



Forested field edges support a greater diversity of wild pollinators in lowbush blueberry (*Vaccinium angustifolium*)



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ABSTRACT

Agricultural landscapes vary widely in the degree to which they provide natural habitat. This is in spite of the fact that the availability of natural habitat has been identified as a critical factor influencing the diversity and abundance of beneficial crop insects, including native pollinators. We examined the effect of the type of field edge habitat (forested or deforested) on the abundance and diversity of bee species foraging in 15 managed lowbush blueberry fields in the vicinity of St. Stephens, New Brunswick, Canada. Additionally, we tested whether edge habitat type was associated with differences in pollen limitation, fruit set, and seed set of adjacent lowbush blueberry plants. Finally, we used GIS to determine the influence of larger scale land use patterns on the pollinator community and crop success of individual fields. Our forested field edges were distinguished as having lower light availability, greater canopy cover, and a greater bee nesting habitat index than deforested edges. Forested edges also had a greater diversity of bees. In particular, they supported more species of cleptoparasitic bees than deforested edges. Meanwhile, the abundance of non-parasitic (i.e., pollen-seeking) bees was greater along deforested edges. Blueberry plants along deforested edges tended to have more flowers, higher fruit set and marginally higher seed set than plants along forested edges. We found no difference in pollen limitation between edge types, suggesting that differences in fruit set were due to resource limitation. At the landscape level, we found no association among the amount of forest cover surrounding a field and the abundance or diversity of pollinators. However, on the forested edges of fields, we did find a positive correlation between the amount of forest surrounding a field and the abundance of pollinators. Our finding that forested edges had greater nesting habitat index and higher diversity of bees together suggest that the maintenance of areas of natural habitat within agricultural ecosystems helps to support greater pollinator diversity.

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1. Introduction

Pollination is vital to the health of managed and natural ecosystems, and is, consequently, an important component of the global economy (Robertson and Swinton, 2005; Potts et al., 2010). In natural ecosystems, pollinators support the basis of terrestrial food webs by providing pollination services that are essential to the persistence of many plant species (Knight et al., 2005b). In agricultural systems, 35% of global crop-based food production benefits from pollination (Klein et al., 2007). Unfortunately, both managed (Levy, 2011) and wild pollinators (Biesmeijer et al., 2006; Potts et al., 2010; Koh et al., 2016) are experiencing rapid declines.

In spite of the declines, wild bees have been found to improve fruit set in crops whether managed pollinators are present or not (Brittain et al., 2013; Garibaldi et al., 2013). Therefore, by promoting conditions that maintain diverse and abundant wild pollinator communities, we may be able to mitigate the impact of declining reliability of managed pollinators on crop production (Winfree et al., 2007a). Moreover, management schemes that promote species conservation on agricultural lands, which make up c. 40% of the global ice-free land mass (Foley et al., 2011), may help to preserve biodiversity in general (Driscoll et al., 2013).

Although many factors are involved in the decline of wild pollinator populations, the loss of high quality habitat is emerging as a major player (Potts et al., 2010; Kennedy et al., 2013; Koh et al., 2016). In a synthesis, Winfree et al. (2009) found a negative impact of habitat loss on both the abundance and diversity of native bee species. Furthermore, Williams et al. (2010) reported that bees were less abundant in disturbed relative to intact habitats; with

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the magnitude of the response depending on bee life history and the disturbance type. Several recent meta-analyses have confirmed that habitat disturbance is negatively correlated with pollinator species richness (Ricketts et al., 2008), pollinator abundance (Montero-Castano and Vila, 2012), and fruit set of animal-pollinated plant species (McKechnie and Sargent, 2013). Given the association between the availability of quality habitat and the diversity and abundance of wild pollinators, it is critical that we improve our understanding of how the management of natural areas in agroecosystems impacts pollinators.

Habitat requirements for wild bees include sites for nesting and a reliable supply of floral resources throughout the breeding season (Sardinas et al., 2016). One of the most common approaches to restoring bee habitat in agricultural settings is through the creation of hedgerows, or the planting of narrow strips of flowering shrubs and forbs along the edges of agricultural fields. Hedgerows can function as a refuge from pesticides and help to provide a continuity of floral resources, especially when crops are not in flower. Accordingly, hedgerows have been found to enhance the species richness of wild pollinators in agricultural systems (M'Gonigle et al., 2015). However, hedgerows are unlikely to provide suitable nesting habitat (Sardinas et al., 2016), especially for bees that require forested areas for nesting (e.g., cavity nesters).

Forests, on the other hand, may be a better source for bee nesting habitat, at least for some species (Ricketts et al., 2008; Moisan-DeSerres et al., 2015). However, the evidence to support the idea that intact forest and forest remnants provide critical habitat for wild bees is mixed. Although some bees are clearly forest specialists, particularly tree cavity nesters such as carpenter bees, in general, studies show that bee abundance and species richness tend to be lower in forests than in more open habitats (Winfree et al., 2007b, 2011). However, most of these studies have looked at species richness and abundance in aggregate, which means that they tell us nothing about whether particular species (i.e., forest specialists) are disappearing when forest is converted to agriculture (Winfree et al., 2011). Indeed, few studies have examined temporal and spatial turnover across habitat types – which may tell a different story. For example, Tylianakis et al. (2005), studying Hymenopteran diversity across a habitat gradient in Ecuador, discovered that while open, agricultural areas tended to have higher species richness in certain months, forests and abandoned coffee farms tended to have higher species richness through time. Several studies have reported that cavity-nesters tend to be more sensitive to changes in land use than ground nesters (Williams et al., 2010; Burkle et al., 2013). Overall, very little is known about how various land use types impact bee nesting (Sardinas et al., 2016) and more work is needed to improve our understanding of how different bee species respond to land management schemes (Winfree et al., 2011).

To date, much of our understanding of the role of landscape characteristics on pollinator communities and pollination services in agriculture come from studies carried out in areas of intensive agricultural use, such as California's central valley (reviewed by Winfree et al., 2011; Kennedy et al., 2013). Yet, if we want to advise managers on how to manage land to maximize the retention of wild pollinators, we also need studies in areas that exemplify a range of agricultural intensity and habitat types, including those of eastern Canada (e.g., Sheffield et al., 2008, 2013a). The cultivation of lowbush blueberry in New Brunswick, Canada, is unique because of the relatively high availability of natural habitat in the vicinity of growing areas. Unlike the majority of agricultural crops, lowbush blueberry is a wild plant that is native to the areas where it is farmed. Rather than planting into tilled soil, as in conventional agriculture, farmers remove the tree canopy from existing lowbush blueberry stands through a combination of deforestation and burning. The resulting landscape is a mosaic of managed blueberry

fields and intact Jack Pine (*Pinus banksiana*) forest, which is ideal for studying the role of forest remnants on crop pollination. Lowbush blueberry is buzz-pollinated, meaning that it is not effectively pollinated by honey bees, and depends on a diverse assemblage of wild pollinators to set fruit (Javorek et al., 2002; Fulton et al., 2015).

In this study we trapped pollinators and measured reproductive success of lowbush blueberry along forested and deforested field edges in order to address the following questions: (1) do the two edge types differ significantly in terms of their ability to provide a diversity of nesting habitats? (2) are there differences in the abundance and/or diversity of wild bees along the two edge types? (3) are there differences in reproductive success (i.e., flower number, fruit set) of blueberry plants found at the two edge types? (4) are plants in our fields pollen limited, and if so, does pollen limitation differ at the two edge types? Finally, we use GIS to explore whether landscape level differences in the use of lands surrounding blueberry fields impacts pollinator abundance and diversity and/or plant reproductive success.

2. Methods

2.1. Study system

Vaccinium angustifolium Ait. (Ericaceae), commonly known as lowbush blueberry, is a self-incompatible, clonal, perennial shrub native to northeastern North America (Vander Kloet, 1988). In southern New Brunswick, where this study took place, white, bell-shaped flowers are borne in clusters from May to June and berries ripen from late July to August. Pollen release of lowbush blueberry flowers occurs through the sonication of poricidal anthers, which is mainly carried out by native bees in the genera *Bombus* and *Andrena* (Javorek et al., 2002). Management of lowbush blueberry typically includes the biennial levelling of plants through either mechanical mowing or controlled burns. After levelling, plants require a full year, known as a 'sprout year', to recover and set fruit. Fruit is harvested from the fields in the years alternate to pruning, known as a 'crop year.' In this manner, only half of all fields in production are harvested in any given year (Agrifoods and Agriculture Canada, 2012).

2.2. Experimental design

A total of 15 managed lowbush blueberry fields were selected from an area of mixed forest and agricultural lands surrounding St. Stephen, New Brunswick, Canada (45°12'N, 67°17'W). Four fields were surveyed in 2010, and an additional 11 were surveyed in 2011. All selected fields had one edge bordering an area of undisturbed forest and an opposite edge bordering deforested habitat (see Table S1 in Supporting information).

2.2.1. Bee abundance and diversity

At the forested and deforested edges of each field, a transect line for sampling pollinators was placed among blueberry plants in a line parallel to and approximately 3 m from the edge. In 2010, five yellow pan traps (12 oz. plastic bowls; 17.6 cm diameter × 3.7 cm depth; Creative Converting, Clintonville, WI, USA) were dispersed along the length of each transect, approximately 8 m from one another. Traps were filled with a solution of water and propylene glycol. Captured insects were collected daily at 24-h intervals for 24 consecutive days from May 11 to June 4 ($N=24$ sampling periods). In 2011, the 2010 trapping protocol was modified to include yellow (28-3125-51 Lemon Yellow, Touch of Color, Creative Converting) and blue (28-3043-51 White) pan traps, in an attempt to increase the diversity of Hymenoptera attracted to the bowls (Campbell and Hanula, 2007). Transect lines contained six traps

(two per color), set out for one 24-h period per week, during the flowering period, May 17 until June 6 ($N=5$ sampling periods). Although pan traps may not always accurately reflect foraging bee diversity (Popic et al., 2013), we believe they are adequate for our purposes here. Netting has been highlighted as an alternate method for determining species diversity and abundance, however, it can be susceptible to collector bias, is harder to standardize, and, similar to pan traps, may miss taxa such as cleptoparasites that may not be captured near flowers (Roulston et al., 2007). To mitigate the existing criticisms of pan traps, we staked our traps at a height in line with the flowering canopy (~15 cm off the ground) rather than using ground-level traps (Tuell and Isaacs, 2009). Additionally, the use of multiple colours of pan traps is known to improve sampling diversity (Toler et al., 2005). Finally, our use of a paired edge design means that collection biases are consistent within and across fields.

All trapped bees were collected, stored in 70% ethanol, pinned and identified to species or, if that was not possible, to morphospecies (i.e., coarse groupings based on morphological characteristics (Oliver and Beattie, 1996)). Bees were identified using keys from several resources (Mitchell, 1960, 1962; LaBerge, 1971, 1980; Bouseman and LaBerge, 1978; McGinley, 1986; Michener, 2007). Samples from all pan traps along each transect were combined to estimate individual bee abundance and species diversity, calculated as the Simpson's diversity index (Simpson, 1949). Bee abundance was scaled by the total number of trapping hours and by the number of bowls, in order to account for variation in protocol by year.

2.2.2. Plant reproductive success

For each of the 15 fields, a transect line parallel to, and approximately 1 m towards the center of the field from the pan trap transect line, was established along each forested and deforested edge. Before the onset of flowering, 20 plants along each transect were haphazardly selected and marked. Study plants were selected to be at least 3 m apart in order to minimize the possibility of selecting clones (Bell et al., 2009). On each marked plant, two flowering stems were haphazardly selected; one stem was randomly assigned to a hand pollination treatment, while the other was assigned as the control. Hand pollination was performed daily during the entire flowering period (i.e., May 14–31 in 2010, May 17–June 6 in 2011). First, supplemental pollen was collected from unmarked plants by sonicating the back of the flower heads using an electric toothbrush and catching the falling pollen in a microcentrifuge tube. Collected pollen was then transferred to the anthers of all open flowers on one of the target stems. Flowers on the control stem of each pair were left open to ambient levels of pollination (i.e., open-pollinated). The total number of flowers produced by each stem over the growing season was determined by weekly counts of all open flowers and flower buds on the stem. Once fruit had matured, all berries from each marked stem were collected in early July and frozen in plastic bags at -18°C for transportation to the lab. Fruits were subsequently counted, and a subset of berries were thawed and dissected to count seeds. Seed count was estimated for the entire stem using the subset of berries.

2.2.3. Edge environment

Environmental data for all 15 fields were measured in the spring of 2012. Three sampling locations were selected along each field edge, approximately 20 m apart, and various measurements were taken at each location to determine light level, plant diversity, soil composition and nesting substrate diversity. Light level was measured in cloudless conditions on a single day between May 19–24 between 10 a.m. and 2 p.m., using a digital light meter (Fisher Scientific, Cat No. S90198). Because of variability in light-

level readings on the same day, canopy cover at each sampling location was also estimated using a spherical densitometer (Model A, Forest Densimeters, Rapid City, SD), by counting the number of points on the mirror grid covered by vegetation when held 1 m off the ground, and dividing by the total number of points on the mirror grid. Plant community diversity was determined by counting all plant species within a $0.5\text{ m} \times 0.5\text{ m}$ quadrat. Quadrat diversity was then calculated as Simpson's index of diversity (Simpson, 1949). To determine soil composition, three 20 g samples of topsoil were collected per sampling location and sent to the University of Guelph Agriculture and Food Laboratory Services to analyze pH, soil moisture, available nitrogen (NH_4^+ and NO_3^-), phosphorus (P), and potassium (K) levels. Finally, an index of nesting substrate diversity was determined by placing a $5\text{ m} \times 5\text{ m}$ plot at each sampling location and then exhaustively searching for the presence of potential pollinator nesting substrates (e.g., bare ground, leaf litter, vegetation, rocks, hollow twigs, dead wood, rodent burrows, rock cavities). The index of nesting diversity was calculated as the number of different nesting substrates recorded in the plot (Potts et al., 2003), averaged per edge.

2.3. Effect of surrounding land use

To determine the effect of the amount of forest (vs. other land use) on bee community and blueberry reproduction in the lands surrounding our experimental fields, circular zones of 1 km radius, chosen as a distance greater than the average foraging range of most native bee species collected in the pan traps (Gathmann and Tscharrntke, 2002; Greenleaf et al., 2007), were defined around a single geo-referenced point, representing the entry point from the main road into each field, using ArcGIS v.10 (ESRI, 2011). We grouped land cover into six categories using the codes from satellite maps obtained from Natural Resources Canada (Government of Canada, 2009a,b).

2.4. Statistical analyses

To test the hypothesis that the presence of forest adjacent to a field influences wild bee abundance and diversity we used linear mixed effects models, with field included as a random effect. Bee abundance was square-root transformed, and bee diversity was arc-sin square-root transformed in order to comply with the assumption of normality (Sokal and Rohlf, 1995). Because cleptoparasitic bees rely on a host species to collect pollen and rear their young, they are not expected to spend as much of their time foraging (Sheffield et al., 2013b). Therefore, to tease apart the effect of bee life history type (i.e., cleptoparasitic vs. pollen-collecting) on our edge effects we ran two separate analyses: one with all bee types and one without cleptoparasitic bees (Table 2).

To test whether field edge type was associated with differences in pollen limitation and plant reproductive success we fit additional GLMMs for fruit and seed set of open-pollinated blueberry stems, as well as for the pollen limitation of fruit and seed set between edge types. Fruit and seed set models were tested using fruit and seed counts per stem respectively, with the number of flowers per stem being included as an offset term (Zuur et al., 2009). All GLMMs included field as a random effect (or plant nested within field for the analysis of pollen limitation) and were fit with a negative binomial distribution to account for zero-inflation (Bolker, 2008). Because field edge type was significantly associated with bee abundance and diversity, these variables were excluded as confounding factors and assessed separately. We assessed whether the abundance and diversity of pollinating bees altered fruit or seed set using this separate model.

For all analyses of bee abundance, bee diversity, reproductive output, and pollen limitation, interaction effects were included to determine if field area, surrounding land use (i.e., forest cover), and sampling year were important factors affecting the results (i.e., whether they influenced model fit). Where appropriate, continuous predictors (i.e., field area, forest cover) were scaled and centered to improve interpretation of model coefficients. An information theoretic approach was used to compare the second-order Akaike's Information Criterion (AICc) and AICc weights between a subset consisting of the most plausible models. The model with the lowest AICc was selected as the optimal model. Significance of terms was determined using Wald chi-square tests (Bolker, 2008).

Paired *t*-tests were used to detect differences in several measured variables of forested and deforested field edges.

All statistical analyses were carried out using R Statistical Software (v.3.0.2) (R Development Core Team 2013). Mixed-effects models were fit using the *lme()* function in the *nlme* package, *glmer()* in the *lme4* package for binary data, and the *glmmadmb()* function for reproductive output and pollen limitation data. All means are reported as \pm SE.

3. Results

3.1. Bee abundance and diversity

In total, we identified 27 different species or morphospecies of bees trapped across the 15 fields. In order of decreasing abundance, these included representatives from the genera *Andrena*, *Nomada*, *Lasioglossum*, *Apis*, *Osmia*, *Bombus*, *Sphecodes*, *Augochlorella*, *Augochlora*, and *Ceratina*. Bee abundance was significantly lower along forested than deforested edges, while bee diversity showed the opposite trend, with forested edges exhibiting a significantly higher diversity of bees than deforested edges (Fig. 1, Table 1). When bee life history type was examined more closely, we discovered that cleptoparasitic bees were more abundant along forested edges ($X^2(1) = 40.32$, $P < 0.0001$) while non-parasitic (i.e., pollen-carrying) bees were more abundant along deforested edges (Table 1). When cleptoparasitic bees were excluded from the dataset, there was no longer a relationship between edge and bee diversity, indicating that the differences in species richness among edges was driven by the presence of more cleptoparasitic species along forested edges.

3.2. Plant reproductive success

The average number of open flowers per stem on adjacent blueberry plants ranged from 11.7 to 46.9 flowers/stem and was significantly lower along forested (21.8 ± 1.68 flowers/stem) compared to deforested edges (29.77 ± 3.04 flowers/stem) ($t = -3.07$, $df = 14$, $P = 0.0083$). In the optimal model testing fruit set of open-pollinated stems, field area and year improved model fit (Table 2), but did not significantly interact with edge type (Table 3). Overall, fruit set was higher on deforested edges and was also higher in 2010 than 2011 (Table 3). Fruit set was not associated with the abundance ($X^2(1) = 2.31$, $p = 0.128$) or diversity ($X^2(1) = 0.04$, $P = 0.837$) of pollinating bees. While edge type predicted fruit set, it only marginally predicted seed set in open-pollinated stems, and field area, forest cover or sampling year did not alter the effect of edge (Table 2; Table 3). Like fruit set, seed set was also higher in 2010 than 2011 (Table 3). There was no relationship between seed set and the abundance ($X^2(1) = 1.57$, $P = 0.2099$) or diversity ($X^2(1) = 0.28$, $P = 0.5955$) of pollinating bees.

Despite a detectable effect of pollination treatment on both seed and fruit set, it did not significantly interact with edge type (Table 3). The effect of edge and pollination treatment on seed and

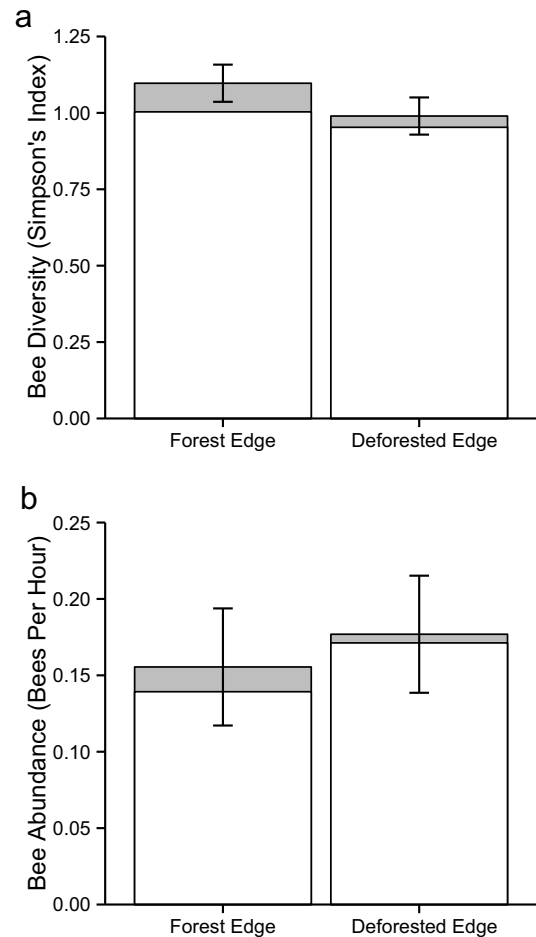


Fig. 1. a. Bee diversity (measured as Simpson's Index) for pan traps at the forested and deforested edges of lowbush blueberry fields. Shading represents the portion of each sample that is represented by cleptoparasitic species. b. Bee abundance (bees collected per hour) for pan traps at the forested and deforested edges of lowbush blueberry fields. Shading indicates the proportion of each sample that is represented by cleptoparasitic species.

Table 1

Effects of forested and deforested field edges on local bee abundance and diversity. Optimal models selected by AIC are presented, with *P* values determined through Wald chi-squared tests.

Variable	Estimate	SE	df	<i>F</i>	<i>P</i>
Pollinating and cleptoparasitic bees:					
Bee abundance					
intercept	0.155	0.0192	1,13	78.2	<0.0001
edge	0.021	0.00746	1,13	8.24	0.0131
forest cover	0.0146	0.0195	1,13	0.0869	0.773
edge × forest cover	-0.0179	0.00759	1,13	5.60	0.0342
Bee diversity					
intercept	1.10	0.0304	1,14	182e01	<0.0001
edge	-0.107	0.0362	1,14	8.77	0.0103
Pollinating bees:					
Bee abundance ^a					
intercept	0.124	0.0992	1,14	82.7	0.0001
edge	0.0319	0.00886	1,14	13.0	0.0029
forest cover	0.00272	0.0174	1,13	0.0246	0.878
edge × forest cover	-0.0166	0.00814	1,13	4.14	0.0627
Bee diversity					
intercept	1.00	0.0374	1,14	991	0.0001
edge	-0.0505	0.0417	1,14	1.47	0.246

Bold indicates *P*-values less than 0.05.

^a Significance of main effect terms calculated in the absence of non-significant interaction terms.

Table 2
Summary of model selection testing edge (edge) effect on fruit set and seed set (A, B) and whether pollen supplementation (pol) differs per edge (edge x pol) (C, D). The effect of forest cover (frs), field area (fld) and sampling year (yer) were also included to see if they improve the predictive value of edge. Only competitive models with $\Delta AICc < 2$ are shown (Burnham and Anderson, 2002).

Model	Intercept	AICc	$\Delta AICc$	w_i
A) Fruit Set (Open Pollinated)				
edge + yer + fld + edg:yer + edg:fld	−0.521	3593.4	0.00	0.410
edge + yer + edg:yer	−0.541	3594.0	0.580	0.306
edge + yer + frs + edg:yer + edg:frs	−0.552	3595.0	1.56	0.188
B) Seed Set (Open Pollinated)				
edge + yer + fld + edg:yer + edg:fld	3.02	7032.2	0.00	0.439
edge + yer + edg:yer	2.98	7033.0	0.780	0.297
C) Pollen Limitation (Fruit Set)				
edge + pol + yer + edg:pol + edg:yer + yer:pol + edg:pol:yer	−0.581	7156.8	0.00	0.510
edge + pol + yer + fld + edg:pol + edg:yer + yer:pol + edg:fld + fld:pol + edg:pol:yer + edg:pol:fld	−0.558	7157.4	0.620	0.375
D) Pollen Limitation (Seed Set)				
edge + pol + yer + fld + edg:pol + edg:yer + yer:pol + edg:fld + fld:pol + edg:pol:yer + edg:pol:fld	2.94	14285.4	0.00	0.359
edge + pol + yer + edg:pol + edg:yer + yer:pol + edg:pol:yer	2.91	14286.5	1.06	0.211
edge + pol + edg:pol	2.43	14286.5	1.10	0.207

Table 3

Optimal model selected to test edge effect on fruit set and seed set (A, B) and whether pollen supplementation differs per edge (edge x pollination) (C, D). The interaction of field area and sampling year with edge are also included where they improve model fit.

Model	Estimate	SE	X ²	df	P
A) Fruit Set (Open Pollinated) ^a					
intercept	−0.561	0.0912			
edge	0.112	0.0510	4.79	1	0.0286
field area	0.0861	0.045	3.75	1	0.0529
year	−0.429	0.103	17.4	1	3.12e-05
edge × field area	0.0565	0.0480	1.39	1	0.239
edge × year	0.112	0.117	0.920	1	0.338
B) Seed Set (Open Pollinated) ^a					
intercept	3.00	0.155			
edge	0.117	0.643	3.29	1	0.0699
field area	0.144	0.0778	3.43	1	0.0641
year	−0.629	0.178	12.5	1	0.000400
edge × field area	0.0844	0.0625	1.82	1	0.177
edge × year	0.0412	0.150	0.0753	1	0.784
C) Pollen Limitation (Fruit Set) ^a					
intercept	−0.594	0.0862			
edge	0.0944	0.0406	5.41	1	0.0200
pollination	0.0733	0.0282	6.76	1	0.00934
year	−0.4519	0.0964	22.0	1	2.74e-06
edge × pollination	−0.0304	0.0565	0.291	1	0.590
edge × year	0.0442	0.0903	0.239	1	0.625
pollination × year	−0.0623	0.0630	0.979	1	0.323
edge × pollination × year	−0.1594	0.0126	1.60	1	0.206
D) Pollen Limitation (Seed Set) ^a					
intercept	2.91	0.157			
edge	0.0894	0.0533	2.82	1	0.0931
pollination	0.0758	0.0387	3.84	1	0.0500
field area	0.124	0.0789	2.47	1	0.116
year	−0.625	0.180	12.1	1	0.000495
edge × pollination	0.019	0.168	0.00560	1	0.941
edge × field area	0.0864	0.0651	1.76	1	0.184
pollination × field area	−0.0777	0.0527	2.17	1	0.140
edge × year	0.0707	0.155	0.209	1	0.648
pollination × year	0.157	0.126	1.57	1	0.210
edge × pollination × field area	0.00524	0.0746	0.0049	1	0.944
edge × pollination × year	−0.160	0.179	0.804	1	0.370

Bold indicates *P*-values less than 0.05.

^a Significance of main effect terms calculated in the absence of non-significant interaction terms.

fruit set did not differ with forest cover, field area, or sampling year (Table 2; Table 3).

3.3. Edge environment

Forested and deforested edges exhibited significant differences in terms of light intensity, canopy cover and nesting substrate (Table 4). As expected, light intensity was higher and canopy cover was lower along deforested edges compared to forested edges, while the nesting substrate index was higher along forested edges compared to deforested edges. Blueberry plants adjacent to forested edges had fewer flowers per stem than those adjacent to deforested edges (Table 4).

3.4. Surrounding land use

On average, lands in the 1 km radius surrounding our fields were composed of forest (63.4%), other blueberry fields (26.0%), successional shrubs (5.1%), and other types of agriculture (0.81%). We did not detect an overall effect of the percentage of forest cover surrounding a field on bee abundance or diversity (Table 1). However, there was a positive association between the percentage of land covered by forest and the bee abundance along a field's forested edge, suggesting that fields embedded in more forested landscapes either support or attract a greater abundance of bees.

Table 4

Mean (SE) of environmental variables between forest and deforested edges of lowbush blueberry fields.

Environmental variable	Forested	Deforested	t_{14}	<i>P</i>
Light (fc)	287 (48.3)	466 (40.8)	−2.93	0.010
Canopy cover (%)	33.8 (7.55)	7.24 (3.18)	−3.46	0.00381
Plant diversity	0.489 (0.0237)	0.451 (0.0272)	−1.64	0.0869
Nesting substrate index	4.89 (0.336)	3.80 (0.281)	−2.51	0.0249
Soil moisture (% dry)	65.0 (6.46)	60.0 (4.90)	−0.787	0.444
Soil NH ₄ ⁺ (mg/kg dry)	66.5 (18.3)	67.6 (17.8)	−0.0509	0.960
Soil NO ₃ [−] (mg/kg dry)	58.0 (18.6)	76.9 (16.4)	−0.752	0.464
Soil P (mg/L soil dry)	18.7 (4.22)	23.9 (5.28)	−1.23	0.239
Soil K (mg/L soil dry)	97.8 (10.0)	105.7 (9.50)	−1.05	0.310
Soil pH	4.58 (0.09)	4.57 (0.0881)	0.0550	0.957

Bold indicates *P*-values less than 0.05.

4. Discussion

When pollinator habitat is disturbed or removed through human activity, the availability of wild bee nesting and/or foraging resources may be reduced, which can lead to a decrease in the abundance and diversity of wild pollinators (Winfree et al., 2009). Here we study the impacts of the removal of adjacent forest on the abundance and diversity of wild bee species, and the resulting crop yields, in an agricultural landscape. We found a higher diversity, but lower abundance of bees along forested than along deforested edges of lowbush blueberry fields. Blueberry plants in our study fields were significantly pollen limited, but there were no differences in pollen limitation among field edge types. Although plants at deforested edges had significantly more flowers and higher fruit set than those along forested edges, the lack of difference in pollen limitation suggests that differences in fruit set between edges were likely driven by resource, not pollinator, limitation. Further, we discovered that, while forested edges harboured more species of bees overall, the difference in diversity could largely be attributed to a higher number of cleptoparasitic bee species trapped along forested edges. Finally, we did not find a universal impact of large scale landscape use on the bee community or plant reproductive success, although, we report a positive association between the abundance of bees along the forested edges of fields and the proportion of forest cover in the lands surrounding.

The higher diversity of bees trapped along forested edges may be explained by a greater availability of nesting habitat. Higher nesting substrate index values (Table 4) along forested edges strongly suggest that more nesting opportunities were available to accommodate a greater diversity of bee species. When cleptoparasitic bees were removed from the diversity analysis, the effect of edge disappeared, suggesting that cleptoparasitic species are driving the higher Simpson's diversity index on forested edges. Cleptoparasitic bees are impacted by any habitat disturbance that disrupts the nesting of their host species. The presence of cleptoparasitic bees can therefore be an indication of high quality nesting habitat because they cannot be sustained without adequate host nests (Sheffield et al., 2013b). In our case, cleptoparasites were mostly from the subfamily Nomadinae, which parasitize a wide variety of host species (Michener, 2007). Our findings are consistent with a recent study of cleptoparasitic bee diversity across a wide spectrum of habitat disturbance types. Sheffield et al. (2013b) reported that areas characterized as low human disturbance, such as old fields and woodlands, contained a higher diversity of cleptoparasitic bee species than those with higher levels of disturbance, such as actively managed apple orchards. This is consistent with our findings, as well as with a growing literature demonstrating that undisturbed and semi-wild areas are particularly important for the conservation of bees with specialist requirements (e.g., above ground nesters, parasites, etc.) (Senapathi et al., 2015; Le Feon et al., 2016).

Although forested edges generally provided a greater diversity of nesting habitat, the abundance of pollinating bees tended to be higher along deforested edges. This finding suggests that while pollinating bees may nest along forested edges, they appear to prefer to forage along deforested edges, at least during the blueberry flowering season. This could be driven by our finding that blueberry plants along deforested edges experienced more sunlight, higher ambient temperatures, and produced more flowers per stem, on average, than plants along forested edges. Similar sized solitary bees to the ones caught in our study have been shown to have foraging distances of 100–1000 m depending on body size (Gathmann and Tschardt, 2002), while *Bombus* species can reportedly travel up to 1750 m (Walther-Hellwig and

Frankl, 2000; Knight et al., 2005a), and *Apis mellifera* up to 5 km (Beekman and Ratnieks, 2000). Given that the maximum distance between our transects was 100 m, even the smallest bees we caught would likely have had the ability to nest near, or within, the forested edge while still foraging throughout the adjacent blueberry field. We note that because our pollinator sampling was limited to the period of time (~3 weeks) that blueberry plants were in bloom, our bee sampling could be biased against finding bees along the forested edge. In addition to having a higher nesting index, the forested edges likely also harbour a wider variety of non-crop flowering plant species, which could provide critical forage during the period that blueberry is not in bloom. Previous studies have found that, due to temporal and spatial differences in bee foraging patterns, forests may provide seasonal resources that are not captured by 'snapshot' sampling regimes such as the one applied here (Tylianakis et al., 2005).

While bee species richness has been shown to be positively correlated with fruit and seed set in many studies (Steffan-Dewenter and Tschardt, 1997; Klein et al., 2003; Hoehn et al., 2008), we found no association. Lower fruit or seed set along forested edges could be indicative of either pollen or resource limitation; our pollen supplementation experiment helps to tease apart these factors. We found pollen limitation of fruit and seed set along both forested and deforested edges, but no difference between the two edge types (Table 3). Therefore, even though bees were more abundant along deforested edges, there was no associated reduction in pollen limitation. Fulton et al. (2015), in a study of lowbush blueberry in this same region, similarly found that in spite of clear pollen limitation, the addition of managed pollinators had only a limited, mixed impact on fruit set. They argued that factors other than pollination, including differences in plant resource availability, likely explain a large amount of variation in fruit set among plants and fields. In our fields, differences in fruit set are quite likely due to greater resource limitation on the forested edge: our environmental measures indicate that soil conditions along the two edge types were similar, but that plants along the shadier forested edges receive significantly less sunlight. Increased fruit abortion has been associated with low light levels in a number of crops (Cantagallo et al., 2004; Marcelis et al., 2004), including high-bush blueberry (Kim et al., 2011).

Recently, several prominent studies have made the case that in order to successfully conserve pollinator diversity, we need to move away from arguments that are predominantly agriculturally motivated (Kleijn et al., 2015; Senapathi et al., 2015). Our study illustrates why this is true – while we found little support for the hypothesis that habitat conservation alters pollen limitation or crop yields, we found plenty of support for the hypothesis that habitat is critical for pollinator diversity. Unfortunately, we know very little about what constitutes 'quality habitat' for wild pollinators. Most studies of pollinator habitat in agroecosystems have focused on broad categories, such as distance to 'natural' and 'semi-natural' areas (reviewed by Winfree et al., 2011), but not on what specific habitat characteristics are important to pollinator conservation. Moreover, there is little consensus about how to assess nesting capacity (Sardinas and Kremen, 2014), making it difficult to recommend what type of habitat to conserve or restore. Compounding this, most existing habitat assessment tools are intended for cavity nesting species, those that nest in hollow twigs, rotting wood, and other pre-formed cavities (Ehnstrom, 2001), even though the vast majority of native bee species are ground nesters (Cane, 1991). Finally, greater intensification is the dominant trend in agricultural landscapes, and land managers may fear that conserving habitat for mutualists could reduce profits, even though the opposite has been shown to be the case for some systems (e.g., Ricketts and Lonsdorf, 2013).

4.1. Conclusions

Globally, wild pollinators are in critical decline, largely due to the conversion of pollinator habitat to agriculture. Areas with a relatively low intensity of agricultural use, such as the lowbush blueberry growing regions of eastern Canada, are still in a good position to conserve critical pollinator habitat. We demonstrate that the presence of forested habitat along the edge of managed lowbush blueberry fields is associated with higher species diversity, but a lower overall abundance, of wild bees. Our finding of more cleptoparasitic species and a greater diversity of nesting habitat at forested edges, along with a higher abundance of pollinating bees at deforested edges, leads us to conclude that wild bees in these fields are likely nesting near the forested edges, but preferentially foraging closer to the flower-rich deforested edges during the blueberry bloom period. Although we find little support for the idea that the maintenance of natural or semi-natural habitat near fields directly increases crop yields, our study supports the idea that these areas provide critical habitat for nesting, especially for bees with specialized life histories. Growers and policy makers for these regions need to keep in mind that lowbush blueberry, with its unique reliance on wild pollinators, may be particularly vulnerable to the habitat loss that often accompanies an increase in the intensification of agriculture.

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