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Diverse heathland bee communities provide limited pollination services for lowbush blueberry species

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ABSTRACT

Providing pollinators, especially bee species, with floral and nesting requirements is essential in order to ensure the pollination service they provide is maintained, especially in agroecosystems. Here, we investigated the importance of floral and nesting provisions provided by common and rare plant species in heathland habitat to maintain pollination services in cultivated blueberry fields in Nova Scotia, Canada. Bee species, along with their associated floral records were collected in late May and June 2016, within coastal, inland, and highland heathlands. We also compared measured rates of blueberry flower visits by bees, as well as flower abundance and resulting fruit set, in natural coastal barrens and managed lowbush blueberry fields. Our results indicate that heathland habitats support a high diversity of bees, 97% of which are known pollinators of provincial fruit crops and efficient pollinators of blueberry. Our study also resulted in one new provincial record, *Osmia nigriventris* (Zetterstedt), for Nova Scotia. Estimates of blueberry fruit set calculated from bee visits underestimated observed fruit set in both natural and managed barrens habitat, with both measures indicating suboptimal fruit set. The presence of high-quality lowbush blueberry pollinators like *Andrena* and *Bombus* visiting berry-producing plants and rare plant species like golden heather, *Hudsonia ericoides* Huder (Cistaceae), show that heathlands represent key floral and nesting elements that should be targeted in agroecosystem conservation efforts for important blueberry pollinators and other berry-pollinating bee species.

INTRODUCTION

In Atlantic Canada (Nova Scotia, Prince Edward Island, New Brunswick, and Newfoundland and Labrador), wild (lowbush) blueberry, *Vaccinium angustifolium* Aiton (Ericaceae), is a key economic commercial berry crop for the region (Cutler et al. 2015; Drummond 2019). Roughly 28% of Canada's fruit and berry production in 2016 was from eastern Canada, substantially more than Ontario's 15% production (AAFC 2017). Most research to date has focused on the importance of wild bee pollination, as lowbush blueberry relies on bees capable of sonication for cross-pollination and maximal fruit set (Javorek et al. 2002; Isaacs & Kirk 2010; Tuell & Isaacs 2010; Hicks 2011; Blaauw & Isaacs 2014). Very little is known about alternative forage plants that are essential in lowbush blueberry productivity at the agricultural scale (Stubbs et al. 1992). This is surprising as unlike many other orchard crops (e.g., highbush blueberry, apples), wild blueberry is not planted, and develops from native existing stands (Drummond 2019). Ensuring the proper nesting and alternative foraging resources are available for wild bees is paramount, particularly, to safeguard against localized declines or annual fluctuations in agricultural landscapes in regions where unusual weather conditions occur (Bartomeus et al. 2013; Forrest 2015).

Heathland ecosystems along the coast of Northeastern North America were historically very extensive (Foster & Motzkin 2003), but many heathlands are now significantly fragmented and decreasing at alarming rates due to afforestation, invasive species, and urban spread (Foster & Motzkin 2003; Oberndorfer et al. 2009). Coastal heathlands have been the subject of many conservation efforts in the past decade as they not only are important habitats culturally (e.g., Peggy's Cove, Nova Scotia), but they are also habitat for many rare plant species such as *Hudsonia ericoides*

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and Canada buffaloberry (*Shepherdia canadensis* Nutt (Elaeagnaceae)) (Oberndorfer et al. 2009). This shrub-dominated habitat also supports many common berry-producing plant species such as: serviceberry (*Amelanchier* spp., (Rosacaea)), chokeberry (*Photinia melanocarpa* Michaux (Rosaceae)), and wild blueberry, all of which, require varying degrees of insect visits for pollination (Oberndorfer et al. 2009; Cameron & Bondrup-Nielsen 2013).

To our knowledge, pollinator communities, and plant-pollinator dynamics of natural heathland habitats have not been investigated in North America. This is rather surprising given wild blueberry naturally occurs in heathland habitats. Therefore, during spring 2016, we investigated wild bee communities of three distinct heathland habitats: coastal, inland and highland heathland throughout the province of Nova Scotia, Canada. Our main objectives of this study were to: (1) examine the abundance and identity of wild bee species visiting flowers of common and rare berry- producing shrubs of each distinct heathland habitats. (2) compile floral records for each bee species in each of three heathland habitats. (3) use wild bee visitation rates to compare estimates of lowbush blueberry (*Vaccinium angustifolium*) yields from commercial and natural heathland.

METHODS

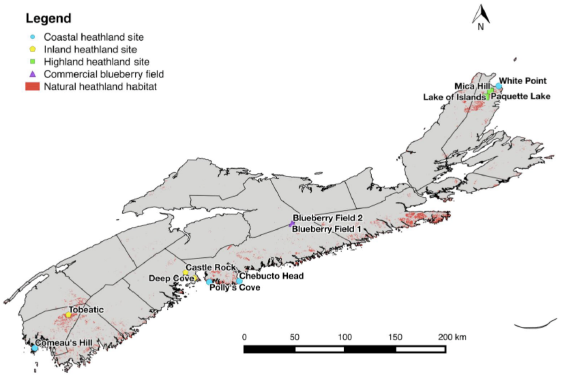
Heathland site selection

Berry producing plant species bloom in the spring in Nova Scotia. Accordingly, our sampling of wild bees targeted the last week of May and the month of June in 2016. The heathland site-selection process was informed by large-scale provincial spatial vegetation data sets (e.g., NSDNR's Spatially Related Forest Resources Information System) and finer-scale previously collected field data of flowering species (e.g., unpublished plant community data, Basquill Lundholm & Porter 2010 - 2015). We define heathland as low-nutrient habitat that is dominated by ericaceous shrubs and features low tree canopy cover, humus-rich soils, and (often) exposed conditions (Oberndorfer et al. 2009). Coastal heathlands are directly adjacent to the ocean and are influenced by coastal environmental factors. Inland heathlands are not directly impacted by coastal influences (e.g., salt spray) and are maintained by non-coastal processes (e.g., history of grazing or fire, bedrock exposure, etc.). In Nova Scotia, highland heathlands occur only on Cape Breton Island and can be distinguished by outcrop plant communities that are boreal or alpine in nature; these highland heathlands can be much more extensive than those located on the mainland and are subject to strong winds (les suêtes).

We selected 10 field sites across the province (Figure 1, Table S1) that represented coastal, inland, and highland heathland habitat, and attempted to include sites that featured populations of select rare plant species (Table 1). Once identified as a potential bee sampling location, we visited each site prior to the bee survey to verify that the habitat was appropriate (i.e., many berry-producing shrubs, satisfied our definition of heathland, accessible). We did not randomly select sites but attempted to cover as much of the distribution of each heathland type in the province (with a minimum of three sites per heathland type), with the stipulation that each site had to include lowbush blueberry.

Populations of *Hudsonia ericoides* were located at Chebucto Head, Polly's Cove, and Castle Rock. White Point was the only site to host *Shepherdia canadensis*, and the two uncommon species of northern blueberry (*Vaccinium boreale* Hall & Aalders (Ericaceae)), and bog blueberry (*Vaccinium uliginosum* L. (Ericaceae)) were located at highland sites only (Paquette Lake, Mica Hill, Lake of Islands). A population of northern highbush blueberry (*Vaccinium corymbosum* L. (Ericaceae)) was located at Comeau's Hill and was included in the bee survey as this is a relatively uncommon species with a southern distribution.

Figure 1. Map of sampling locations in Nova Scotia. Extent of natural heathland habitat was mapped using Nova Scotia Department of Natural Resources data (2015) from the Spatially Related Forest Resources information system.



Sampling of bee species

Although it is preferable to sample bees under favourable conditions (sunny, temperatures ≥10 °C, low wind) (Drummond 2002), these criteria are not frequently met in the spring in Nova Scotia, especially in foggy, windy heathlands. Therefore, we undertook sampling of bees as long as temperatures were not cold, 10 °C or above and

Table 1. Early flowering (May–June) berry-producing plant species and target rare plant species found in Nova Scotia heathland habitat.

Berry producing species		Rare species
Amelanchier spp.	*Photinia* spp.	*Hudsonia ericoides*
Aralia nudicaulis	*Prunus* spp.	*Shepherdia canadensis*
Arctostaphylos uva-ursi	*Ribes* spp.	*Vaccinium boreale*
Cornus canadensis	*Rubus* spp.	*Vaccimium. uliginosum*
Gaylussacia spp.	*Sambucus racemosa*	
Ilex mucrontata	*Vaccinium* spp.	
Maianthemum spp.	*Viburnum nudum*	

there was no rain. Pan traps and timed aerial net collections were used to sample bees as the combination of both these methods is known to yield a more comprehensive sample of bee diversity (Wilson et al. 2008). Following Lebuhn et al. (2003), two 50-m transects were centred in regions with the densest bloom of berry-producing plants and arranged in an X formation with 30 coloured bowls (10 each of white, blue, and yellow bowls) spaced 1–3 m apart. Pans were set at 09:00, and picked up after 17:00.

In addition to pan trapping, four 30-minute aerial net collection periods were conducted on the same day as bowl sampling (1 day per site): two 30-minute net collections occurred in the morning, 09:00–12:00 after the bowl traps were set up, and two occurred in the afternoon, 12:00–15:00, by walking the 50 m x 50 m square surrounding the intersection of the two-bowl trap transects. Both sampling methods were used as the combination of these methods yields a more comprehensive sample of bee diversity (Wilson et al., 2008). For bees that were caught with nets, we recorded the floral host and identified each plant to species. When bees were observed to forage at a site but were not visiting berry-producing species, we collected them on non-berry producing plant species (e.g., rhodora (*Rhododendron canadense* Torr. (Ericaceae)), and pale bog laurel (*Kalmia polifolia* Wangeh (Ericaceae)) to ensure that at least some bees were collected at each site.

Identification of bee species

All specimens were identified to genus level using Packer et al. (2007), and Mitchell (1960 & 1962) and then to species level using published taxonomies (and revisions): Gibbs (2010 & 2011) for metallic *Lasioglossum* spp., Gibbs et al. (2013) for non-metallic *Lasioglossum* spp; Laberge and Ribble (1975), LaBerge (1969, 1973, 1977, 1980, 1985, 1989), for *Andrena* spp.; Laverty & Harder (1988) for *Bombus* spp.; Mitchell (1960, 1962) for *Halictus* spp.; Rehan and Sheffield (2011) for *Ceratina* spp.; and, Rightmyer et al. (2010) for non-metallic *Osmia* spp. Bees were also assigned to functional guilds according to Sheffield et al.(2013). A subset of bee specimens caught were sent to the Packer Collection (PYCU) at York University for expert verification by Sheila Dumesh. Furthermore, specimens of tentative provincial records of *Lasioglossum* and *Osmia* were sent to Dr. Jason Gibbs at the University of Manitoba for expert verification.

Blueberry monitoring

Site selection

At all blueberry sites, we delineated 10 monoculture patches of lowbush blueberry measuring 0.9 m × 0.9 m (equivalent to $1yd^2$) with flagging tape. At Polly's Cove and Chebucto Head, we identified and flagged patches as they were encountered via pedestrian survey, as monoculture patches of lowbush blueberry were relatively uncommon in natural heathland. Given most wild bee species fly <1 km (Zurbuchen et al. 2009), at the farm, we established two sites (with ten patches each) to sample both field margin/forest adjacent (blueberry field 1) and field center (blueberry field 2) environments to capture variation within a large commercial farm. The two sites were separated by 1.5 km. Each of the two blueberry field locations, patches were separated by at least 5 m. Together, we used these observations to calculate an estimate of percent berries at harvest and the observed fruit set for the plants in these different environments.

Blueberry visitation rates

We compared wild bee visits to lowbush blueberry in cultivated fields to bee visits to lowbush blueberry in natural heathland according to a standardized protocol (Drummond 2002). Together, we used counts of flowers and fruit to calculate an estimate of percent berries at harvest and the observed fruit set for the plants in these different environments. We included two coastal heathlands, Polly's Cove and Chebucto Head, for comparison, chosen for ease of access. Bees were monitored between 1–7 June 2016 (once at each site) in monoculture patches of blueberry on days without rain and with temperatures (10 °C or above). Our monitoring protocol followed that of Drummond (2002). We recorded the number of honeybees, bumblebees, and other wild bees entering each monoculture patch of lowbush blueberry during a 30-minute observation period. Five patches were monitored in the morning (09:00–12:00) and five in the afternoon (12:00–15:00) at each site. Estimated harvestable percentage of blueberries was calculated using bee visit rates, following Drummond (2002) using the equation:

$$\textbf{\% Berries} = 14.5 + 7.8\,(N_{\text{honeybees}}) + 17.7\,(N_{\text{native bees}})$$

Along with bee monitoring, we identified and marked six blueberry clones using flagging tape at each patch. On each clone, we tagged five stems with embroidery floss. We recorded the number of flowers on each stem of every tagged clone (1–7 June 2016) for all patches, for a total of 300 stems per site (1200 stems overall). After petal fall in June, we counted immature fruits (28 June – 6 July 2016) on all previously tagged stems at all sites, excluding all stems that had been grazed or affected by botrytis blight. We calculated initial percent fruit set (prior to summer drop) following the equation:

$$\%\,Fruit = \left(\frac{N_{fruit}}{N_{flowers}}\right) \times 100$$

Although this cannot predict the final percentage of berries available at the final harvest, it does constrain the maximum percent fruit possible for a given site in a given year and indicates the percentage of flowers that were successfully pollinated.

Statistical analyses

To assess bee inventory completeness and species richness across all heathland habitats, we generated sample-based and individual-based species accumulation curves (n = 11 sampling events - Chebucto Head was sampled twice due to poor weather) with estimated richness (100 runs without replacement) using EstimateS 9.1.0 (Colwell 2005). All other data analyses were performed using R version 3.1.2 (R Core Team 2014).

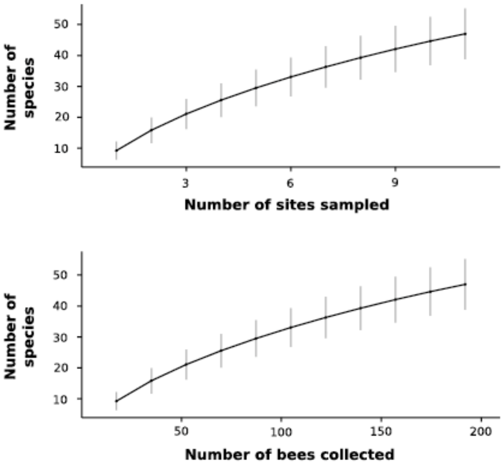
Means reported in-text are associated with one standard error (mean ± SE). We assessed differences in proportions of bee guilds among heath types by using Chi-square test of proportions. We used a Kruskal-Wallis test to assess differences in the percentage of immature fruit set by lowbush blueberry, bee visitation rates to lowbush blueberry in commercial farm and coastal heathland sites, and rates of bee capture on rare and berry-producing plant species across three heathland habitats as normality of residuals was violated.

RESULTS

Heathland bee diversity & abundance

A total of 193 bees were collected, comprising nine genera and 43 species, from 10 heathland collection locations (Figure 2, Table S3) from 21 May – 27 June 2016. Species richness was similar across heathland habitat types, with the greatest number (±SE) of bee species recorded in inland habitat (11.7 ± 2.7) and the fewest in coastal habitat (8 ± 2.8) surveyed here, with highland heathlands displaying intermediate bee species richness (9 ± 1). Our collection includes a new provincial record for *Osmia nigriventris* (Zetterstedt, 1838). Our surveys also detected a species previously considered rare in North American collections, *Osmia laticeps* (Thomson 1872) (last recorded in Nova Scotia in 1932 - species determination by M. Rightmyer, San Diego Natural History Museum, San Diego, CA.

Figure 2. Individual and sample-based species accumulation curves across all heathland sites; error bars = 95% confidence intervals.



Overall, solitary ground-nesting bees, bumblebees, and social ground-nesting bees were the best-represented guilds and cavity-nesting species the worst represented guilds at heathlands (Figure 3). No significant differences were found among guilds in heathland habitat types, with the exception of, significantly fewer social ground-nesting bees and significantly more social parasites in highland heathlands (χ^2 = 8.95, P = 0.009; χ^2 = 7.31, P = 0.03, respectively) relative to inland heathlands with coastal sites displaying an intermediate abundance of both bee guilds (Figure 3).

Lasioglossum spp. (32% of the total), *Bombus* spp. (26%), and *Andrena* spp. (23%) were the most common genera found in heathland habitat in late May and June, and *Bombus vagans* (33 of 193) was the most abundant bee, followed by *Lasioglossum ephialtum* (27), and *Lasioglossum planatum* (12) (Figure 3, Table S3). Of the n = 47 bee species collected, 22 were singletons (47%) (Table S3). A PERMANOVA on bee species composition of all three heathland habitat types revealed no significant differences (F = 1.06, P = 0.4).

Floral host associations

Several berry-producing plant species featured flowers that attracted diverse bee species (Figure 4, Table S3).

Figure 3. **Guild structure of heathland bee communities according to proportion caught with combined collection methods within each heathland type (n = 3). *denotes significant difference in tests of proportions with between individuals caught per guild ($\chi^2 = 5.8$, $p < 0.05$).**

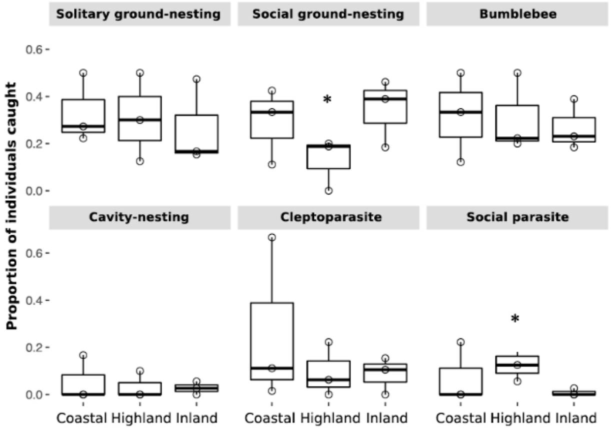
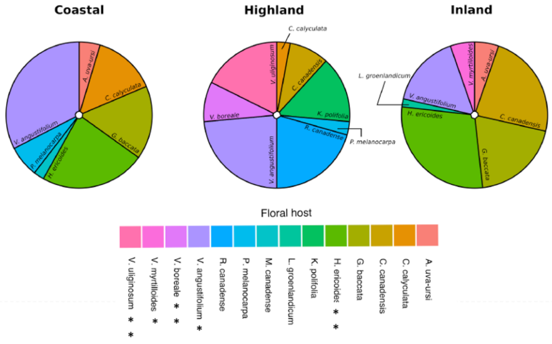


Figure 4. **Proportion of spring bee visits to all recorded floral hosts according to heathland habitat type. ** Denotes rare plant species and * denotes wild blueberry species.**

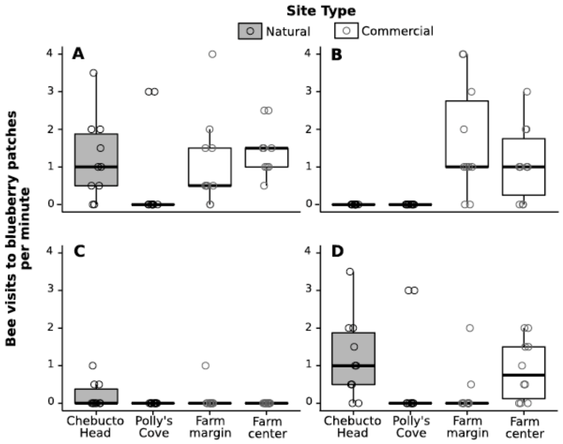


Excluding the 10 parasitic species we collected, 32 of the 33 non-parasitic species found in heathlands in this study (97%) have been collected previously in lowbush blueberry fields in NS, NB, PEI, or ME, and 19 non-parasitic species have also been found in apple orchards in the Annapolis Valley (Table S3). We frequently captured bees on lowbush blueberry in all heathland habitats, with a total of 16 bee species visiting this host. Bees visited several berry-producing plants across heathland sites, including black huckleberry (*Gaylussacia baccata* Koch (Ericaceae)), black chokeberry (*Aronia melanocarpa* Medik (Rosaceae)), bearberry (*Arctostaphylos uva-ursi* Spreng (Ericaceae)), and bunchberry (*Cornus canadensis* L. (Cornaceae)). However, bees were also attracted to ericaceous species that do not produce berries, such as leatherleaf (*Chamaedaphne calyculata* Moench (Ericaceae)), *Rhododendron canadense*, and *Kalmia polifolia*. Several bee species repeatedly visited rare species. We repeatedly captured *Andrena carlini, Andrena ceanothi, Andrena regularis,* and *Andrena w-scripta* on *Hudsonia ericoides*. In total, this rare plant was visited by four species of *Andrena*, one bumblebee, one small carpenter bee, three parasitic *Nomada*, and five halictid bees. Although *Andrena rufosignata* was the only repeat visitor to *Vaccinium uliginosum*, together *Vaccinium uliginosum* and *Vaccinium boreale* were visited by four species of *Andrena*, three species of bumblebee, and one small halictid species (Figure 4).

Lowbush blueberry visitation & fruit set

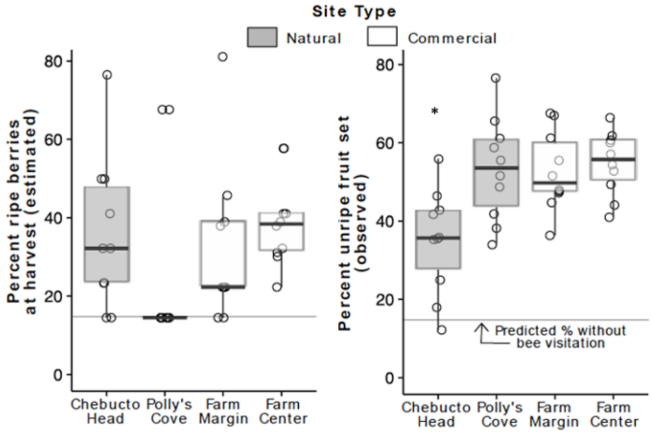
The number of bees observed visiting lowbush blueberry per minute differed among the sites monitored and by bee type (Figure 5a-d). When we combined visits from all bees, visitation rates were not significantly different between commercial or natural lowbush blueberry patches (t = 5.50, *P* = 0.114, Figure 5a). When honeybees were excluded it remained non-significant, with visitation rates of wild bees to commercial blueberry patches lower relative to those observed in natural heathland (t = 5.00, *P* = 0.12, Figure 5d). We did not observe any honeybees foraging at lowbush blueberry in natural coastal heathland sites monitored, and we observed very few bumblebees foraging in lowbush blueberry patches monitored at any site (Figure 5b and c).

Figure 5. **Count of bees visiting lowbush blueberry patches per minute in both commercial fields and natural heathland. A: all bees, B) honeybees only, C) bumblebees only, D) all wild bees (i.e., honeybees excluded). No significant differences were found at $p < 0.05$.**



Interestingly, though higher visitation rates of wild bees were observed in natural heathlands, observed fruit set was significantly lower ($F = 13.38$, $P < 0.0001$) in heathlands relative to commercial blueberry farm patches. Immature fruit set was lowest at Chebucto Head (35%) relative to all other sites (53-55%) (Figure 6a). Mature fruit set at harvest (as predicted from bee visits) did not differ significantly ($F = 4.81$, $P = 0.16$) between commercial and natural lowbush blueberry patches, ranging from a minimum of 25% ± 7.1%) at Polly's Cove and a maximum of 39% ± 3.6%) at the center of the commercial blueberry field (Figure 5). Of the lowbush blueberry patches monitored at Polly's Cove, 80% were predicted to provide at most 14.5% mature fruit, contributing to the low overall estimate of mature fruit set for that site.

Figure 6. Observed percent unripe blueberry fruit set and estimated percent ripe berries at harvest. Unripe fruit set calculated from flower vs. fruit count in June-July; percent berries at harvest estimated from bee visits according to Drummond (2002). Line indicates expected percent fruit set without any visits from bees (14.5%). * denotes significant difference at $p < 0.05$.



DISCUSSION

We found concerning low abundances of bees during the spring bloom of the berry-producing heathland species for which they are key pollinators. Of the species that were found in our study, there was a high proportion of visits from effective pollinators like *Andrena* spp., *Bombus* spp., and *Lasioglossum* spp. (Javorek et al. 2002; Cutler et al. 2015). The increased pollination efficacy of these bee taxa (relative to European honeybees) may buffer their provisioning of pollination services despite low abundances (Javorek et al. 2002; Cutler et al. 2015).

Though some wild bee species are robust to cold weather, fog, light rain, and high winds, our data suggest that it is plausible that adverse conditions from unseasonal weather events impacted species in heathlands. Wetter spring conditions will reduce the number of optimal foraging days in May and June, with the potential to further impact pollination services provided to spring-blooming species and later fruit development, though some species can extend their bloom period in response to poor weather (Southwick & Southwick 1986). The minimum temperature at which a bee can take flight is dependent on solar radiation; on days that are cool and sunny, bees are able to take flight at lower ambient temperatures relative to cool and cloudy days (Vicens & Bosch 2000). Better resolution of the tolerance limits of our wild species of *Andrena* spp. and *Lasioglossum* spp. would improve our understanding of spring pollination services provided by heathland bee communities.

Bee diversity & abundance in heathlands

Our study resulted in a new provincial record of *Osmia nigriventris* and included a species (*Osmia laticeps*) that was previously considered rare in North American museum collections since the 1990s. These findings, coupled with a high proportion of singletons (47%), suggests that heathland habitat may be representative of a community with many rare species in comparison to other habitats.

In highland heathlands, more of the ground-nesting bees tended to be solitary than social. This could stem from colony development, as foundresses may have been rearing the first generation of worker daughters at the time our collections took place. It is also possible that colder temperatures favour solitary lifestyles, particularly in socially polymorphic bee species (e.g., *Augochlorella aurata*, several species of *Lasioglossum*) (Packer 1990; Sheffield et al. 2014). Thus, we would expect to see fewer individuals of these species if no worker generations are being reared or if worker generations have not yet emerged to forage.

Bumblebees are known to be tolerant of cold temperatures, wind, and even light rain (Tuell et al. 2010); however, they appeared in low abundance in heathlands in early spring while queens were busy brooding in May and early June. As a result, queens are the only bumblebees available to pollinate in the early spring and must divide their energy between foraging and brooding (Pyke et al. 2011). We observed many social parasites (particularly in highland heathlands) actively foraging in June, which suggests high occupancy by their hosts (non-parasitic bumblebees). Thus, delayed colony development due to unseasonal weather conditions (e.g., highland habitat in Cape Breton) will limit the number of bumblebees available to pollinate spring blooming plants. Relative to their workers, pollination services rendered by queen bumblebees result in more seeds per fruit, but fewer fruits overall (Kudo et al. 2011).

Cavity nesting species we did detect, nest in pithy plant stems (*Ceratina* spp.), under rocks (*Osmia inermis,* Zetterstedt), or in dead wood that has been bored by other insects (*Osmia nigriventris*), (Packer et al. 2007; Rightmyer et al. 2010). Locations far from the forested margins of heathlands may offer very few nesting opportunities for bees that occupy cavities in wood. Some species of *Osmia* appear robust to adverse weather and can forage in cold temperatures, light rain, and moderate wind (Vicens & Bosch 2000). Members of this genus also overwinter in adult form, tend to fly early in the spring, and forage on species that occurred at our sites (Sheffield et al. 2003). Our detection of very low abundances of spring-flying *Osmia* may stem from inadequate nesting opportunities within the heathlands sampled, or inappropriate capture techniques (net and bowl). Trap nests may have better sampled this group of bees (Stubbs et al. 1992).

Floral associations

Adding and maintaining floral and nesting resources in proximity to agircultual land has been shown to increase the diversity and abundance of wild pollinators visiting these crops (Tuell et al. 2010; Cutler et al. 2015). It is important however, to fully understand which provisions are essential for effective pollinators in specific cropping systems (Winfree et al. 2015). In our study, effective blueberry pollinators: *Andrena* spp*.*, *Lasioglossum* spp, and *Bombus* spp were frequent visitors to all berry-producing species, and almost all of the non- parasitic bee species that we collected in heathlands in the spring are known to visit lowbush blueberry (Cutler et al. 2015). These results suggest that heathlands represent key floral and nesting elements for effective blueberry pollinators, that should be targeted in lowbush blueberry agroecosystem conservation.

Among our focal rare species, we were unable to sample repeatedly on *Shepherdia canadensis* or *Vaccinium boreale*, though the early flowering period of *Shepherdia. canadensis* and the small size of its flowers likely favor visits by fly pollinators (Gervais et al. 2018). At most, we captured three bees during 30 minutes of continuous observation on *Vaccinium uliginosum*. Decreased attention from bees can lead to pollen limitation in rare species (Bruninga-Socolar et al. 2016). Deposition of pollen from co-flowering species (e.g., from more abundant ericads) can further reduce fertilization of rare plant species (Van Rossum et al. 2013; Carvalheiro et al. 2014) and many of our provincial ericaceous species share pollinators (Reader 1975; Rathcke 1988), as we observed here. Both *Vaccinium boreale* and *Vaccinium uliginosum* inhabit highland heathlands in Cape Breton, often occurring on exposed outcrops of bedrock hilltops. Bumblebees have been shown to only collect nectar, but not pollen, when *Vaccinium uliginosum* host populations are small (Mayer et al. 2012). Their fidelity is positively related to patch size (Van Rossum et al. 2013); thus, the smaller patches of *Vaccinium uliginosum* on these outcrops appear to be receiving infrequent, low quality visits from bumblebees.

In contrast, a relatively diverse bee pollinator assemblage visited *Hudsonia ericoides*. Several andrenid bees repeatedly visited this rare plant, as did their parasites (*Nomada*). We observed many *Nomada* frequently searching near *Hudsonia ericoides* for hosts, suggesting that *Andrena* are important pollinators of this provincially rare plant. The distribution of *Hudsonia ericoides* is southern around the province, which likely improves its window of opportunity for pollination, and we observed more favourable pollination dynamics for this species in inland heathlands that were not affected by coastal winds. Additionally, *Hudsonia ericoides* presents a simple floral morphology and its yellow colouration stands out from that of primarily pink and white co-flowering species, though we have no data on UV reflectance patterns. These floral attributes may allow foragers to effectively locate even small populations of this species.

Blueberry visitation & fruit set

Based on commercial fruit set targets (~60% fruit set) (Drummond 2002), we found that pollination rates were suboptimal in managed fields and in natural heathland using both measures of bee observation (visits/minute) and counts of flowers. Pollen limitation, and a subsequent reduction in fruit set, has been previously documented in Nova Scotia lowbush blueberry fields, but adverse weather conditions were not a factor (Fulton et al. 2015). Immature fruit set represents the maximum possible fruit set, as yield of harvestable berries decreases following mid-summer fruit drop, foraging by pests (birds, mammals), insect damage (e.g., blueberry spanworm, *Itame argillacearia* Packard (Geometridae)), or fungal pathogens (e.g., mummy berry**,** *Monilinia vaccinii-corymbosi* Reade). Thus, final berry yield is likely even lower than we predicted in managed fields, as management practices (e.g., mowing, spraying of agrochemicals) can impact yields (Vanbergen et al. 2013). Mature fruit set estimated from bee visits did not correspond with observed immature fruit set. At one coastal heathland site (Polly's Cove), fruit appeared to be set through self-fertilization alone. This indicates that flower and fruit counts, which represent an integrated assessment of pollinator activity throughout the bloom period, are needed to corroborate fruit set estimates based on bee visitation rates. In addition, given that nocturnal pollinators contribute to lowbush blueberry fruit sets in commercial fields (Cutler et al. 2012), it is highly likely they also contribute to pollination of berry-producing plants in heathland habitats.

CONCLUSIONS

Our results suggest that fruit set is suboptimal in the coastal heathlands monitored, likely due to weather. We recommend that measures of pollination services, particularly in agroecosystems, not be based solely on bee visits. Incorporating fruit counts, along with bee visits, provides a more precise assessment of pollination services in agroecosystems. In locations that experience spring seasons dominated by unpredictable weather conditions, our results suggest that despite heathlands making up only 3% of Nova Scotia's landmass, they are a storehouse of important blueberry pollinators and other berry-pollinating bee species. We strongly recommend further investigation into wild bee species of heathland habitats in Atlantic Canada to determine if our observations of a low abundance of spring-flying bees is representative of heathland bee communities, or continued evidence of the decline of wild bees to due changes in environmental conditions.

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SUPPLEMENTARY ANALYSIS

There is limited literature on the impact of temperature on species included within the bee fauna of Northeastern North America; however, several studies have explored the thermal limits of non-native congeners of bee species in Nova Scotia (Table S2). Very limited literature describes the wind speed or precipitation limits of different bee species. Based on our review of the literature and observations by Drummond (2002) of bees foraging on lowbush blueberry blooming in Maine, minimum daily temperatures below 15 °C, wind speeds above 30 km/h, and rainfall events above 1.0 mm were considered to represent adverse foraging conditions for bees.

To characterize the foraging conditions experienced by wild bees in Nova Scotia, we accessed Environment Canada historical weather data for June 2016 from four weather stations that were located relatively near to regions that were sampled in this project and for which relatively complete recent records were available: Yarmouth RCS, Shearwater RCS, Upper Stewiacke RCS, and Ingonish RCS. Minimum daily temperature, total daily rainfall, and maximum wind speed all impact bee foraging activity. Maximum daily wind speed values presented in this report represent either the maximum wind gust recorded by Environment Canada for a given date or, when those data were not available, the maximum hourly wind speed reported for that date. Minimum daily temperatures presented in this report represent the minimum daily temperature recorded by Environment Canada at a given weather station between sunrise and sunset for June 2016 (05:00 – 20:00).

Historical weather conditions for June 2016 from weather stations in close proximity for our sampling locations, showed that overall weather conditions were less than optimal for wild bee species throughout Nova Scotia (Figure S1). Overall mean weather conditions for the province revealed that maximum temperatures were less than 15 °C for 7 out of 14 days (50%). There were no days with wind gusts <30 km/h and 8 out of 14 days (58%) exhibited total daily precipitation >1mm during peak blueberry bloom (Figure S1).

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Figure S1. Daily mean weather conditions for weather stations in close proximity to sampling areas in June 2016. Solid red lines indicate adverse condition thresholds: maximum temperature <15 °C; Maximum wind gust >30 km/h, total daily precipitation >1.0 mm.

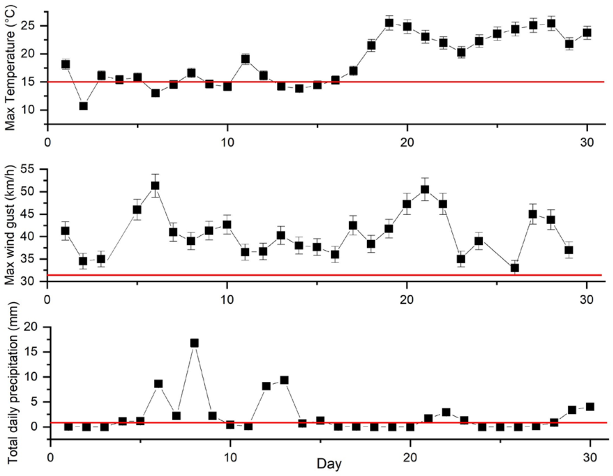

Table S1. Field site and survey information from natural and commercial blueberry fields in Nova Scotia. Survey A refers to the first survey, with B referring to the second per site. LBB refers to surveys of lowbush blueberry flower, fruit, and bee visitor counts. Lowbush blueberry survey dates not included.

Site	Survey(s)	Capture dates	Berry Producing plants	Rare plant species
Comeau's Hill	A, B	June 5	+	
Tobeatic	A, B	May 21	+	
Castle Rock	A, B	June 18	+	+
Deep Cove	A, B	June 17	+	
Polly's Cove	A, B, LBB	June 16	+	+
Chebucto Head	A, B, LBB	May 26, June 27	+	+
Lake of Islands	A, B	June 23	+	+
Paquette Lake	A, B	June 11	+	+
Mica Hill	A, B	June 20	+	+
White Point	A, B	June 10	+	+
Blueberry Field 1	LBB	N/A	+	
Blueberry Field 2	LBB	N/A	+	

Table S2. Foraging tolerances of several bee species under various weather conditions.

Bee species	Minimum Flight Temperature	Wind Speed	Rain	Source
Andrena carlini & *regularis*	13	N/A	Foraging occurred in "mild" rain	LaBerge & Schrader 1978
Andrena clarkella	8	N/A	N/A	Stone & Willmer 1989
Andrena fulva	12	N/A	N/A	Stone & Willmer 1989
Andrena nigroaenea	9	N/A	N/A	Stone & Willmer 1989
Apis mellifera	15	Flew in 16 km/h wind	N/A	Tuell & Isaacs 2010
Apis mellifera	12	N/A	N/A	Vicens & Bosch 2000
Apis mellifera	13	Unaffected by recorded wind speeds: max. 30.8 km/h; mean 8.9 km/h	N/A	Frier et al. 2016
Bombus edwardsii (workers and queens)	2.5	N/A	N/A	Stone & Willmer 1989
Bombus impatiens	10	Flew in 16 km/h wind	N/A	Tuell & Isaacs 2010
Bombus lapidarius	9,4	N/A	N/A	Corbet et al 1993, Stone & Willmer 1989
Bombus pascuorum	6	N/A	N/A	Corbet et al 1993
Bombus spp. queens	0	N/A	N/A	Heinrich 2004
Bombus spp.	5	Unaffected by recorded wind speeds: max. 30.8 km/h; mean 8.9 km/h	N/A	Frier et al. 2016
Bombus terrestris	6,3	N/A	N/A	Corbet et al 1993, Stone & Willmer 1989
Bombus terricola	5	N/A	N/A	Stone & Willmer 1989
Bombus vosnesenskii (queen)	2, 6	N/A	N/A	Stone & Willmer 1989, Heinrich 2004
Bombus vagans	5	N/A	N/A	Stone & Willmer 1989
Colletes cunicularius	10	N/A	N/A	Stone & Willmer 1989
Megachile rotundata	13.5, 16.5	Flew at wind speeds up to 25.7 km/h	N/A	Corbet et al 1993 ref Lerer et al 1982 Stubbs et al. 1994
Megachile willoughbiella	16	N/A	N/A	Stone & Willmer 1989
Osmia cornuta	10	Unaffected by moderate wind (26 km/h), few females flew in 50 km/h wind (no other bee species observed at this speed)	0.9 mm/h	Vicens & Bosch 2000
Osmia ribifloris	10	Flew at wind speeds up to 24.1 km/h		Stubbs et al. 1994
Osmia rufa	5	N/A	N/A	Stone & Willmer 1989
Most native bees and honeybees	16	N/A	N/A	Heinrich 2004
Other native species	<10	Decreased flower visitation rates at speeds above 11 km/h	N/A	Inouye & Pyke 1988
Other native species	15	Flew in 16 km/h wind	N/A	Tuell & Isaacs 2010

Table S3. Bee species floral associations and abundances by heathland habitat type. Bolded bee species are known to specialize on lowbush blueberry pollen during bloom, (**) denotes bee species known to forage in lowbush blueberry fields and/or on lowbush blueberry, (***) denotes bee species known to forage in both lowbush blueberry fields and apple orchards, † denotes singletons.

		Floral hosts (Number of bees visiting host sp.)			**Abundance**		
Bee species		**Berry**	**Non-berry**	**Rare**	**Coastal**	**Inland**	**Highland**
Andrenidae							
Andrena	*algida***†	*C. canadensis (1)*				1	
	bradleyi***	*V. angustifolium (1)*	*C. calyculata (2)*	*V. uliginosum (1)*	1		3
	carlini***			*H. ericoides (3)*	2	1	
	ceanothi**	*V. angustifolium (2),* *G. baccata (1)*		*H. ericoides (2)*	5		
	*cressonii****	*C. canadensis (3)*				3	
	mandibularis***			*V. uliginosum (1)*	1		1
	*melanochroa****†				1		
	regularis***	*C. canadensis (2)*	*L. groenlandicum (1)*	*H. ericoides (4)*	1	6	
	rufosignata***	*G. baccata (2),* *P. melanocarpa (1),* *V. angustifolium (1)*		*V. boreale (1),* *V. uliginosum (2)*	2	2	3
	vicina***	*C. canadensis (2),* *G. baccata (1),* *M. canadense (1),* *V. angustifolium (1)*	*C. calyculata (1)*		3	4	
	*w-scripta****			*H. ericoides (5)*		5	
Apidae							
Bombus	*bimaculatus****†	*A. uva-ursi (1)*			1		
	*fernaldae***	*C. canadensis (1),* *V. angustifolium (3)*	*K. polifolia (2)*	*V. boreale (1)*	2		5
	*insularis***†	*V. angustifolium (1)*				1	
	*perplexus****†	*V. angustifolium (1)*			1		
	*sandersoni****†		*K. polifolia (1)*				1
	ternarius***	*G.baccata (2)*	*C. calyculata (1),* *R. canadense (1)*	*H. ericoides (1),* *V. uliginosum (1)*	1	3	3
	vagans**	*A. uva-ursi (2),* *C. canadensis (3),* *G. baccata (8),* *P. melanocarpa (1),* *V. angustifolium (1),* *V. myrtilloides (3)*	*K. polifolia (2),* *R. canadense (2)*	*V. boreale (1)*	9	14	10
Ceratina	*calcarata****		*C. calyculata (2)*		5		
	*mikmaqi***		*C. calyculata (1)*	*H. ericoides (1)*	5		
Nomada	bidentate spp.	*A. uva-ursi (1)*			1	1	
	cressonii†			*H. ericoides (1)*		1	
	depressa		*R. canadense (1)*	*H. ericoides (1)*	1		1
	gracilis	*V. angustifolium (1)*				1	2
	luteoloides†			*H. ericoides (1)*		1	
	cf. *cressonii/depressa/townesi/capillata*	*V. angustifolium (1)*			1	2	1
Halictidae							
Augochlorella	*aurata****	*C. canadensis (3)*		*H. ericoides (1)*		4	
Halictus	*rubicundus****	*G. baccata (1),* *V. angustifolium (1)*			1	1	
Lasioglossum	*cressonii****	*A. uva-ursi (1),* *P. melanocarpa (1)*			1	1	
	*ephialtum***	*G. baccata (1),* *V. angustifolium (3)*		*H. ericoides (1),* *I. uliginosum (1)*	18	5	4

Table S3 cont'd.

		Floral hosts (Number of bees visiting host sp.)			**Abundance**		
Bee species		**Berry**	**Non-berry**	**Rare**	**Coastal**	**Inland**	**Highland**
	*inconditum***	*C. canadensis (1),* *G. baccata (1),* *P. melanocarpa (1),* *V. angustifolium (2)*	*R. canadense (2)*		1	1	7
	*laevissimum****†	*V. angustifolium (1)*			1		
	*oblongum****			*H. ericoides (1)*	1	2	
	*pilosum***			*H. ericoides (2)*		2	
	*planatum***	*V. angustifolium (1)*		*H. ericoides (2)*	10	4	1
	*tenax***†					1	
	versans†				1		
Sphecodes	*atlantis*†		*R. canadense (1)*				1
	*ranunculi***†					1	
			Megachilidae				
Osmia	*inermis***†	*V. angustifolium (1)*				1	
	laticeps†				1		
	nigriventris†						1
	*proxima***†	*G.baccata (1)*				1	

Note: Bees captured using bowl traps are not associated with a floral host; therefore, counts in the habitat columns will not always reflect sum of counts on floral hosts.

Note: Foraging preferences of bee species from: Bushmann & Drummond 2015; Cutler et al. 2015; Hicks 2011; Lomond & Larson 1983; Moisan-Deserres et al. 2014a, 2014b; Müller 2010; Nilsson 2009; Russo et al. 2015; Sheffield et al. 2003; Stubbs et al. 1992.