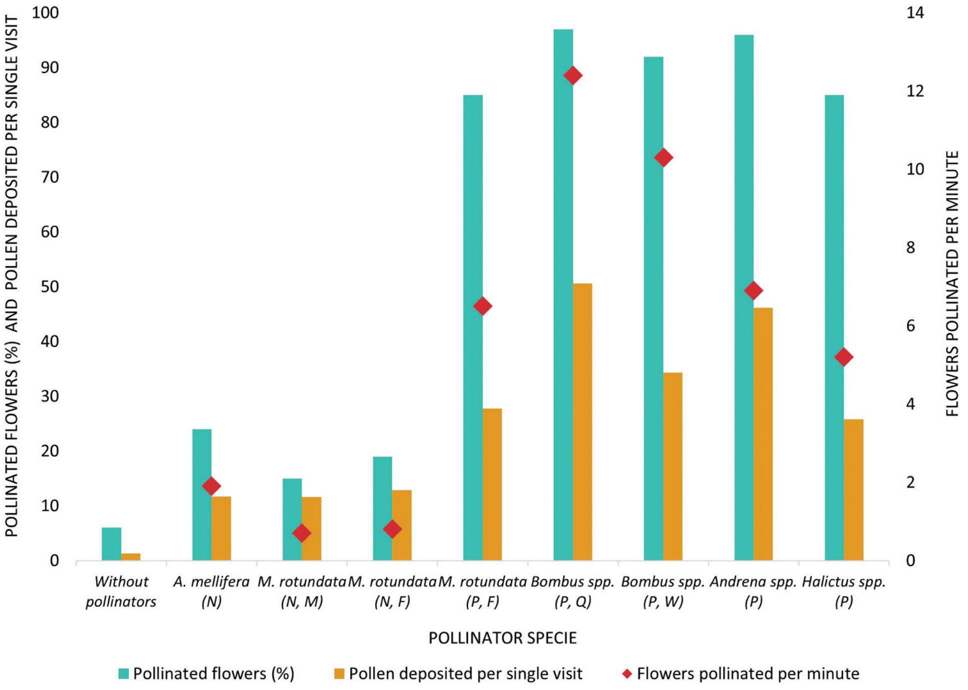

Figure 8. Pollination effectiveness on lowbush blueberry (*Vaccinium angustifolium*) flowers by different species of bees (Hymenoptera: apoidea). The pollination percentage for each taxon was calculated as the number of pollinated stigmata divided by the total number of flowers visited. N, nectar; P, pollen; M, male; F, female; Q, queen; W, worker (adapted from Javorek et al., 2002).

lower part of the receptacle, while larger bees such as honey bees preferred the apical stigmata at the top of the receptacle (Chagnon et al., 1993; Hoehn et al., 2008).

The presence of poricidal anthers in lowbush blueberry flowers determines the foraging preferences of pollinators, with some preferring pollen and others preferring nectar depending on their ability to sonicate (Buchmann, 1983). Honey bees are more interested in lowbush blueberry nectar than in pollen, as their total pollen loads contain less than 14% of *V. angustifolium* pollen (Dufour et al., 2020). In contrast, pollen-foragers of *Bombus* and *Andrena* genera can be three to six times more effective than nectar-foragers like *A. mellifera* and *Megachile rotunda* Fabr (Gagnon et al., 2011; Javorek et al., 2002). Javorek et al. (2002) also found a higher tetrad deposition in pollen-foragers such as *Bombus* spp., which can deposit around 50 tetrads per visit, compared with honey bee or leafcutting bees that can deposit around 12 tetrads per visit. Pollen-foragers also had pollination percentages exceeding 85%, while nectar-foragers exhibited pollination percentages below 25% (Figure 8).

Bee Population Declines

Since the early 2000s, the decline of pollinating insects has been documented worldwide (Biesmeijer et al., 2006; Cane and Tepedino, 2001; Council, 2006; Klein et al., 2017). Despite their crucial role in supporting terrestrial ecosystems, there is a lack of data to accurately quantify declines in many regions of the world for most wild pollinator taxa (Goulson et al., 2015). Bumble bees (*Bombus* spp.) are the group of pollinators with more available information (Cameron et al., 2011; Soroye et al., 2020). In Canada, for example, of 41 known bumble bee species, seven are officially at risk or endangered (COSEWIC, 2023). Studies on lowbush blueberry report both no decline (Drummond and Hoshide, 2024) and a decline (Table 3) in wild pollinator abundance. Drummond and Hoshide (2024) found no significant reduction in wild pollinator abundance in Maine based on a linear statistical approach.

However, it revealed large annual fluctuations, leading to unpredictability and potential risks for production. Moreover, Drummond et al. (2017) suggest a population decline in *Osmia* spp. mason bees over time.

Various factors can influence the decline in the abundance and diversity of wild bees. The main ones include agricultural intensification and urban development (Goulson et al., 2015), monotonous diets associated with pollination of large monocultures (Koh et al., 2016; Sánchez-Bayo and Wyckhuys, 2019; St Clair et al., 2020), competition for floral resources and nesting sites (Goulson et al., 2015), the impact of climate change on pollinators' life cycles and the phenology of angiosperms (Goulson et al., 2015; Pyke et al., 2016; Soroye et al., 2020), pesticides (Cameron and Sadd, 2020; Sánchez-Bayo et al., 2016), and parasite and disease spillover (Colla et al., 2006; Goulson et al., 2015; Hicks et al., 2018; Meeus et al., 2011).

The impact of these factors on lowbush blueberries has been insufficiently explored. This review found only a few studies that partially evaluated these factors (Table 3). The main causes of pollinator diversity decline in lowbush blueberry context include the distance of fields from natural habitats or forest edges (moisan-De Serres et al., 2014), the poor dietary value of pollen (Dufour et al., 2020), competition for floral resources with commercial pollinators (Eaton and Nams, 2012), climate change (Drummond et al., 2017), and pathogen transmission from commercial colonies to native pollinators (Bushmann et al., 2012; Hicks et al., 2018). The landscape surrounding lowbush blueberry fields plays a crucial role, both positively and negatively, in influencing bee diversity and abundance. Its effects are discussed in the following section.

Table 3. Factors that can potentially affect wild bee abundance and diversity in lowbush blueberry crops.

Factor	Findings in lowbush blueberry crops	References in the lowbush blueberry context
Transformed landscapes by agricultural intensification	Forest edges in lowbush blueberry fields attract a high abundance and diversity of pollinators, which decreases as the distance from this natural habitat increases.	(moisan-De Serres et al., 2014)
Monotonous diets	Reduction in the diversity, availability, and quantity of floral resources. Resulting in poor dietary value of pollen.	(Dufour et al., 2020)
Competition for floral resources	There is a negative interaction between honey bees and wild bees in lowbush blueberry fields. The effect of honey bees on yield and blossoms set is reduced in smaller fields that have a high abundance of wild bees.	(Eaton and Nams, 2012)
Climate change	A 29-year analysis of the effect of climate change on the native bee community and bee foraging in lowbush blueberries show a reduction in the optimal density of wild pollinators required for blueberry pollination during bloom, with direct impacts on bee abundance and pollination	(Drummond et al., 2017)
Pathogen spillover	This study found wild bumble bees within commercial *B. impatiens* colonies used for lowbush blueberry pollination. They found pathogens such as *Crithidia bombi, Apicystis bombi, Vairimorpha bombi, Vairimorpha ceranae* and *Ascosphaera* spp. in commercial individuals and native bumble bees inside commercial colonies	(Bushmann et al., 2012; Hicks et al., 2018)

Blueberry Landscape Limitations

The landscape surrounding lowbush blueberry fields affects wild bee diversity and abundance (Du Clos et al., 2022; Jesson et al., 2014). For example, surrounding flowering plant heterogeneity and diversity can increase wild bee abundance and diversity at the field level (Bushmann and Drummond, 2020). The study carried out by moisan-De Serres et al. (2014) showed a higher abundance of wild bees when blueberry fields had forested edges, and McKechnie et al. (2017) found a greater nesting habitat and a greater richness of cleptoparasitic bees in forested edges compared with deforested ones. Cutler et al. (2015) found that the abundance of the smallest species of bees is reduced as the distance from the field edge increases. Du Clos et al. (2022) found that power line corridors near lowbush blueberry fields can offer high-quality floral resources and refugia for bees, enhancing their abundance and richness, especially in agricultural landscapes that lack resources. However, Du Clos et al. (2020) found that certain cover types with abundant floral resources, such as lowbush blueberry fields, their surroundings, and urban areas, can increase wild bee diversity and abundance. These studies reaffirm the importance of natural habitat conservation both within and around agricultural exploitations.

However, forested edges do not always ensure a higher bee diversity. Some studies show that lowbush blueberry fields incrusted in coniferous and deciduous forests have low wild bee diversity (Bushmann and Drummond, 2020; Du Clos et al., 2020). Other studies show that deforested edges host a higher non-parasitic bee (pollen-seeking bees) abundance, which can be explained because deforested edges have higher light levels and lower canopy overlapping, changing foraging behaviors (McKechnie et al., 2017).

Some studies reported possible alternatives to wild bee conservation in lowbush blueberry landscapes. Venturini et al. (2017, 2018) demonstrated the long-term benefits of pollination reservoirs (PRs), increasing bee abundance and lowbush blueberry fruit set. They compared different types of PRs, including clover, a wildflower mix, and natural regeneration. Their findings indicated that clover was the most frequently visited PR by social bees, such as honey bees and bumble bees. This was followed by the wildflower mix, while natural regeneration was the least visited (see section 6 for more on PR economics). Stubbs et al. (1997) found that providing wooden trap-nest blocks increased bee abundance from the genus *Osmia* during the lowbush blueberry bloom. Asare et al. (2017) and Bushmann and Drummond (2015) found that organic systems, apart from being economically preferable to conventional ones, could also increase bumble bee richness. Finally, Groff et al. (2016) developed a geospatial tool (BeeMapper) for blueberry growers to predict the abundance of lowbush blueberry wild bee pollinators in the landscape surrounding their fields in Maine. This type of tool aims to improve pollinator conservation plans, the placement of commercial colonies, and the understanding of wild bee populations in mass-flowering crops.

The deforestation generated by new blueberry fields developed from the forest is one of the most recent concerns of this productive system, perpetuating one of the most common externalities of conventional agricultural systems (Major, 2021). Blueberries require much light to ensure their correct growth, which exerts pressure on deforestation in the surroundings of the crop, with a direct impact on the habitat of wild pollinators. This study did not find the exact annual deforestation rates for lowbush blueberry production. However, some reports in the news have shown concerns and alarming figures in New Brunswick, Canada, where 8,000 ha of forest areas have been transformed into lowbush blueberry fields (Trozzo, 2023). Future studies to develop blueberry fields in a more environmentally way are essential.

Commercial Pollinators

Even though some wild pollinators are highly effective in blueberry pollination, variations in wild bee abundance and landscape factors can limit wild bee availability. Therefore, relying on wild pollinators might not allow growers to reach the desired fruit set, increasing their need for managed pollinators, especially honey bees (*Apis mellifera*), the common eastern bumble bee (*Bombus impatiens*), alfalfa leafcutter bees (*Megachile rotundata*) (Table 4), and bees of the genus *Osmia* spp (Bushmann and Drummond, 2020; Hanes et al., 2013).

Table 4. Characteristics of the principal commercial pollinators used in lowbush blueberry crops.

Commercial pollinator/ Characteristics	Honey bees (Apis mellifera)	Common eastern bumble bee (Bombus impatiens)	Alfalfa leafcutting bee (Megachile rotundata)
Origin	Europe, western Asia, and Africa	Eastern North America	Eurasian
Sociality	Eusocial	Primitively eusocial (solitary and social phases)	Solitary and gregarious
Life cycle	Perennial	Annual	Annual – sometimes bivoltine
Colony size	50,000–60,000 individuals	Up to 540 individuals	-
Introduction for lowbush blueberry pollination	Earlies 60's in the USA	1990 in the USA and Canada	1990 in the USA and Canada
Recommended density	1–25 colonies/ha	4–10 colonies/ha	20,000–50,000 bees/ha
Foraging temperature	13°C and 23°C	10°C to 32°C	Foraging activity is reduced at temperatures below 21°C
Distance	Up to 5 km	400 meters	Up to 120 meters from the domes
Pollination parameters	Shorter tongue (6.6 mm). 1.9 flowers pollinated/minute. 11.7 pollen tetrads deposited/ visite	Longer tongue (7.2 mm)	0.7–6.5 flowers pollinated/ minute. 11.6–27.8 pollen tetrads deposited/visite
Fidelity	Around 14% of pollen loads carried by honey bees are from the *Vaccinium* genus	Around 60% of pollen loads carried by bumble bees are from the *Vaccinium* genus	-
Buzz pollination	No	Yes	No

Honey Bees

North American Beekeeping

In Canada, the contribution of pollination corresponds to a value of Canadian agricultural crops of 2.57 billion dollars per year, of which 235 million corresponds to the cultivation of blueberries (Agriculture and Agri-Food Canada, 2017). Lowbush blueberry is the main crop pollinated commercially in Quebec (MAPAQ, 2018; Maucourt et al., 2017). The beekeeping industry of the Canadian province of Quebec represents an annual economic activity of nearly $25.4 million (Government of Canada, 2022). In 2020, Quebec had 485 beekeepers and 67,200 hives, of which 34,339 were rented for blueberry pollination (ISQ, 2021). In New Brunswick, approximately 32,500 hives are used annually for lowbush blueberry pollination, including both local (9,500 colonies) and imported hives (23,000) (Agriculture, Aquaculture and Fisheries, 2024). Estimates for Nova Scotia and Prince Edward Island are less frequently published.

In the USA, 2.8 million honey bee colonies are transported annually for pollination services and honey production (Collum et al., 2023). The demand for migratory beekeeping in blueberry crops in Maine has grown enormously in recent years. In 1960, only 500 colonies were transported for lowbush blueberry pollination, but this number grew to 25,000 in 1985, 60000 in the 2000s, and 77,000 in 2015 (Collum et al., 2023; Drummond, 2002a).

Honey Bee Foraging Activity

Honey bees are native to Europe, western Asia, and Africa, and were introduced to North America by European settlers during the 19th century (Forget and Turcotte, 1997). Specific biological characteristics of honey bees give them advantages and disadvantages for commercially pollinating lowbush blueberries (Table 5). The most important advantages to lowbush blueberry pollination include the high number of individuals (Boucher et al., 2013; CRAAQ, 2018), the use of a communication system (Drummond, 2002b), and the long distances that bees can travel in search of resources (moisan-De Serres, 2013). On the other hand, their foraging activity is reduced at temperatures below 12°C

Table 5. Advantages and disadvantages of honey bees as commercial pollinators of lowbush blueberry.

Advantages	Disadvantages
The ***high number of individuals*** (between 50,000 and 60,000 workers of which around 50% are foragers (Boucher et al., 2013; CRAAQ, 2018)) could compensate for the lack of individual efficiency (Javorek et al., 2002; moisan-De Serres, 2013).	Their ***foraging activity is reduced at temperatures below 12°C*** and at wind speeds above 19 km/h (common spring conditions during blueberry pollination) (Arrington and DeVetter, 2018)
Honey bees are ***polylectic,*** which means they can be adapted to pollinate a wide range of plants (Goulson, 2010).	Because of their polylectic condition, ***they can target other rewarding plants*** when resources are scarce (unfavorable for unattractive crops such as lowbush blueberry) (Drummond, 2002a; Dufour et al., 2020)
Honey bees have a ***communication system*** to locate floral resources and they possess the capacity to learn how to manipulate flowers with complex morphologies (Drummond, 2002b).	Honey bees have been reported to do ***secondary nectar robbing*** in highbush blueberry (*V. corymbosum*) and rabbiteye blueberry (*V. ashei* Reade) (Benjamin and Winfree, 2014; Sampson et al., 2004)
Honey bees can travel up to 5 km from the colony, which allows them to ***pollinate a large area of flowers*** (moisan-De Serres, 2013).	They ***do not carry out the buzz pollination*** or sonication required to remove pollen from the poricidal anthers (Arrington and DeVetter, 2018; Javorek et al., 2002)
Honey bees can be ***easily transported*** during blooming periods of different crops (Drummond, 2002b).	Honey bees have ***shorter tongues*** than bumble bees, making it more difficult to access nectar (Courcelles et al., 2013; Wahengbam et al., 2019).

(Arrington and DeVetter, 2018), they do not carry out buzz pollination (Arrington and DeVetter, 2018; Javorek et al., 2002), and they have shorter tongues than bumble bees, making it difficult to access nectar (Courcelles et al., 2013; Wahengbam et al., 2019).

Nectar robbing can decrease honey bee pollination efficiency in *Vaccinium* flowers. Primary nectar robbers access nectar by biting holes into tubular flowers, often without pollinating them, while secondary robbers, like honey bees, take nectar from these holes (Irwin et al., 2010). Studies show that honey bees engage in secondary robbing in highbush blueberry (*V. corymbosum*) and rabbiteye blueberry (*V. ashei*) flowers, with nectar robbing rates reaching 42.7% in some highbush varieties (Benjamin and Winfree, 2014; Courcelles et al., 2013; Sampson et al., 2004). In rabbiteye blueberries, when carpenter bees rob 4 to 50% of flowers, 65 to 100% of honey bees also rob them, though this does not affect fruit set but does impact seed set negatively (Dedej, 2004; Sampson et al., 2004). The effects of nectar robbing in lowbush blueberries remain unstudied.

Recommended Densities and Strengths

The introduction of honey bees for pollinating lowbush blueberries must be timed precisely, as it significantly affects both fruit set and seed set (Jesson et al., 2014; WSU, 2021). Normally, pollinators are introduced when approximately 10 to 20% of the lowbush blueberry flowers in a field are open and will remain until the petals fall, for a total of three weeks of pollination (Arrington and DeVetter, 2018; Chagnon et al., 2015; Drummond, 2002a). The timing of colony introduction must be respected to ensure foraging in the blueberry rather than the other nearby flowers (Olmstead and McCallum, 2019). The introduction of honey bee colonies can increase fruit set by 70% to almost 100% (Dufour et al., 2020). The increase in colony densities causes an increase in the size and number of fertilized seeds (Aras et al., 1996; WSU, 2021). In contrast, other research carried out in Newfoundland did not find an improvement in fruit set variables with honey bee supplementation, and conversely, lower levels of wild pollinators were observed (Hicks, 2011).

Despite the existence of various recommendations for optimal densities of colonies of honey bees for lowbush blueberry pollination (Chagnon et al., 2015; Gagnon et al., 2011; Savard, 2014), they are still imprecise and variable (between 1 to 25 honey bee colonies/ha). This variability is explained by factors such as the fluctuation of native bee populations associated with lowbush blueberry fields (Drummond et al., 2017) or colony strength. For this reason, Drummond (2020a)suggested that bee forager density within a field is a more accurate predictor of fruit set and yield than colony density. On the other hand, the study carried out by Grant et al. (2021) on highbush blueberries determined that colony strength significantly impacts yields, suggesting that increased colony strength could provide better pollination benefits without increasing colony density. These results could also apply to lowbush blueberries.

Additionally, a meta-analysis carried out in 16 different cropping systems suggests that there is a limit where colony addition no longer contributes to increased yields (Rollin et al., 2019). This limit was determined for lowbush blueberry by Eaton and Nams (2012) in Nova Scotia, who established a maximum of 4 colonies/ha. Up to this density, they observed competition between honey bees and wild bees, as well as erratic effects of commercial pollination on yields. Drummond (2002a) developed a linear model to predict fruit sets based on the density of honey bees and wild bees foraging in one square meter of lowbush blueberry. Monitoring forager densities allows the adjustment of required colony densities to obtain the desired fruit set. However, optimal colony densities for pollination supplementation remain to be determined precisely in both agronomic and economic terms.

Colony strength is a parameter widely used as an indicator of the health of colonies that are used for blueberry pollination. This strength is often evaluated in the number of frames covered with bees. Normally, colonies are considered in good condition when they have between six and ten full frames of brood in all stages of development, distributed in a two-story hive (Drummond, 2002a). A colony with 30,000 bees is considered stronger than two colonies of 15,000 since the proportion of foraging bees in relation to nurse bees is greater (Isaacs et al., 2016). Some research demonstrates that the number of foragers does not follow a linear relationship with the number of bee frames (Fukuda, 1983). It is, therefore, important to complement these evaluations with parameters of foraging activity.

Impact of Pollination on Honey Bee Health

Some studies have demonstrated the negative impacts of blueberry pollination on the health of honey bee colonies (Colwell et al., 2017; Drummond, 2022; Drummond et al., 2021; Dufour et al., 2020). As previously mentioned, and discussed extensively in the final section, lowbush blueberry production heavily depends on colony rentals. Therefore, this section aims to provide a broader perspective on the challenges associated with commercial pollination by honey bees. Honey bees are generalist pollinators that need a diversified diet to meet their nutritional requirements. Lowbush blueberry fields are normally large monocultures that limit the presence of other plant species from which bees could benefit. By eating a monofloral diet during pollination, colony development is slowed (Dufour et al., 2020). Huber (2016) reported a content of 13% of raw proteins in the pollen of the highbush blueberry (*V. corymbosum*), while Colwell et al. (2017) reported a content of 9.8% for *V. angustifolium* and *V. corymbosum*. This content is below the requirements of bee colonies (around 20%). Lower crude protein content leads to brood reduction after the lowbush blueberry pollination period (Drummond, 2022; Drummond et al., 2021; Dufour et al., 2020). Drummond et al. (2021) also found that brood reduction was associated with the negative effect of *Varroa* infestation. Furthermore, pesticide exposure has been reported to impact colony health. Drummond (2022) found that exposure to the fungicide propiconazole may reduce the number of sealed brood and workers during and shortly after bloom. This effect was observed in colonies located in fields treated with the fungicide compared to those in untreated fields.

The low yields of lowbush blueberry fields in some regions, the increase of its surfaces, and the possible decline in the wild pollinator populations exert pressure that leads to the increase in the number of colonies needed for blueberry pollination. Colony augmentation could increase the risk of transmission of viral diseases (Gisder and Genersch, 2017). Pathogens and parasites, and their related diseases, are major concerns in beekeeping. Varroosis (*Varroa destructor* (Anderson and Trueman)) is a major health issue in Canadian beekeeping and the leading cause of winter mortality (Currie et al., 2010; Ferland et al., 2022). *Varroa* is the most common parasite in southeastern Quebec, with almost half of the colonies infested (Claing, 2019). Our research team, found a higher proportion of colonies infested with *Varroa* when the recommended density of lowbush blueberry was doubled, as well as a slowdown in the colony strength gain (unpublished data, manuscript in preparation). The increased risk of pathogen and parasite transmission associated with higher colony densities could worsen the existing colony shortage, further contributing to economic constraints (see section 6 for more on the economic constraints of commercial pollination).

Drummond et al. (2021) and Dufour et al. (2020) reported a higher level of *Vairimorpha ceranae* (Fries) during and after lowbush blueberry pollination, respectively. However, to our knowledge, there have been no studies evaluating the impact of increased colony/hectare densities on bee health in lowbush blueberry fields.

Bumble Bees

North American Species

Among the 265 species of bumble bees (*Bombus* Latrielle: Apidae) reported worldwide, six species are commercially farmed, *Bombus terrestris* (L.) and *B. impatiens* being the most common in Europe and North America, respectively (Gekière et al., 2022; Goulson and Hughes, 2015; Williams and Jepsen, 2021). The commercial use of bumble bees began in Europe in 1987 for the pollination of greenhouse tomatoes. In Canada and the USA, the use of bumble bees for pollination services dates to the 1990s, when the common eastern bumble bee (*B. impatiens*) was used for the pollination of lowbush blueberries in New Brunswick and Maine (Drummond, 2012a). Then, in the early 2000s, it was used in Nova Scotia, and it was introduced in Quebec in 2006 (Desjardins and de Oliveira, 2006; Palmier and Sheffield, 2019). *Bombus impatiens* is a species native to eastern North America whose natural distribution in Canada was limited to southern Ontario and Quebec (Laverty and Harder, 1988). Since the species was introduced for commercial pollination, it has become established in other provinces such as British Columbia, New Brunswick, Nova Scotia, and Prince Edward Island (Palmier and Sheffield, 2019).

Biology

Bumble bees are insects considered primitively eusocial because of their simpler social organization than that of honey bees (Goulson, 2010). The colored patterns on the tergites of their abdomen are a common way to identify bumble bee species. *Bombus impatiens* is the only North American species that has only the first tergite with pale yellow pubescence, while the rest of the tergites are totally black (Palmier and Sheffield, 2019).

Unlike bees of the genus *Apis* like the honey bee, bumble bees have an annual life cycle. In temperate regions, its cycle is divided into a solitary phase, a social phase, and a competitive phase (Hefetz and Grozinger, 2017). The solitary phase begins when a mated queen emerges from diapause to search for a nesting area and initiate a new colony. During this phase, the queen forages and takes care of the brood. It is, therefore, no different than solitary bees. Following their emergence, the first workers will forage and take care of the nest, while the queen only lay eggs (Goulson, 2010). This period is the social phase, and the colony then undertakes exponential growth, reaching populations of up to 540 individuals in the case of *Bombus impatiens* (Cnaani et al., 2002). Finally, the competition phase begins at the end of the foraging season when the production of workers ceases and is replaced by the production of future queens (gynes) and males (Hefetz and Grozinger, 2017). Diploid larvae will develop into gynes and haploid eggs will develop into males. At this time, the workers compete with each other and with the queen to lay eggs and thus contribute to the population of males in the nest (Holman, 2014). The gynes and males will then mate, and the young mated queens will seek out a suitable underground site where they will spend the next six to nine months in diapause before initiating a new nest the following spring (Hefetz and Grozinger, 2017).

Foraging Activity and Effectiveness

Unlike honey bees, bumble bees are well adapted to pollinating lowbush blueberry (Javorek et al., 2002). Their longer tongue (7.2 mm in *B. impatiens*) than that of the honey bee (6.6 mm) allows them to seek nectar in deeper floral structures (Austin and Dunlap, 2019; Balfour et al., 2013). The study of Courcelles et al. (2013) demonstrated that highbush blueberry cultivars with longer and narrower corollas (10.2 mm) received significantly more visits from bumble bees than from honey bees. Additionally, pollen deposition on the stigma by honey bees can be doubled when they follow *B. impatiens* queens pollinating (Drummond, 2016)

In addition, compared to honey bees, bumble bees can forage during periods of low solar radiation and light rain (Brown and Rains, 2006; Isaacs et al., 2016). Bumble bees can forage at temperatures ranging from 10°C to 32°C, whereas honey bees prefer temperatures between 13°C and 23°C for good foraging activity (Decourtye et al., 2016). Some studies suggest that worker polymorphism, in addition to being linked to the division of labor (Couvillon et al., 2010; Goulson, 2010), is a characteristic that allows adaptation to different foraging conditions. Larger bumble bees can, therefore forage better at colder temperatures, while smaller bumble bees forage at warmer temperatures (Peat et al., 2005).

Bumble bees can visit more flowers over time and transfer pollen efficiently. For example, bumble bee queens can transfer between four and eight times more pollen to the stigma of lowbush blueberry flowers than honey bees (Drummond, 2016; Isaacs et al., 2016; Javorek et al., 2002). They have a vibrational behavior known as sonication, achieved via the rapid vibration of their wings. Sonication makes it possible to shake the anthers more effectively, release the pollen grains more easily, and accumulate them on their body. The collected pollen will be transferred from flower to flower on the stigma. While three visits from a honey bee per flower are required to ensure pollination, only one visit from a bumble bee is sufficient in highbush blueberries (Isaacs et al., 2016). In addition, bumble bees are more faithful to the crop they pollinate compared to honey bees because their foraging distance is shorter, around 400 m, while the honey bee can forage up to 5 km (Desjardins and de Oliveira, 2006). This fidelity was also demonstrated in lowbush blueberry fields. Around 60% of pollen loads carried by bumble bees are from the *Vaccinium* genus (Drummond, 2012a; moisan-De Serres et al., 2014).

Recommended Densities

Stocking recommendations for commercial bumble bees in lowbush blueberry fields are also variable. In Quebec, for example, Desjardins and de Oliveira (2006) recommended 688 individuals per hectare, which means two to four colonies/hectare, depending on the colony strength. In Maine, recommendations are between seven and nine colonies/hectare with 150 or 200 worker bees per colony (Drummond, 2012a; Stubbs and Yarborough, 2002). Stubbs and Drummond (2001) compared three different colony densities of *B. impatiens* (5, 7.5, and 10 colonies/ha) in lowbush blueberry fields in Maine. Each bumble bee density was compared with a density of 7.5 honey bee hives/ha. In this study, no significant differences were found between the different densities evaluated in any pollination effectiveness parameter (% fruit set, berry weight, or seeds per berry). Only the percentage of harvested berries (yield) was higher in fields stocked with 10 *B. impatiens* colonies/ha. Although some studies evaluate different stocking densities, the limits of stocking densities remain unknown.

Impact of Pollination on Bumble Bee Health

Lowbush blueberry fields, spanning several dozen hectares, offer limited quality, quantity, and temporal availability of floral resources (Cameron and Sadd, 2020). Therefore, during pollination services in blueberry fields, blueberry becomes almost the only floral resource that bumble bees consume. However, as described before, its pollen has a low protein content. Pollen provides micronutrients (proteins, lipids, sterols, and amino acids) essential for development and reproduction (Cameron and Sadd, 2020) and is essential for the adult immunity in bumble bees (Brunner et al., 2014; Cameron and Sadd, 2020). While we did not find studies directly linking the health status of commercial bumble bee colonies or their pollination effort to production parameters (such as yield or fruit set) in lowbush blueberry, the impact of pollination on colony health remains remarkably relevant for ecological concerns, such as pathogen spillover. In this context, a reduction in immunity plays a critical role.

Few studies have analyzed the connection between lowbush blueberry pollination and commercial bumble bee diseases. In this review, only two papers were found that studied this interaction. Bushmann et al. (2012) evaluated the prevalence of *Vairimorpha* infection in wild bumble bees foraging in lowbush blueberry fields where commercial *B. impatiens* were used. They found a 5.48% global infection level in wild bumble bees, and a 6.9% infection rate in commercial *B. impatiens*, with no significant differences or evidence of possible pathogen spillover. However, the infection rates varied among different bumble bee species, with 46.2% of *B. terricola* individuals being infected. For their part, Hicks et al. (2018) evaluated colonies pre-used in lowbush blueberry pollination and later used in cranberry fields. They found a higher prevalence of *Apicystis bombi, Vairimorpha ceranae*, and *Ascosphaera* spp. in colonies used in both lowbush blueberry and cranberry pollination than in colonies only used in cranberry fields. Findings related to spillover in wild bumble bees are discussed in the last section.

Leafcutter Bees

Use in Lowbush Blueberry Fields

The alfalfa leafcutter bee, *Megachile rotundata* (Hymenoptera: Megachilidae), is a solitary and gregarious Eurasian species (Stubbs and Drummond, 1997a). This species is the most produced and widely managed solitary bee in the world (Pitts-Singer and Cane, 2011). It was accidentally introduced to the USA in 1930 and began to be commercially used for alfalfa pollination in the 1960s in western North America. Its foraging evaluation began in 1992 in Maine, and during the late 1990s, it was introduced to lowbush blueberry fields in Canada (Savard, 2014; Stubbs and Drummond, 1997a). It is not aggressive, which facilitates its handling.

Despite its commercial introduction for lowbush blueberry pollination, its use is less frequent than that of bumble bees or honey bees due to some biological limitations. First, this species is vulnerable to low temperatures, which can prolong the emergence and mating period and even cause death below −5°C (moisan-De Serres, 2013; Stubbs and Drummond, 2001). This is problematic as the spring weather conditions in which lowbush blueberry blooms are usually cold and humid. Furthermore, the emergence *M. rotundata* naturally coincides with summer flowering plants, and it is much more active in summertime. Thus, blueberry pollination involves the release of *M. rotundata* at least one month before its natural flight period. This can increase bivoltinism (the production of a second generation in the same year) by 7 to 30%. Bivoltinism can generate a reduction in the recovery and maintenance of populations that will be used in the next period of pollination (Sheffield, 2008).

Biology

Megachile rotundata is a solitary species whose life cycle starts at the beginning of spring when the pre-pupa begins its pupal development. Adults then emerge at the beginning of summer (Sgolastra et al., 2019). Like many other solitary species, *M. rotundata* is protandrous. This means that males emerge two or three days before females, to be ready to mate when females emerge (Pitts-Singer and Cane, 2011). Females only mate once with a single male. After mating, females usually nest in pre-established hollows above the ground using leaf fragments. There, they will lay their eggs (under ideal conditions, they will lay two eggs per day), and they will raise the larvae by providing food (Pitts-Singer and Cane, 2011).

A female can spend 5–6 hours per day foraging for food. At first the female will mainly forage pollen but will progressively increase the nectar supply (Pitts-Singer and Cane, 2011). The male progeny will receive 17% less food than the female. Embryogenesis will take two to three days. The larvae will pass through five larval instars (20 days) to finally become a pupa (15 days) (Pitts-Singer and Cane, 2011; Sgolastra et al., 2019). The pre-pupas will be in a pre-wintering state for later hibernation. This species may present bivoltinism according to temperatures, nutrition, photoperiods, or emergency induction by interrupting the metamorphosis of developing bees (Helm et al., 2018). In warmer regions, it can produce up to four generations (Sgolastra et al., 2019). Adults can be active from June or July according to latitude, and their life span is between seven and eight weeks.

Foraging Activity and Recommended Densities

The stocking recommendation for lowbush pollination with alfalfa leafcutter bees is between 20,000 and 50,000 bees/hectare, depending on the desired fruit set (MacKenzie et al., 1997; Stubbs and

Drummond, 1997a, 1997b). Higher densities are desired in places with frequent frost during bloom periods because of the lower cold tolerance of *Megachile* (Sheffield, 2008). Alfalfa leafcutter bees are typically placed in the middle of the field inside domes to protect them from cold temperatures. They are often used in conjunction with commercial honey bees and bumble bees because they forage in a range relatively short (up to a maximum of 120 meters from the domes) (Savard, 2014). Their foraging activity is reduced at temperatures below 21°C. However, they have been observed foraging on blueberry bloom from 13°C in northwestern Alberta (Stubbs and Drummond, 1997a). Stubbs and Drummond (1997a) showed that females of *M. rotundata* visit one flower per stem to collect pollen and spend 2.4 seconds per flower. This is a desirable trait because of the self-incompatibility of lowbush blueberry flowers. Pollination with *M. rotundata* can improve the fruit set by 30% over background pollination (Stubbs and Drummond, 2001).

Leafcutter Bee Health

Lowbush blueberry pollination's impact on *Megachile rotundata* health has not been studied yet. Like the honey bee, alfalfa leafcutter bees can be affected by diseases such as chalkbrood (*Ascosphaera aggregata*). Although this disease is related to *Ascosphaera apis*, which infects *A. mellifera*, so far, no crossed infection has been reported between species (Pitts-Singer and Cane, 2011). Disease transmission from *Megachile* to wild pollinators during lowbush blueberry pollination remains underknown.

Other Commercial Pollinators

Other pollinators have been explored as potentially manageable for lowbush blueberry pollination. For example, the solitary cavity-nesting species *Osmia ribifloris*, native to Northwestern USA, has a high affinity for *Vaccinium* pollen and a good activity during spring even with inclement weather (DeVetter et al., 2022). This species was introduced in Maine for lowbush blueberry pollination in the 1990s (Stubbs et al., 1994). However, *O. ribifloris* presents a lower performance than *A. mellifera* and other wild pollinators because of its incapacity to sonicate flowers (DeVetter et al., 2022). *Colletes validus* has also been considered as potentially manageable for lowbush blueberry pollination. This solitary ground-nesting species is native to Northeastern America. Like *O. ribifloris*, it has a high affinity for *Vaccinium* pollen and good activity during spring and inclement weather, but it can sonicate flowers (DeVetter et al., 2022).

Commercial Pollination Limitations and Risks

The Risks of Introducing Commercial Bumble Bee Hives

The introduction of commercial bumble bees for lowbush blueberry pollination has affected both disease spillover and the abundance of wild bumble bee species. As explained in Section 4, wild pollinators can contribute between 30% and 55% of the fruit set in blueberry fields. Therefore, this section pretends to establish the link between the challenges associated with commercial pollination and its impact on wild pollinators, beyond purely productive parameters. Commercial *B. impatiens* are reservoirs of different pathogens, mites, and viruses (Sachman-Ruiz et al., 2015). Pathogen transmission can occur in the presence of wild bumble bees inside commercial colonies due to drifting or honey robbing (Graystock et al., 2015). Hicks et al. (2018) reported for the first time the presence of wild bumble bees within commercial *B. impatiens* colonies, which were used for lowbush blueberry and/or cranberry pollination in Newfoundland and Labrador. It is hypothesized that wild bumble bees were attempting to steal provisions from commercial colonies. This study found pathogens such as *Crithidia bombi, Apicystis bombi, Vairimorpha bombi, Vairimorpha ceranae* and *Ascosphaera* spp. in commercial individuals and native bumble bees inside commercial colonies. They also found *C. bombi*, *V. bombi, and A. bombi* in bees collected away from commercial colonies and on the same field.

The presence of *V. bombi* and *Chrithidia bombi* in commercial colonies has been linked to the decline of bumble bees in North America, particularly species like *Bombus terricola*, *B. occidentalis* (Greene), and *B. affinis* (Cresson) (Evans et al., 2008; Winter et al., 2006). For instance, *B. terricola* used to be a common pollinator found at high densities in lowbush blueberry fields in Maine, while *B. impatiens* was not reported in the region in the 1960s (Boulanger et al., 1967). Since the introduction of *B. impatiens* as a commercial pollinator for lowbush blueberry, there has been a decrease in the abundance of *B. terricola* (Bushmann et al., 2012). At the same time, the abundance of *B. impatiens* has increased, possibly because the commercial queens are able to overwinter successfully, they have a varied diet and emerge early (Bushmann et al., 2012; Jacobson et al., 2018; Stubbs and Drummond, 2001).

Given the current gaps in legislation and the insufficient information of pathogen loads in reared bumble bee industries, some experts propose the introduction of a clean-stock certification program for these facilities. This program aims to minimize parasites, pests, and diseases to acceptable levels. More details about the program can be found in Strange et al. (2023).

Another risk with commercial *Bombus* colonies is the gene introgression with the release of commercial queens and gynes into wild populations (Gurel and Sakli, 2021; Miller et al., 2023). Gurel and Sakli (2021) reported this risk in *B. terrestris*, which has a higher production of gynes in colonies placed directly in fields rather than in greenhouses. Queen excluders have been proposed to avoid commercial queen escapes (Miller et al., 2023). These excluders could also avoid the entrance of wild queens into commercial colonies. In apple orchards, wild bumble bee queens have been reported in commercial *B. impatiens* colonies, which can become an ecological trap for nest-searching *Bombus* queens (Miller et al., 2023). Each commercial colony without a queen excluder was found to have an average of ten wild *B. impatiens* queens. However, the number of queens per colony was reduced to an average of one in the presence of a queen excluder. Personal observations have revealed that, in lowbush blueberry fields, *B. impatiens* colonies frequently nest beneath commercial colonies of the same species, both with and without queen excluders (Figure 9). However, no studies have yet assessed the potential risks this behavior poses to wild populations or evaluated the effectiveness of queen excluders in preventing unintended interactions in these environments.

Figure 9. a) *Bombus impatiens* colonies have been observed nesting underneath commercial *B. impatiens* colonies deployed for pollination in lowbush blueberry fields. b) Zoom of the colony. No analysis was conducted to determine whether the observed colonies originated from wild queens or escaped queens from commercial colonies. Photos Ana María Quiroga-Arcila and Charles-Antoine Gagnon.

The Economic Constraints of Commercial Pollination

The demand for pollination services in lowbush blueberry fields has gradually grown over the years. However, a combination of different factors, such as climate change, high honey bee colony winter losses, reduced availability of strong honey bee colonies in early spring (during lowbush blueberry bloom), and colony importation policies from some regions/countries to others generates a shortage of honey bee colonies (Collum et al., 2023).

Honey bee colony mortalities cause shortages for lowbush blueberry pollination. As beekeeping is an agricultural production, honey bee losses have been more documented compared to wild pollinators. Unusually high mortalities have been reported, particularly in the USA (59% colony losses between 1947 and 2005) and in Europe (25% colony losses between 1985 and 2005) under the name of colony collapse disorder (CCD) (Krupke et al., 2021). In the USA, between the years 1980 and 2005, 2.1 million managed colonies were lost, going from 4.5 million to 2.4 million, with annual losses of around 30% (Collum et al., 2023; Drummond, 2002a). *Varroa* is one of the leading causes of winter mortality, together with the high incidence of viruses (Ferland et al., 2022). For more detailed information regarding pesticide impact, please refer to the third section, subsection on Crop Management.

In Canada, the reality is not so different, as, in 2022, winter mortality was 45.5% for the country as a whole and 48.4% for the province of Quebec, almost double the annual average for the period 2007–2021. In the case of the Maritime provinces, winter mortality was 19.8% in New Brunswick, 15.3% in Nova Scotia, and 51.9% in Prince Edward Island (Ferland et al., 2022). Winter mortality should normally remain below the 15% threshold (MAPAQ, 2018). Like in the USA, high *Varroa destructor* infestation levels have been identified as the cause of this important mortality in Quebec and in Prince Edward Island. Since 2006, nuc production has significantly increased to address high colony mortality and meet pollination and colony replacement needs (Goulson et al., 2015; MAPAQ, 2018; Maucourt et al., 2017).

Honey bee colony shortages are causing an increase in rental prices for lowbush blueberry pollination services and driving up the demand for other commercial pollinators such as bumble bees or alfalfa leafcutter bees (Stevens et al., 2015). Colony rental prices for lowbush blueberry pollination have increased significantly in the last few years (Asare et al., 2017; Hanes et al., 2013). In the case of Quebec, in only four years, there has been an increase of 48%, from USD $99.30 in 2018 to USD $146.87 in 2022. The highest increase occurred between 2021 and 2022, when the price increased by 21.5% (ISQ, 2024). The rising cost of commercial pollination is a significant risk for blueberry production, as it accounts for about 46% of all production costs. With the increasing demand for commercial pollinators, the rising costs and the impacts on honey bee colony health, the sustainability of blueberry farms is threatened (Asare et al., 2017). Blueberry producers are seeking alternatives, such as bumble bees, to address this problem (Stevens et al., 2015), despite the associated risks mentioned before. Maritime provinces like New Brunswick have developed lowbush blueberry pollination strategies to meet projected colony needs by 2029—estimated at 17,000 local colonies and 40,000 imported ones. However, the number of colonies available in 2022 would only cover 56% and 58% of these needs, respectively. The strategy includes support programs to boost colony numbers, promotion of alfalfa leafcutter bees, partnerships with bumblebee suppliers, and efforts to support healthy native bee populations (Agriculture, Aquaculture and Fisheries, 2024).

Adopting pollination reservoirs (PRs), on-farm areas with pollen- and nectar-rich plants, can support wild bee populations (Venturini et al., 2017). Venturini et al. (2017) demonstrated that after four years of PR implementation, fruit set increased by 10%, and wild bee abundance rose from 0.4 to 1 bee/m^2/min, with an installation cost of $307.62/ha, which can be offset by net farm income. Economic studies suggest that consumer willingness to pay for wild-pollinated blueberries could further support these investments. Consumers are willing to pay 14% more (an additional $0.51–$0.74 per dry liter) for blueberries pollinated by wild bees, which is 1.75 times the annual cost of establishing wildflower pastures (Hoshide et al., 2018; Stevens et al., 2015). However, growers are typically willing to invest only $140–$188/ha, just 25% of the net income attributable to wild bees (Hoshide et al., 2018). Wild pollinators contribute 40% of net farm income per hectare ($613/ha from a total of \$1,536/ha), while replacing their pollination services with managed bees would cost \$992/ha, exceeding their economic contribution (Hoshide et al., 2018). Additionally, consumers are willing to pay 6.7 times more to support wild pollination than growers are willing to invest, highlighting the need for financial incentives.

The economic risks faced by producers drive them to introduce managed pollinators to secure a desirable fruit set and minimize uncertainty. A potential tool to optimize these investments is the Economic Pollinator Level (EPL), developed by Drummond and Hoshide (2024). EPL estimates the optimal bee density to justify pollination investments, whether renting honey bee colonies or establishing PRs, based on pollination costs per m^2/ha (either honey bee rental costs or establishing pollinator pastures), crop market value per kg, fruit set per bee per m^2/ha, and berry weight (kg). This approach helps balance economic investments while reducing dependence on managed bees. Given the decline in blueberry prices and increasing colony rental costs, government assistance programs may be necessary to encourage PR adoption and mitigate economic risks.

Growers’ Perspectives on Pollination Management

The decision-making process in blueberry farm management is shaped by growers’ cognitive frameworks, also known as their cultural models. A study by Collum et al. (2023) found that lowbush blueberry growers’ perceptions of pollination management are mediated by three cognitive domains: the importance of pollination, sources of pollination, and the uncertainty associated with this practice. Regarding the first domain, multiple studies agree that growers recognize pollinators as essential and acknowledge that their production depends on bees (Collum et al., 2023; Hanes et al., 2013, 2018; Rose et al., 2013). They are also concerned about pollinator health, both for wild and managed bees (Collum et al., 2023; Hanes et al., 2013). Regarding sources of pollination, growers’ perceptions differ between managed and wild pollinators. Managed bees are often associated with more intensive production, usually at the expense of surrounding habitats that support wild bees (Collum et al., 2023). This trade-off increases perceived risk, leading many growers to rent honey bee colonies as a way to regain control and reduce uncertainty. The decline in the use of alfalfa leafcutter bees in Maine is an example of risk-driven decision-making. Although widely used in the 1990s and 2000s, their high maintenance demands led growers to reduce their use in favor of lower-risk alternatives such as honey bees (Collum et al., 2023). Rose et al. (2013) further demonstrated that conventional growers tend to operate larger fields, deploy higher colony densities per field, and have more capital to invest in managed pollination. As a result, they are less likely to use alternative pollinators such as bumble bees. In contrast, organic and integrated pest management (IPM) growers are more open to using alternative pollinators or maintaining their own colonies.

Perceptions of wild bees are generally positive, with multiple studies highlighting their importance (Collum et al., 2023; Hanes et al., 2013, 2018). Hanes et al. (2013) found that 88% of growers implement at least one pollinator conservation measure, typically those requiring minimal labor. However, wild pollinators are often seen as unreliable, leading many growers to rely on managed bees as a way to eliminate risk (Hanes et al., 2013). At the same time, wild bees are sometimes viewed as an insurance policy in case weather conditions negatively affect managed pollinators (Hanes et al., 2013). Nonetheless, growers struggle to identify wild pollinators, rarely conduct rigorous monitoring (Hanes et al., 2018), and remain uncertain about the actual contribution of wild bees to pollination services (Hanes et al., 2013). The third cognitive domain, uncertainty, ultimately drives pollination management decisions. Growers seek to minimize risk, ensuring higher yields and prices while maintaining control over their farms (Collum et al., 2023). This finding is crucial because it shifts the perspective on pollinator conservation and managed colony use. Hanes et al. (2018) demonstrated that pollinator conservation is not inherent in growers’ management strategies, which slows its adoption. Growers question why they should invest time and money into something uncertain (Hanes et al., 2013). Therefore, conservation programs that emphasize wild bees’ role in mitigating uncertainty and reducing risk, along with time- and labor-efficient strategies, could encourage broader adoption.

Conclusion

This review examines the various challenges and concerns associated with lowbush blueberry pollination. It highlights the challenges in blueberry pollination and identifies current research gaps that need to be addressed to understand the subject better. Despite the recent growth of research in Canada and the USA, there is still a gap in understanding the pollination of this berry. One of the significant challenges in lowbush blueberry pollination is its substantial reliance on insect pollinators (Drummond, 2019b; Gagnon et al., 2011). Approximately 74% of visits to lowbush blueberry flowers are made by Hymenoptera insects, primarily bees (moisan-De Serres et al., 2014). Thus, the global decline of bee populations is a pressing issue that significantly affects blueberry production.

Numerous studies have identified key problems faced by bees in agricultural landscapes. In this review, we have identified extensive monocultures as a factor of pressure on bees. This is due to the landscape modifications and reduction of resource availability. Landscapes surrounding blueberry fields influence the diversity and abundance of pollinator species by providing nesting sites and floral resources Dufour et al. (2020); Koh et al. (2016); moisan-De Serres (2013); Sánchez-Bayo and Wyckhuys (2019) (St Clair et al., 2020).; Another critical issue arising from lowbush blueberry monoculture is the limited availability of foraging resources, which fluctuates annually and varies between fields based on the surrounding landscape. This limitation could lead to nutritional deficiencies in pollinators (Dufour et al., 2020, 2020b). While these deficiencies have been primarily studied in honey bees, their impact on other commercial and wild pollinators remains less understood. This review briefly explored current alternatives for increasing floral diversity and availability. Future research should focus on strategies to enhance floral resources while minimizing competition with blueberry flowers for pollinators and reaching the desired fruit set. It also highlighted the lack of knowledge regarding resource competition between commercial and wild pollinators in blueberry fields. Thus, future research should investigate this topic further.

Moreover, pesticide use poses additional risks to pollinators (Choate and Drummond, 2013; Drummond, 2022; Gradish et al., 2012; Gradish et al., 2012). Although some studies have evaluated pesticide residues in commercial pollinators such as honey bees, bumble bees, and leafcutter bees, there is little data on wild pollinators in lowbush blueberry fields. Additionally, more research should focus on pesticide decay rate models, as these could help growers better time pesticide applications to reduce bees' exposure risk (Averill et al., 2024).

The potential decline of wild pollinators and the increasing use of commercial pollinators is one of the most significant challenges found for lowbush blueberry pollination in this review. The potential decline of wild pollinators, combined with the large-scale nature of blueberry farms, and growers intention to minimize risks, ensure higher yields and prices, and maintain control over their production, has resulted in a greater reliance on commercial colonies, with honey bees being the most significant commercial pollinator (Bushmann and Drummond, 2020; Collum et al., 2023; Hanes et al., 2013). This review underscored their advantages and disadvantages in terms of pollination efficiency. In recent years, high winter mortality rates have been recorded in honey bee colonies. Additionally, rising production costs for beekeepers have increased colony rental prices, posing a financial risk for blueberry production (Asare et al., 2017; Hanes et al., 2013). Consequently, there has been a growing interest in using other pollinator species, particularly bumble bees. This review discusses the challenges and risks associated with introducing bumble bees, which currently lack specific legislation. Unfortunately, there is limited information on the risks of using bumble bees in lowbush blueberry farming. Similarly, the impact of commercial pollinators like *Megachile rotundata* on blueberries is entirely unknown. Therefore, we suggest further research on this subject.

Commercial pollination presents additional challenges, such as determining the required densities of commercial pollinators. This variable is difficult to standardize due to regional differences and factors such as the genetic variability inside blueberry fields, the abundance of wild and commercial pollinators in specific fields, the use of different managed pollinators in the same fields, and local environmental conditions (Chagnon et al., 2015; Eaton and Nams, 2012; Gagnon et al., 2011; Rollin et al., 2019; Savard, 2014). Future research should evaluate these parameters at the landscape level.

Finally, this article emphasizes the importance of wild pollinators and suggests that future reviews should compile conservation strategies in the lowbush blueberry context. We also recommend conducting an international survey to determine if native bee decline has occurred in these landscapes. In this review, we also emphasized the economic significance of wild bees by presenting possible strategies and tools to improve their conservation in a financially viable manner. Additionally, this review highlights the importance of incorporating growers' perspectives when developing new conservation strategies, policies, or government programs to encourage wider adoption of these practices. It also emphasizes the need to create accessible and easy-to-understand extension materials to help reduce the existing gap in pollination-related resources for growers.

Acknowledgments

We extend our gratitude to Joseph Moisan-De Serres for his valuable assistance in identifying wild bee specimens. We also thank Pierre-Olivier Martel and Charles-Augustin Déry Bouchard for their technical support. Finally, we are grateful to Club Conseil Bleuet and the blueberry farmers who actively participated in the project and generously allowed us to use their fields. Disclosure of Generative Artificial Intelligence (AI) tools: Grammarly (14.1216.0) was used for language improvement. ChatGPT (4o) was used for language improvement and bibliography formatting.

Disclosure Statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Natural Sciences and Engineering Research Council of Canada (NSERC) under the Alliance Grant program (grant number ALLRP 561308–20);Project Apis m and Costco Wholesale Canada Ltd. (grant agreement number 321); the Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (MAPAQ); the Syndicat des producteurs de bleuets du Québec (SPBQ); the Apiculteurs et Apicultrices du Québec; the Canadian Honey Council; the ClubConseil Bleuet; Biobest; and the Centre de recherche en sciences animales deDeschambault (CRSAD).

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References

Aalders, L.E., and I.V. Hall. 1961. Pollen incompatibility and fruit set in lowbush blueberries. Can. J. Genet. Cytol. 3 (3):300–307. doi: 10.1139/g61-034.

Agriculture and Agri-Food Canada. 2017. Statistical overview of the Canadian honey and bee industry and the economic contribution of honey bee pollination 2016. https://publications.gc.ca/collections/collection_2018/aac-aafc/A71-43-2016-fra.pdf.

Agriculture and Agri-Food Canada. 2023. Statistical overview of the Canadian fruit industry 2022. https://agriculture.canada.ca/sites/default/files/documents/2023-06/FruitReport_2022-eng.pdf.

Agriculture and Agri-Food Canada. 2025. Crop profile for lowbush blueberry in Canada, 2023. https://publications.gc.ca/collections/collection_2025/aac-aafc/A118-10-31-2023-eng.pdf.

Agriculture, Aquaculture and Fisheries. 2010. Croissance et développement du bleuet sauvage. Feuillet de renseignements sur le bleuet sauvage. https://www2.gnb.ca/content/dam/gnb/Departments/10/pdf/Agriculture/WildBlueberries-BleuetsSauvages/a20F.pdf.

Agriculture, Aquaculture and Fisheries. 2024. New Brunswick wild blueberry pollination strategy 2024-2029. Executive Summary. https://www2.gnb.ca/content/dam/gnb/Departments/10/pdf/Agriculture/WildBlueberries-BleuetsSauvages/nb-wild-blueberry-pollination-strategy.pdf.

Aras, P., D. De Oliveira, and L. Savoie. 1996. Effect of a honey bee (Hymenoptera: Apidae) gradient on the pollination and yield of lowbush blueberry. J. Econ. Entomol. 89(5):1080–1083. doi: 10.1093/jee/89.5.1080.

Arrington, M., and L.W. DeVetter. 2018. Increasing honey bee hive densities promotes pollination and yield components of highbush blueberry in western Washington. HortScience. 53(2):191–194. doi: 10.21273/HORTSCI12644-17.

Asare, E., A.K. Hoshide, F. Drummond, G.K. Criner, and X. Chen. 2017. Economic risk of bee pollination in Maine wild blueberry, *vaccinium angustifolium*. J. Econ. Entomol. 110(5):1980–1992. doi: 10.1093/jee/tox191.

Austin, M.W., and A.S. Dunlap. 2019. Intraspecific variation in worker body size makes North American bumble bees (*bombus* spp.) less susceptible to decline. Am. Naturalist 194(3):381–394. doi: 10.1086/704280.

Averill, A.L., B.D. Eitzer, and F.A. Drummond. 2024. Pesticide contamination in native North American crops, part I—development of a baseline and comparison of honey bee exposure to residues in lowbush blueberry and cranberry. Insects 15(7):489. doi: 10.3390/insects15070489.

Bajcz, A.W., and F. Drummond. 2017. Flower power: Floral and resource manipulations reveal how and why reproductive trade-offs occur for lowbush blueberry (*vaccinium angustifolium*). Ecol. Evol. 7(15):5645–5659. doi: 10.1002/ece3.3109.

Balfour, N.J., M. Garbuzov, and F.L.W. Ratnieks. 2013. Longer tongues and swifter handling: Why do more bumble bees (*Bombus* spp.) than honey bees (*Apis mellifera*) forage on lavender (*Lavandula* spp.)? Ecol. Entomol 38(4):323–329. doi: 10.1111/een.12019.

Barai, K., L. Calderwood, M. Wallhead, H. Vanhanen, B. Hall, F. Drummond, and Y.J. Zhang. 2022. High variation in yield among wild blueberry genotypes: Can yield be predicted by leaf and stem functional traits? Agronomy 12(3):617. doi: 10.3390/agronomy12030617.

Bartomeus, I., J.S. Ascher, D. Wagner, B.N. Danforth, S. Colla, S. Kornbluth, and R. Winfree. 2011. Climate-associated phenological advances in bee pollinators and bee-pollinated plants. Proc. Natl. Acad. Sci 108(51):20645–20649. doi: 10.1073/pnas.1115559108.

Beers, L., L. Rowland, and F. Drummond. 2019. Genetic diversity of lowbush blueberry throughout the United States in managed and non-managed populations. Agriculture 9(6):113. doi: 10.3390/agriculture9060113.

Bell, D., F. Drummond, and L. Rowland. 2012. Evidence of functional gender polymorphisms in a population of the hermaphroditic lowbush blueberry (*Vaccinium angustifolium*) 1 this article is part of a special issue entitled "A tribute to Sam Vander Kloet FLS: Pure and applied research from blueberries to heathland ecology". Botany 90(5):393–399. doi: 10.1139/b11-064.

Bell, D., L. Rowland, J. Stommel, and F. Drummond. 2010. Yield variation among clones of lowbush blueberry as a function of genetic similarity and self-compatibility. J. Amer. Soc. Hort. Sci 135(3):259–270. doi: 10.21273/JASHS.135.3.259.

Bell, D., L. Rowland, D. Zhang, and F. Drummond. 2009. Spatial genetic structure of lowbush blueberry, *vaccinium angustifolium*, in four fields in Maine. Botany 87(10):932–946. doi: 10.1139/B09-058.

Benjamin, F.E., and R. Winfree. 2014. Lack of pollinators limits fruit production in commercial blueberry (*vaccinium corymbosum*). Environ. Entomol. 43(6):1574–1583. doi: 10.1603/EN13314.

Biesmeijer, J.C., S.P.M. Roberts, M. Reemer, R. Ohlemüller, M. Edwards, T. Peeters, A.P. Schaffers, S.G. Potts, R. Kleukers, C.D. Thomas, et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313(5785):351–354. doi: 10.1126/science.1127863.

Blüthgen, N., and A.-M. Klein. 2011. Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. Basic Appl. Ecol. 12(4):282–291. doi: 10.1016/j.baae.2010.11.001.

Boucher, C., F. Desjardins, P. Giovenazzo, J. Marceau, A. Pettigrew, H. Tremblay, and N. Tremblay. 2013. Guide gestion optimale du rucher. 2nd ed. Québec, Québec, Canada: Centre de Référence en Agriculture et Agroalimentaire du Québec. https://www.craaq.qc.ca/Publications-du-CRAAQ/gestion-optimale-du-rucher-2e-edition/p/PAPI0103-PDF.

Boulanger, L.W., G.W. Wood, E.A. Osgood, and C.O. Dirks. 1967. Native bees associated with the low-bush blueberry in Maine and Eastern Canada. https://digitalcommons.library.umaine.edu/aes_techbulletin.

Bourgeois, G. 2006. Différentes abeilles butineuses pour la pollinisation du bleuet nain. https://www.agrireseau.net/apiculture/documents/64036/differentes-abeilles-butineuses-pour-la-pollinisation-du-bleuet-nain.

Brown, S., and J. Rains. 2006. Bumble bee (*bombus impatiens*) pollination of field crops in the state of California. Koppert Biol. Syst. https://www.cdfa.ca.gov/Plant/pe/InteriorExclusion/pdfs/CEQA_BumbleBee.pdf.

Brunner, F.S., P. Schmid-Hempel, and S.M. Barribeau. 2014. Protein-poor diet reduces host-specific immune gene expression in *Bombus terrestris*. Proc. R. Soc. B: Biol. Sci 281(1786):20140128. doi: 10.1098/rspb.2014.0128.

Buchmann, S. 1983. Buzz pollination in angiosperms. Floral Cues And Anim. Behav. 73–113. https://digitalcommons.usu.edu/bee_lab_bo/266.

Bushmann, S., and F. Drummond. 2015. Abundance and diversity of wild bees (Hymenoptera: Apoidea) found in lowbush blueberry growing regions of Downeast Maine. Environ. Entomol. 44(4):975–989. doi: 10.1093/ee/nvv082.

Bushmann, S., and F. Drummond. 2020. Analysis of pollination services provided by wild and managed bees (apoidea) in wild blueberry (*vaccinium angustifolium* Aiton) production in Maine, USA, with a literature review. Agronomy 10 (9):1413. doi: 10.3390/agronomy10091413.

Bushmann, S., F. Drummond, L. Beers, and E. Groden. 2012. Wild bumblebee (*Bombus*) diversity and *Nosema* (microsporidia: Nosematidae) infection levels associated with lowbush blueberry (*vaccinium angustifolium*) production and commercial bumblebee pollinators. Psyche: A J. Entomol. 2012(1):1–11. doi: 10.1155/2012/429398.

Calderwood, L., and D.E. Yarborough. 2023. Maine wild blueberry production statistics.

Cameron, S.A., J.D. Lozier, J.P. Strange, J.B. Koch, N. Cordes, L.F. Solter, and T.L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. USA 108(2):662–667. doi: 10.1073/pnas.1014743108.

Cameron, S.A., and B.M. Sadd. 2020. Global trends in bumble bee health. Annu. Rev. Entomol. 65(1):209–232. doi: 10.1146/annurev-ento-011118-111847.

Cane, J.H., and V.J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: Detection, evidence, and consequences. Conserv. Ecol. 5(1). doi: 10.5751/ES-00252-050101.

Chagnon, M., J. Gingras, and D. DeOliveira. 1993. Complementary aspects of strawberry pollination by honey and indigenous bees (hymenoptera). J. Econ. Entomol. 86(2):416–420. doi: 10.1093/jee/86.2.416.

Chagnon, M., A. Pettigrew, D. de Oliveira, and J. Marceau. 2015. Régie des ruches pour la pollinisation du bleuet nain. https://www.agrireseau.net/apiculture/documents/regie_polli_bleuet_marceau_chagnon.pdf.

Chen, Y.-Y., P. Pahadi, L. Calderwood, S. Annis, F. Drummond, and Y.-J. Zhang. 2022. Will climate warming alter biotic stresses in wild lowbush blueberries? Agronomy 12(2):371. doi: 10.3390/agronomy12020371.

Chiasson, G., and J. Argall. 1996. La pollinisation du bleuet sauvage. *Ministère de l'Agriculture et de l'Aménagement Rural Nouveau-Brunswick du N.-B.* https://www2.gnb.ca/content/gnb/fr/ministeres/10/agriculture/content/cultures/bleuets_sauvages/pollinisation.html.

Choate, B., and F. Drummond. 2013. The influence of insecticides and vegetation in structuring *formica* mound ant communities (Hymenoptera: Formicidae) in Maine lowbush blueberry. J. Econ. Entomol. 106(2):716–726. doi: 10.1603/EC12273.

Claing, G. 2019. Prévalence d'agents pathogènes de l'abeille domestique (*Apis mellifera*) au Québec et leur impact sur la mortalité hivernale. https://papyrus.bib.umontreal.ca/xmlui/bitstream/handle/1866/23145/Claing_Gabrielle_2019_memoire.pdf?sequence=4&isAllowed=y.

Cloutier, C., J.-F. Guay, W. Champagne-Cauchon, and V. Fournier. 2021. Overwintering survival of *drosophila suzukii* (diptera: Drosophilidae) in temperature regimes emulating partly protected winter conditions in a cold–temperate climate of Québec, Canada. Can. Entomol. 153(3):259–278. doi: 10.4039/tce.2021.6.

Cnaani, J., R. Schmid-Hempel, and J.O. Schmidt. 2002. Colony development, larval development and worker reproduction in *Bombus impatiens* Cresson. Ins. Soc 49(2):164–170. doi: 10.1007/s00040-002-8297-8.

Colla, S.R., M.C. Otterstatter, R.J. Gegear, and J.D. Thomson. 2006. Plight of the bumble bee: Pathogen spillover from commercial to wild populations. Biol. Conserv. 129(4):461–467. doi: 10.1016/j.biocon.2005.11.013.

Collum, K.K., S.P. Hanes, F. Drummond, and J.E. Leahy. 2023. "We're farmers, not beekeepers": A cultural model of pollination management among lowbush blueberry growers in the United States and Canada. Hum. Organ 82 (2):107–118. doi: 10.17730/1938-3525-82.2.107.

Colwell, M.J., G.R. Williams, R.C. Evans, and D. Shutler. 2017. Honey bee-collected pollen in agro-ecosystems reveals diet diversity, diet quality, and pesticide exposure. Ecol. Evol. 7(18):7243–7253. doi: 10.1002/ECE3.3178.

COSEWIC. 2023. Canadian wildlife species at risk. https://wildlife-species.az.ec.gc.ca/species-risk-registry/virtual_sara/files//species/CSAR%20EN%202023.pdf.

Council, N.R. 2006. Status of pollinators in North America. Natl. Academies Press 1–312. doi: 10.17226/11761.

Courcelles, D.M.M., L. Button, and E. Elle. 2013. Bee visit rates vary with floral morphology among highbush blueberry cultivars (V accinium corymbosum L.). J Appl. Entomol. 137(9):693–701. doi: 10.1111/jen.12059.

Couvillon, M.J., J.M. Jandt, N. Duong, and A. Dornhaus. 2010. Ontogeny of worker body size distribution in bumble bee (*bombus impatiens*) colonies. Ecol. Entomol 35(4):424–435. doi: 10.1111/j.1365-2311.2010.01198.x.

CRAAQ. 2018. Biologie de l'abeille (3e édition). https://www.craaq.qc.ca/Publications-du-CRAAQ/biologie-de-l_abeille-3e-edition/p/PAPI0106-PDF.

Crowl, A.A., P.W. Fritsch, G.P. Tiley, N.P. Lynch, T.G. Ranney, H. Ashrafi, and P.S. Manos. 2022. A first complete phylogenomic hypothesis for diploid blueberries (*vaccinium* section *Cyanococcus*). Am. J. Botany 109(10):1596–1606. doi: 10.1002/ajb2.16065.

Currie, R.W., S.F. Pernal, and E. Guzmán-Novoa. 2010. Honey bee colony losses in Canada. J. Apic. Res. 49(1):104–106. doi: 10.3896/IBRA.1.49.1.18.

Cutler, G.C., V.O. Nams, P. Craig, J.M. Sproule, and C.S. Sheffield. 2015. Wild bee pollinator communities of lowbush blueberry fields: Spatial and temporal trends. Basic Appl. Ecol. 16(1):73–85. doi: 10.1016/j.baae.2014.11.005.

Cutler, G.C., K.W. Reeh, J.M. Sproule, and K. Ramanaidu. 2012. Berry unexpected: Nocturnal pollination of lowbush blueberry. Can. J. Plant. Sci. 92(4):707–711. doi: 10.4141/cjps2012-026.

Decourtye, A., C. Vidau, O. Rollin, F. Requier, C. Rüger, F. Allier, V. le Féon, A. Kretzschmar, J. Devillers, M. Henry, et al. 2016. Fréquentation des cultures par les abeilles mellifères et sauvages : synthèse des connaissances pour réduire le risque d'intoxication aux pesticides. Cah. Agri. 25(4):44001. doi: 10.1051/cagri/2016025.

Dedej, S. 2004. University of Georgia. Bee foraging behavior and pollinating activity on rabbiteye blueberry vaccinium ashei reade. Doctoral Diss. https://getd.libs.uga.edu/pdfs/dedej_selim_200408_phd.pdf.

Desjardins, È.-C., and D. de Oliveira. 2006. Commercial bumble bee bombus impatiens (Hymenoptera: Apidae) as a pollinator in lowbush blueberry (Ericale: Ericaceae) fields. J. Econ. Entomol. 99(2):443–449. doi: 10.1093/jee/99.2.443.

DeVetter, L.W., S. Chabert, M.O. Milbrath, R.E. Mallinger, J. Walters, R. Isaacs, S.P. Galinato, C. Kogan, K. Brouwer, A. Melathopoulos, et al. 2022. Toward evidence-based decision support systems to optimize pollination and yields in highbush blueberry. Front. Sustain. Food Syst 6:1006201. doi: 10.3389/fsufs.2022.1006201.

Drummond, F. 2002a. Honey bees and blueberry pollination. Cooperative extension: Maine wild blueberries. Orono, Maine, USA: University of Maine Cooperative Extension. https://extension.umaine.edu/blueberries/factsheets/bees/629-honey-bees-and-blueberry-pollination/.

Drummond, F. 2002b. Replaces honey bees and blueberry pollination. https://www.maine.gov/dacf/php/apiary/documents/BlueberryPollination.pdf.

Drummond, F. 2012a. Commercial bumble bee pollination of Lowbush Blueberry. Int. J. Fruit. Sci. 12(1–3):54–64. doi: 10.1080/15538362.2011.619120.

Drummond, F. 2012b. Effect of imidacloprid on bumble bees, 2009. Arthropod Manag. Tests 37(1). doi: 10.4182/amt.2012.C8.

Drummond, F. 2016. Behavior of bees associated with the wild blueberry agro-ecosystem in the USA. Int. J. Entomol. Nematol 2(1):27–41. https://api.semanticscholar.org/CorpusID:55764525.

Drummond, F. 2019a. Factors that affect yield in wild blueberry, *vaccinium angustifolium* Aiton. Agric. Res. Technol. Open Access J 22(5). doi: 10.19080/ARTOAJ.2019.22.556212.

Drummond, F. 2019b. Reproductive biology of wild blueberry (*vaccinium angustifolium* Aiton). Agriculture 9(4):69. doi: 10.3390/agriculture9040069.

Drummond, F. 2020a. Estimating the strength of your pollinator force in wild blueberry. University of Maine, Cooperative Extension Wild Blueberries. https://extension.umaine.edu/blueberries/estimating-the-strength-of-your-pollinator-force-in-wild-blueberry/.

Drummond, F. 2020b. Wild blueberry fruit drop: A consequence of seed set? Agronomy 10(7):939. doi: 10.3390/agronomy10070939.

Drummond, F. 2022. Honey bee exposure to the fungicide propiconazole in lowbush blueberry fields. Agronomy 12 (12):3081. doi: 10.3390/agronomy12123081.

Drummond, F., A.L. Averill, and B.D. Eitzer. 2024. Pesticide contamination in native North American crops, part II—comparison of flower, honey bee workers, and native bee residues in lowbush blueberry. Insects 15(8):567. doi: 10.3390/insects15080567.

Drummond, F., E. Ballman, and J. Collins. 2017. Are they weeds or a life force? Or sustainability on the edge. Maine J. Conserv. Sustain. https://umaine.edu/spire/2017/05/04/drummond-et-al/.

Drummond, F., E. Ballman, and J. Collins. 2019. Population dynamics of spotted wing drosophila (drosophila suzukii (Matsumura)) in Maine wild blueberry (*vaccinium angustifolium* Aiton). Insects 10(7):205. doi: 10.3390/insects10070205.

Drummond, F., A.C. Dibble, C. Stubbs, S.L. Bushmann, J.S. Ascher, and J. Ryan. 2017. A natural history of change in native bees associated with lowbush blueberry in Maine. Northeast. Nat. (steuben). 24(m15):49–68. doi: 10.1656/045.024.m1502.

Drummond, F., and A.K. Hoshide. 2024. An economic cost/benefit tool to assess bee pollinator conservation, pollination strategies, and sustainable policies: A lowbush blueberry case study. Sustainability 16(8):3242. doi: 10.3390/su16083242.

Drummond, F., J. Lund, and B. Eitzer. 2021. Honey bee health in Maine wild blueberry production. Insects 12(6):523. doi: 10.3390/insects12060523.

Du Clos, B., F.A. Drummond, and C.S. Loftin. 2022. Effects of an early mass-flowering crop on wild bee communities and traits in power line corridors vary with blooming plants and landscape context. Landsc. Ecol 37(10):2619–2634. doi: 10.1007/s10980-022-01495-9.

Du Clos, B., F.A. Drummond, C.S. Loftin, and T. Pitts-Singer. 2020. Noncrop habitat use by wild bees (Hymenoptera: Apoidea) in a mixed-use agricultural landscape. Environ. Entomol. 49(2):502–515. doi: 10.1093/ee/nvaa001.

Dufour, C., V. Fournier, and P. Giovenazzo. 2020. Diversity and nutritional value of pollen harvested by honey bee (Hymenoptera: Apidae) colonies during lowbush blueberry and cranberry (ericaceae) pollination. Can. Entomol. 152 (5):622–645. doi: 10.4039/tce.2020.29.

Dufour, C., V. Fournier, P. Giovenazzo, and M.E. Saunders. 2020. The impact of lowbush blueberry (*Vaccinium angustifolium* Ait.) and cranberry (*Vaccinium macrocarpon* Ait.) pollination on honey bee (*Apis mellifera* L.) colony health status. PLOS ONE 15(1):e0227970. doi: 10.1371/journal.pone.0227970.

Dunford, N.T. 2022. Blueberries and health. Funct. Food Sci 2(1):1. doi: 10.31989/ffs.v2i1.875.

Eaton, L., R. Glen, and W. Doug. 2004. Efficient mowing for pruning wild blueberry fields. Small Fruits Rev. 3 (1–2):123–131. doi: 10.1300/J301v03n01_12.

Eaton, L., K. MacKenzie, D. McIsaac, and J. Murray. 2004. Pollinating wild lowbush blueberries in Nova Scotia. Lowbush Blueberry Fact Sheet. https://cdn.dal.ca/content/dam/dalhousie/images/sites/wild-blueberry/pdfs/Pollination_Lowbush_Blueberry_NS.pdf.

Eaton, L., and V. Nams. 2012. Honey bee stocking numbers and wild blueberry production in Nova Scotia. Can. J. Plant. Sci. 92(7):1305–1310. doi: 10.4141/cjps2012-045.

Evans, E., R. Thorp, S. Jepsen, and S. Hoffman Black. 2008. Status review of three formerly common species of bumble bee in the subgenus *bombus*. https://www.xerces.org/sites/default/files/2019-10/xerces_2008_bombus_status_review.pdf.

Ferland, J., M. Kempers, K. Kennedy, P. Kozak, R. Lafrenière, C. Maund, C. Menzies, C. Mesher, S. Muirhead, M. Nasr, et al. 2022. Statement on honey bee wintering losses in Canada. https://honeycouncil.ca/wp-content/uploads/2022/08/CAPA-Statement-on-Colony-Losses-2021-2022-FV.pdf.

Forget, A., and L.-M. Turcotte. 1997. Histoire de l'apiculture québécoise. Abbaye cistercienne d'Oka. https://www.apicentris.org/_files/ugd/c4d505_29420dbf653646a69f062e2de88546a1.pdf.

Forney, C.F., S. Qiu, M.A. Jordan, D. McCarthy, and S. Fillmore. 2022. Comparison of volatile compounds contributing to flavor of wild lowbush (*vaccinium augustifolium*) and cultivated highbush (*vaccinium corymbosum*) blueberry fruit using gas chromatography-olfactometry. Foods 11(16):2516. doi: 10.3390/foods11162516.

Fukuda, H. 1983. The relationship between work efficiency and population size in a honeybee colony. Popul Ecol. 25 (2):249–263. doi: 10.1007/BF02515602.

Fulton, M., L.K. Jesson, K. Bobiwash, and D.J. Schoen. 2015. Mitigation of pollen limitation in the lowbush blueberry agroecosystem: Effect of augmenting natural pollinators. Ecosphere 6(11):1–19. doi: 10.1890/ES15-00148.1.

Gagnon, S., M. Chagnon, G. Chiasson, È.-C. Desjardins, and L. Tremblay. 2011. La production du bleuet sauvage dans une perspective de développement durable. La pollinisation du bleuetier. Guide de production du bleuet sauvage. https://www.agrireseau.net/documents/80039/guide-de-production-du-bleuet-sauvage.

Gailīte, A., A. Gaile, and D. Ruņģis. 2020. Genetic diversity and structure of wild *vaccinium* populations - *V. myrtillus*, *V. vitis-idaea* and *V. uliginosum* in the Baltic States. Silva Fenn. 54(5):1–20. doi: 10.14214/sf.10396.

Garibaldi, L.A., I. Steffan-Dewenter, R. Winfree, M.A. Aizen, R. Bommarco, S.A. Cunningham, C. Kremen, L. G. Carvalheiro, L.D. Harder, O. Afik, et al. 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339(6127):1608–1611. doi: 10.1126/science.1230200.

Gekière, A., J. Habay, and D. Michez. 2022. Monitoring of parasites in bumblebee colonies developed from controlled nesting of wild queens (Hymenoptera: Apidae: *Bombus*). OSMIA 10:45–54. doi: 10.47446/OSMIA10.5.

Gisder, S., and E. Genersch. 2017. Viruses of commercialized insect pollinators. J. Invertebr. Pathol. 147:51–59. doi: 10.1016/J.JIP.2016.07.010.

Glass, V.M., D.C. Percival, and J.T.A. Proctor. 2005. Tolerance of lowbush blueberries (*vaccinium angustifolium* Ait.) to drought stress. I. Soil water and yield component analysis. Can. J. Plant. Sci. 85(4):911–917. doi: 10.4141/P03-027.

Goulson, D. 2003. Effects of introduced bees on native ecosystems. Annu. Rev. Ecol. Evol. Syst. 34(1):1–26. doi: 10.1146/annurev.ecolsys.34.011802.132355.

Goulson, D. 2010. Bumblebees: Behaviour, ecology, and conservation. Oxford University Press. https://www.semanticscholar.org/paper/Bumblebees%3A-Behaviour%2C-Ecology%2C-and-Conservation-Goulson/8ca79ee0c8dcfb2d642a279f928450309e27c8b5.

Goulson, D., and W.O.H. Hughes. 2015. Mitigating the anthropogenic spread of bee parasites to protect wild pollinators. Biol. Conserv. 191:10–19. doi: 10.1016/j.biocon.2015.06.023.

Goulson, D., E. Nicholls, C. Botías, and E.L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347(6229). doi: 10.1126/science.1255957.

Government of Canada. 2022. Apiculture au Québec en chiffres. https://www.quebec.ca/agriculture-environnement-et-ressources-naturelles/agriculture/industrie-agricole-au-quebec/productions-agricoles/elevage-abeilles-miel-apiculture#:~:text=Apiculture%20au%20Qu%C3%A9bec%20en%20chiffres,entreprises%20(donn%C3%A9es%20de%202018).

Gradish, A.E., C.D. Scott-Dupree, and C.G. Cutler. 2012. Susceptibility of *megachile rotundata* to insecticides used in wild blueberry production in Atlantic Canada. J. Pest Sci. 85(1):133–140. doi: 10.1007/s10340-011-0391-0.

Gradish, A.E., C.D. Scott-Dupree, A.J. Frewin, and C.G. Cutler. 2012. Lethal and sublethal effects of some insecticides recommended for wild blueberry on the pollinator *bombus impatiens*. Can. Entomol. 144(3):478–486. doi: 10.4039/tce.2012.40.

Grant, K.J., L. DeVetter, and A. Melathopoulos. 2021. Honey bee (*apis mellifera*) colony strength and its effects on pollination and yield in highbush blueberries (*vaccinium corymbosum*). PeerJ 9:e11634. doi: 10.7717/peerj.11634.

Graystock, P., D. Goulson, and W.O.H. Hughes. 2015. Parasites in bloom: Flowers aid dispersal and transmission of pollinator parasites within and between bee species. Proc. R. Soc. B 282(1813):20151371. doi: 10.1098/rspb.2015.1371.

Groff, S.C., C.S. Loftin, F. Drummond, S. Bushmann, and B. McGill. 2016. Parameterization of the InVEST crop pollination Model to spatially predict abundance of wild blueberry (*vaccinium angustifolium* Aiton) native bee pollinators in Maine, USA. Environ. Modell. Softw. 79:1–9. doi: 10.1016/j.envsoft.2016.01.003.

Gumbrewicz, R., and L. Calderwood. 2022. Comparison of wood mulch particle sizes for wild blueberry management in a changing climate. Int. J. Fruit. Sci. 22(1):551–567. doi: 10.1080/15538362.2022.2070577.

Gurel, F., and R. Sakli. 2021. Assessing the reproductive performance of commercial *bombus terrestris dalmatinus* colonies in different conditions and some practical ways to mitigate its invasive risk. Apidologie 52(4):792–800. doi: 10.1007/s13592-021-00865-7.

Hall, I.V., L.E. Aalders, and K.B. McRae. 1982. Lowbush blueberry production in eastern Canada as related to certain weather data. Can. J. Plant. Sci. 62(3):809–812. doi: 10.4141/cjps82-120.

Hall, I.V., D.L. Craig, and R.A. Lawrence. 1983. A comparison of hand raking and Mechanical harvesting of lowbush blueberries. Can. J. Plant. Sci. 63(4):951–954. doi: 10.4141/cjps83-119.

Hanes, S.P., K.K. Collum, A.K. Hoshide, and E. Asare. 2013. Grower perceptions of native pollinators and pollination strategies in the lowbush blueberry industry. Renew. Agric. Food Syst 30(2):124–131. doi: 10.1017/S1742170513000331.

Hanes, S.P., A. Drummond, F. Hoshide, and A. Hoshide. 2018. Assessing wild pollinators in conventional agriculture: A case study from Maine's blueberry industry. HER 24(1). https://www.jstor.org/stable/26506663.

Hefetz, A., and C.M. Grozinger. 2017. Hormonal regulation of behavioral and phenotypic plasticity in bumblebees. Horm. Brain. Behav 2:453–464. doi: 10.1016/B978-0-12-803592-4.00040-7.

Helm, B.R., S. Payne, J.P. Rinehart, G.D. Yocum, J.H. Bowsher, and K.J. Greenlee. 2018. Micro-computed tomography of pupal metamorphosis in the solitary bee *megachile rotundata*. Arthropod Struct. Dev 47(5):521–528. doi: 10.1016/j.asd.2018.05.001.

Hicks, B.J. 2011. Pollination of lowbush blueberry (*vaccinium angustifolium*) in Newfoundland by native and introduced bees. J. Acadian Entomol. Soc 7. https://www.acadianes.org/journal/papers/hicks_11-11.pdf.

Hicks, B.J., B.L. Pilgrim, E. Perry, and H.D. Marshall. 2018. Observations of native bumble bees inside of commercial colonies of *bombus impatiens* (Hymenoptera: Apidae) and the potential for pathogen spillover. Can. Entomol. 150 (4):520–531. doi: 10.4039/TCE.2018.28.

Hoehn, P., T. Tscharntke, J.M. Tylianakis, and I. Steffan-Dewenter. 2008. Functional group diversity of bee pollinators increases crop yield. Proc. R. Soc. B 275(1648):2283–2291. doi: 10.1098/rspb.2008.0405.

Hoffman, G.D., C. Lande, and S. Rao. 2018. A novel pollen transfer mechanism by honey bee foragers on highbush blueberry (Ericales: Ericaceae). Environ. Entomol. 47(6):1465–1470. doi: 10.1093/ee/nvy162.

Hokanson, K., and J. Hancock. 2000. Early-acting inbreeding depression in three species of *vaccinium* (ericaceae). Sex. Plant Reprod. 13(3):145–150. doi: 10.1007/s004970000046.

Holman, L. 2014. Bumblebee size polymorphism and worker response to queen pheromone. PeerJ 2(1):e604. doi: 10.7717/peerj.604.

Hoshide, A.K., F.A. Drummond, T.H. Stevens, E.M. Venturini, S.P. Hanes, M.M. Sylvia, C.S. Loftin, D.E. Yarborough, and A.L. Averill. 2018. What is the value of wild bee pollination for wild blueberries and cranberries, and who values it? Environments 5(9):98. doi: 10.3390/environments5090098.

Huber, G. 2016. University of British Columbia. An investigation of highbush blueberry floral biology and reproductive success in British Columbia. Doctoral Diss. doi: 10.14288/1.0300154.

IBO. 2023. Global state of the blueberry industry report. https://www.internationalblueberry.org/2023-report/.

Irwin, R.E., J.L. Bronstein, J.S. Manson, and L. Richardson. 2010. Nectar robbing: Ecological and evolutionary perspectives. Annu. Rev. Ecol. Evol. Syst. 41(1):271–292. doi: 10.1146/annurev.ecolsys.110308.120330.

Isaacs, R., J. Gibbs, E. May, E. Hanson, and J. Hancock. 2016. Invest in pollination for success with highbush blueberries. Michigan State University Extension. https://extension.msu.edu/experts.

ISQ. 2021. Faits saillants de l'enquête sur l'apiculture au Québec. Enquête. https://statistique.quebec.ca/fr/fichier/faits-saillants-de-lenquete-sur-lapiculture-au-quebec-enquete-2020.pdf.

ISQ. 2024. Statistiques relatives à la location de colonies à des fins de pollinisation selon le type de culture, Québec. https://statistique.quebec.ca/fr/produit/tableau/925.

Jacobson, M.M., E.M. Tucker, M.E. Mathiasson, and S.M. Rehan. 2018. Decline of bumble bees in northeastern North America, with special focus on *bombus terricola*. Biol. Conserv. 217:437–445. doi: 10.1016/j.biocon.2017.11.026.

Javorek, S.K., K.E. Mackenzie, and S.P. Vander Kloet. 2002. Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (ericaceae: *Vaccinium angustifolium*). Ann. Entomol. Soc. Am. 95 (3):345–351. doi: 10.1603/0013-8746(2002)095[0345:CPEABH]2.0.CO;2.

Jensen, K.I.N., and D.E. Yarborough. 2004. An overview of weed management in the wild lowbush blueberry - past and present. Small Fruits Rev. 3(3–4):229–255. doi: 10.1300/J301v03n03_02.

Jesson, L., D. Schoen, C. Cutler, and S. Bates. 2014. La pollinisation du bleuet nain. Synthèse des résultats de recherche de l'Initiative canadienne de pollinisation. https://www.uoguelph.ca/canpolin/New/Blueberry%20booklet%20FINAL%20French%20high%20res.pdf.

Kalt, W., A. Cassidy, L.R. Howard, R. Krikorian, A.J. Stull, F. Tremblay, and R. Zamora-Ros. 2020. Recent research on the health benefits of blueberries and their anthocyanins. Adv. Nutr. 11(2):224–236. doi: 10.1093/advances/nmz065 .

Klein, S., A. Cabirol, J.M. Devaud, A.B. Barron, and M. Lihoreau. 2017. Why bees are so vulnerable to environmental stressors. Trends Ecol. Evol. 32:268–278. doi: 10.1016/j.tree.2016.12.009.

Koh, I., E.V. Lonsdorf, N.M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T.H. Ricketts. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl. Acad. Sci. USA. 113(1):140–145. doi: 10.1073/pnas.1517685113.

Krupke, C.H., G. Hunt, and R.E. Foster. 2021. Protecting honey bees from pesticides. Purdue. Ext. https://extension.entm.purdue.edu/publications/E-53/E-53.html.

Laverty, T.M., and L. Harder. 1988. The bumble bees of eastern Canada. Can. Entomol. 120(11):965–987. doi: 10.4039/Ent120965-11.

MacKenzie, K., D. Rogers, and S. Javorek. 1997. The alfalfa leafcutting bee, *megachile rotundata* fabr.: An alternative managed pollinator of lowbush blueberry. Acta. Hortic 446(446):87–90. doi: 10.17660/ActaHortic.1997.446.11.

Madrid, M., and R. Beaudry. 2020. Small fruits: Raspberries, blackberries, blueberries. In Controlled and modified atmospheres for fresh and fresh-cut produce, eds. M.I. Gil and R., Beaudry, 335–346. Cambridge, Massachusetts, USA: Elsevier. doi: 10.1016/B978-0-12-804599-2.00020-X.

Major, C. 2021. Exploring the opportunities and constraints to the success of Newfoundland's wild lowbush blueberry (*vaccinium angustifolium* Aiton) industry. Guelph, Ontario, Canada: University of Guelph. https://atrium.lib.uoguelph.ca/server/api/core/bitstreams/1f4d8d94-7491-47ee-8e5f-42cc728b194f/content.

Mallinger, R.E., H.R. Gaines-Day, C. Gratton, and N.E. Raine. 2017. Do managed bees have negative effects on wild bees? A systematic review of the literature. PLOS ONE 12(12):e0189268. doi: 10.1371/journal.pone.0189268.

Manning, P., and C.G. Cutler. 2013. Potential nocturnal insect pollinators of lowbush blueberry. https://www.researchgate.net/publication/264309290.

MAPAQ. 2018. Portrait-diagnostic sectoriel de l'apiculture au Québec. https://www.mapaq.gouv.qc.ca/fr/Publications/Portrait_Diagnostic_sectoriel_Apiculture_complet.pdf.

MAPAQ. 2022. Portrait-diagnostic sectoriel de l'industrie du bleuet sauvage au Québec. https://www.mapaq.gouv.qc.ca/fr/Publications/Monographiebleuet.pdf.

Maucourt, S., V. Fournier, and P. Giovenazzo. 2017. Comparison of three methods to multiply honey bee (*apis mellifera*) colonies. Apidologie 49(3):314–324. doi: 10.1007/s13592-017-0556-9.

McGregor, S.E. 1976. Insect pollination of cultivated crop plants. In Agricultural research service, 411. Washington, DC, USA: US Department of Agriculture. https://www.ars.usda.gov/arsuserfiles/20220500/onlinepollinationhandbook.pdf.

McKechnie, I.M., C.J.M. Thomsen, and R.D. Sargent. 2017. Forested field edges support a greater diversity of wild pollinators in lowbush blueberry (*vaccinium angustifolium)*. Agric. Ecosyst. Environ. 237:154–161. doi: 10.1016/j.agee.2016.12.005.

Meeus, I., M.J.F. Brown, D.C. De Graaf, and G. Smagghe. 2011. Effects of invasive parasites on bumble bee declines. Conserv. Biol. 25(4):662–671. doi: 10.1111/j.1523-1739.2011.01707.x.

Michener, C.D. 2007. The bees of the world. 2nd ed. The Johns Hopkins University Press, Baltimore.

Miller, O., C. Hale, L. Richardson, D. Sossa, A. Iverson, S. McArt, K. Poveda, and H. Grab. 2023. Commercial *bombus impatiens* colonies function as ecological traps for wild queens. J. Appl. Ecol 60(4):592–600. doi: 10.1111/1365-2664.14353.

moisan-De Serres, J. 2013. Influence du paysage de bleuetières sur les communautés de pollinisateurs indigènes du Lac-St-Jean et évaluation du potentiel de pollinisation des pollinisateurs du bleuet nain. http://hdl.handle.net/20.500.11794/24158.

moisan-De Serres, J., M. Chagnon, and V. Fournier. 2014. Influence of windbreaks and forest borders on abundance and species richness of native pollinators in lowbush blueberry fields in Québec, Canada. Can. Entomol. 147(4):432–442. doi: 10.4039/tce.2014.55.

moisan-De Serres, J., M. Girard, M. Chagnon, and V. Fournier. 2014. Pollen loads and specificity of native pollinators of lowbush blueberry. J. Econ. Entomol. 107(3):1156–1162. doi: 10.1603/EC13229.

Morrissette, R., A. Francoeur, and J.M. Perron. 1985. Importance des abeilles sauvages (Apoidea) dans la pollinisation des bleuetiers nains (*Vaccinium* spp.) en Sagamie, Québec. Rev. Entomol. Québec 30(1–2):44–53. http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=7429441.

Morvan, S., M.C. Paré, A. Schmitt, J. Lafond, and M. Hijri. 2022. Limited effect of thermal pruning on wild blueberry crop and its root-associated microbiota. Front Plant. Sci. 13:954935. doi: 10.3389/fpls.2022.954935.

Myra, M., K. Mackenzie, and S.P. Vander Kloet. 2004. Investigation of a possible sexual function specialization in the Lowbush Blueberry (*vaccinium angustifolium* Aiton. Ericaceae). Small Fruits Rev. 3(3–4):313–324. doi: 10.1300/J301v03n03_08.

Native Plant Trust. 2022. *Vaccinium myrtilloides* (velvet-leaved blueberry): Go botany. 25 Jul. 2022. https://gobotany.nativeplanttrust.org/species/vaccinium/myrtilloides/.

Noone, R.E., S.M. Doucet, P.L. Jones, and B. Beres. 2022. Pollination ecology of lowbush blueberry (*vaccinium angustifolium* Aiton) in an island ecosystem. Can. J. Plant. Sci. 102(3):710–721. doi: 10.1139/cjps-2021-0216.

Olmstead, S., and R. McCallum. 2019. Gestion des ruches d'abeilles domestiques pour la pollinisation des bleuets sauvages. Fredericton, Nouveau-Brunswick, Canada: Ministère de l'Agriculture, de l'Aquaculture et des Pêches, Gouvernement du Nouveau-Brunswick. https://www2.gnb.ca/content/dam/gnb/Departments/10/pdf/Agriculture/Beekeeping-Apiculteurs/gestion-B.3.0.pdf.

Palmier, K., and C. Sheffield. 2019. First records of the common eastern bumble bee, *bombus impatiens* Cresson (Hymenoptera: Apidae, apinae, Bombini) from the Prairies Ecozone in Canada. Biodivers. Data J. 7:e30953. doi: 10.3897/BDJ.7.e30953.

Peat, J., B. Darvill, J. Ellis, and D. Goulson. 2005. Effects of climate on intra- and interspecific size variation in bumble-bees. Funct. Ecol 19(1):145–151. doi: 10.1111/j.0269-8463.2005.00946.x.

Pitts-Singer, T.L., and J.H. Cane. 2011. The alfalfa leafcutting bee, *megachile rotundata*: The world's most intensively managed solitary bee. Annu. Rev. Entomol. 56(1):221–237. doi: 10.1146/annurev-ento-120709-144836.

Proctor, M., P. Yeo, and A. Lack. 1973. The natural history of pollination.

Province du Nouveau-Brunswick. 2018. Stratégie du Nouveau-Brunswick en matière de production du bleuet sauvage 2013–2018. https://www2.gnb.ca/content/dam/gnb/Departments/10/pdf/Agriculture/WildBlueberries-BleuetsSauvages/StrategieBleuetSauvage.pdf.

Pyke, G.H., J.D. Thomson, D.W. Inouye, T.J. Miller, and D.P.C. Peters. 2016. Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. Ecosphere 7(3). doi: 10.1002/ECS2.1267.

Rodriguez-Mateos, A., T. Cifuentes-Gomez, S. Tabatabaee, C. Lecras, and J.P.E. Spencer. 2012. ProcyanidProcyanidIn, anthocyanin, and chlorogenic acid contents of highbush and Lowbush Blueberries. J. Agric. Food Chem. 60 (23):5772–5778. doi: 10.1021/jf203812w.

Rollin, O., L.A. Garibaldi, and T. Diekötter. 2019. Impacts of honeybee density on crop yield: A meta-analysis. J. Appl. Ecol 56(5):1152–1163. doi: 10.1111/1365-2664.13355.

Rose, A., F.A. Drummond, D.E. Yarborough, and E. Asare. 2013. Maine wild blueberry growers: A 2010 economic and sociological analysis of a traditional downeast crop in transition. Maine Agric. Exp. Station 445. https://digitalcommons.library.umaine.edu/cgi/viewcontent.cgi?article=1017&context=aes_miscreports.

Sachman-Ruiz, B., V. Narváez-Padilla, and E. Reynaud. 2015. Commercial *bombus impatiens* as reservoirs of emerging infectious diseases in central México. Biol. Invasions 17(7):2043–2053. doi: 10.1007/s10530-015-0859-6.

Sampson, B.J., R.G. Danka, and S.J. Stringer. 2004. Nectar robbery by bees *xylocopa virginica* and *apis mellifera* contributes to the pollination of Rabbiteye Blueberry. J. Econ. Entomol. 97(3):735–740. doi: 10.1603/0022-0493(2004)097[0735:NRBBXV]2.0.CO;2.

Sánchez-Bayo, F., D. Goulson, F. Pennacchio, F. Nazzi, K. Goka, and N. Desneux. 2016. Are bee diseases linked to pesticides? – A brief review. Environ. Int 89-90:7–11. doi: 10.1016/j.envint.2016.01.009.

Sánchez-Bayo, F., and K.A.G. Wyckhuys. 2019. Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232:8–27. doi: 10.1016/j.biocon.2019.01.020.

Savard, J. 2014. La pollinisation des bleuetières. Bull. www.agrireseau.qc.ca/rap.

Sgolastra, F., S. Hinarejos, T.L. Pitts-Singer, N.K. Boyle, T. Joseph, J. Lūckmann, N.E. Raine, R. Singh, N.M. Williams, and J. Bosch. 2019. Pesticide exposure assessment paradigm for solitary bees. Environ. Entomol. 48(1):22–35. doi: 10.1093/ee/nvy105.

Sheffield, C.S. 2008. Summer bees for spring crops? Potential problems with *megachile rotundata* (fab.) (Hymenoptera: Megachilidae) as a pollinator of lowbush blueberry (ericaceae). J. Kans. Entomol. Soc 81(3):276–287. doi: 10.2317/JKES-710.23.1.

Soroye, P., T. Newbold, and J. Kerr. 2020. Climate change contributes to widespread declines among bumble bees across continents. Science 367(6478):685–688. doi: 10.1126/science.aax8591.

Statistics Canada. 2024. Fruit and vegetable production, 2023. https://www150.statcan.gc.ca/n1/daily-quotidien/240216/dq240216d-eng.htm.

St Clair, A.L., G. Zhang, A.G. Dolezal, M.E. O, A.L. Toth, and G. DeGrandi-Hoffman. 2020. Diversified farming in a monoculture landscape: Effects on honey bee health and wild bee communities. Pollinator Ecol. Manag 49 (3):753–764. doi: 10.1093/ee/nvaa031.

Stevens, T., A.K. Hoshide, and F. Drummond. 2015. Willingness to pay for native pollination of blueberries: A conjoint analysis. Int. J. Agric. Mark 2(4):068–077. https://www.researchgate.net/publication/281414018_Willingness_to_pay_for_native_pollination_of_blueberries_A_conjoint_analysis.

Strange, J., S. Colla, L. Davies Adams, M. Duennes, E. Evans, L. Figueroa, D. Lehmann, H. Moylett, L. Richardson, B. Sadd, et al. 2023. An evidence-based rationale for a North American commercial bumble bee clean stock certification program. J. Pollinat. Ecol 33:1–13. doi: 10.26786/1920-7603(2023)721.

Strik, B.C., and D. Yarborough. 2005. Blueberry production trends in North America, 1992 to 2003, and predictions for growth. Horttechnology. 15(2):391–398. doi: 10.21273/HORTTECH.15.2.0391.

Stubbs, C., and F. Drummond. 1997a. Management of the alfalfa leafcutting bee, *megachile rotundata* (Hymenoptera: Megachilidae), for pollination of wild lowbush blueberry. J. Kans. Entomol. Soc 70(2). http://www.jstor.org/stable/25085759.

Stubbs, C., and F. Drummond. 1997b. POLLINATION OF WILD LOWBUSH BLUEBERRY, VACCINIUM ANGUSTIFOLIUM BY THE ALFALFA LEAFCUTTING BEE, MEGACHILE ROTUNDATA. Acta. Hortic 446 (446):189–196. doi: 10.17660/ActaHortic.1997.446.28.

Stubbs, C., and F. Drummond. 2001. *Bombus impatiens* (Hymenoptera: Apidae): An alternative to *apis mellifera* (Hymenoptera: Apidae) for Lowbush Blueberry Pollination. J. Econ. Entomol 94(3):609–616. https://academic.oup.com/jee/article/94/3/609/2217314.

Stubbs, C., F. Drummond, and S.L. Allard. 1997. Bee conservation and increasing *osmia* spp. In Maine lowbush blueberry fields. Northeast Nat. (steuben) 4(3):133. doi: 10.2307/3858708.

Stubbs, C., F. Drummond, and E. Osgood. 1994. *Osmia ribifloris biedermannii* and *megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. J. Kans. Entomol. Soc 67(2). https://about.jstor.org/terms.

Stubbs, C., and D.E. Yarborough. 2002. Commercial bumble bee (*Bombus impatiens*) management for wild blueberry pollination. https://extension.umaine.edu/blueberries/302-commercial-bumble-bee-bombus-impatiens-management-for-wild-blueberry-pollination/.

Takeda, F., W. Yang, C. Li, A. Freivalds, K. Sung, R. Xu, B. Hu, J. Williamson, and S. Sargent. 2017. Applying new technologies to transform blueberry harvesting. Agronomy 7(2):33. doi: 10.3390/agronomy7020033.

Tasnim, R., F. Drummond, and Y.J. Zhang. 2021. Climate change patterns of wild blueberry fields in downeast, Maine over the past 40 years. Water 13(5):594. doi: 10.3390/w13050594.

Trozzo, L.-P. 2023. La disparition de la forêt acadienne vue du ciel. Radio Canada. https://ici.radio-canada.ca/info/long-format/2025012/peninsule-acadienne-tracadie-bleuet-champ-tir.

USHBC. 2023. Export database - Canada - consumer preferences. https://ushbc.blueberry.org/for-exporters/export-database/.

Vasiliev, D., and S. Greenwood. 2021. The role of climate change in pollinator decline across the Northern Hemisphere is underestimated. Sci. Total Environ. 775:145788. doi: 10.1016/j.scitotenv.2021.145788.

Venturini, E., F. Drummond, A.K. Hoshide, A.C. Dibble, and L.B. Stack. 2017. Pollination reservoirs in lowbush blueberry (Ericales: Ericaceae). J. Econ. Entomol. 110(2):tow285. doi: 10.1093/jee/tow285.

Venturini, E.M., F. Drummond, and A.K. Hoshide. 2018. Organic establishment of pollination reservoirs in the lowbush blueberry (*Ericales: Ericaceae*) agroecosystem. Open Agric. 3(1):393–403. doi: 10.1515/opag-2018-0044.

Wahengbam, J., A. Raut, and N. Banu. 2019. Role of bumble bee in pollination. Ann. Biol. 35(2):290–295. https://www.researchgate.net/publication/337857136.

Williams, P., and S. Jepsen. 2021. Bumblebee Specialist group report 2020. https://bumblebeespecialistgroup.org/wp-content/uploads/2021/02/BBSG-Annual-Report-2020.pdf.pdf.

Winter, K., L. Adams, T. Robbin, D. Inouye, L. Day, J. Ascher, and S. Buchmann. 2006. Importation of non-native bumble bees into North America: Potential consequences of using *bombus terrestris* and other non-native bumble bees for greenhouse crop pollination in Canada, Mexico, and the United States. https://www.researchgate.net/publication/31227280.

WSU. 2021. Washington small fruit conference. https://extension.wsu.edu/wam/2021-washington-small-fruit-conference/.

Yarborough, D.E. 2004. Factors contributing to the increase in productivity in the wild blueberry industry. Small Fruits Rev. 3(1–2):33–43. doi: 10.1300/J301v03n01_05.