

Article

Large Remaining Forest Habitat Patches Help Preserve Wild Bee Diversity in Cultivated Blueberry Bush

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Abstract: Global declines in wild and managed bee populations represent a major concern for the agricultural industry. Such declines result, in part, from the loss of natural and semi-natural habitats in and around agricultural ecosystems. However, remaining forest patches in heavily modified landscapes represent nesting habitats that may be crucial to preserving wild bees and their services. Because wild bees are the main pollinators of fruit crops, preserving potential nesting habitats might be particularly important for the crops' yield and profitability. Here, we assessed whether the abundance and richness of visiting wild bees in blueberry crops relates to the amount of surrounding forest cover and if so, whether those relationships varied with spatial scale. Specifically, we sampled wild bee communities in 18 blueberry fields during the blooming period in Montérégie, Quebec, Canada, where sampling consisted of pan trap triplets and direct observation of flower visitors on blueberry bushes. Then, we quantified the proportion of forest in radii of 0.5 km, 1 km, and 2 km around each field. Wild bee abundance was positively related to the proportion of forest habitat surrounding the crop field, but the relationship for wild bee richness was less clear. Moreover, these relationships were strongest at 1 and 2 km radii of measured land cover. Overall, pollinator diversity was highest when at least 30% of the surrounding landscape consisted of forest patches, representing a total area of at least 1 km². Our results suggest that preserving large habitat patches in agricultural landscapes can help prevent further decline in wild bee diversity while maximizing pollination services to fruit crops.

Keywords: native bees; pollination ecology; biodiversity; pollinator conservation; habitat modification; scale; fruit crops



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1. Introduction

Agricultural ecosystems rely on both domesticated and wild bees for pollination [1]. Although managed honey bees (*Apis mellifera* Linnaeus) pollinate many crops, wild bees enhance pollination and yields even in the presence of honey bees [2–5]. Indeed, bee pollination services contribute to the productivity of >75% of the world's crop species [6,7]. Therefore, wild bees can substitute for the services that managed pollinators provide, replacing them either fully or partially [8], while often being more efficient [9]. Wild bees can also enhance productivity in plants that self-pollinate, and for which managed pollination is rare [8]. Clearly, as managed honey bees around the world face serious threats from diseases, pesticides, and other causes, wild bees represent an important insurance policy for agro-ecosystems [5].

Natural forest remnants in intensive agricultural landscapes can provide safe haven for insect pollinators [2,4]. Natural and semi-natural habitats around agricultural fields provide food and nesting resources that contribute to the long-term persistence of wild bee populations [8]. The presence of forest cover surrounding crop systems can therefore exert a

positive influence on wild bee diversity and the services they provide [3,4,8]. Nevertheless, explicit quantification of the amount of natural habitat necessary to maximize the diversity of visiting crops, as well as the spatial scale at which natural habitat availability has an influence, is crucial to inform landscape management.

Wild bees are an essential but underrated player in the production of blueberries in North America. In Canada, highbush blueberries (*Vaccinium corymbosum* L.) are the largest fruit commodity, representing an average market value of USD 220 M between 2015 and 2020 [10]. Despite producers relying heavily on honey bees for pollination, wild bees are the most efficient pollinators of highbush blueberry [11–14]. This likely results from wild bees' co-evolutionary history with highbush blueberries [14,15], which allows bees to deposit more pollen grains to the stigma per flower visit [13–15]. Furthermore, northern wild bees can forage during the cool, wet spring weather [13,15] typical of the highbush blueberry blooming season at northern latitudes (May–June). Nevertheless, it remains unclear how much natural habitat is required to sustain wild bee diversity and associated pollination services in blueberry fields.

Here, we assess whether the wild bee community observed in blueberry bushes during blooming relates to the adjacent natural cover. We predicted that the abundance and richness of wild bees in blueberry fields increase with the proportion of surrounding forest habitat. Furthermore, we investigated the spatial extent at which these relationships are strongest.

2. Materials and Methods

2.1. Study Area

The study was conducted in 18 highbush blueberry (*Vaccinium corymbosum* L.) fields (sampling sites) in Montérégie, Quebec, Canada (Figure 1). Fields included Patriot, Blueray, Burkley, and Bluecrop varieties, and had a surface area of at least 0.5 ha (Supplementary Material; Table S1). The sites were separated from one another by an average minimum distance of ~10 km (min. ~5 km and max. min. ~24 km). The study region included crops of corn, soybean, and hay, as well as smaller quantities of apple orchards, vineyards, and small fruit plantations, such as strawberry and blueberry fields [16]. Regarding natural land cover, the landscape consists of fragmented coniferous and deciduous forest patches, and semi-natural areas, such as grasslands, meadows, hedgerows, marshlands, pastures, and abandoned fields [17].

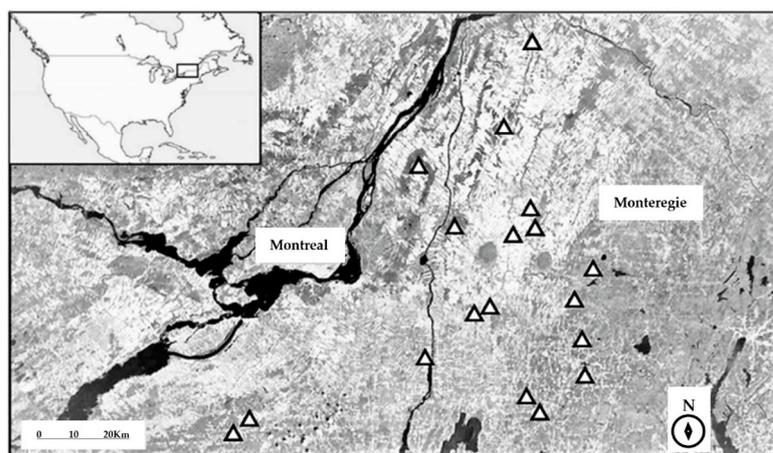


Figure 1. Distribution of highbush blueberry fields sampled in Montérégie region in Quebec, Canada. Triangles indicate the location of study sites.

2.2. Wild Bee Sampling

We performed two visiting rounds to each sampling field throughout the blooming season, from 23 May 2017 to 9 June 2017. At each field, we deployed 10 sampling stations in

a grid, with at least 10 m separating each station (Figure 2). We established a standardized quadrant distribution that would sample as much terrain as possible without exceeding the size of smaller crops. This distribution began at the western middle point of each field and progressed towards the east. To have a better representation of the bee community present in each field, we implemented two complementary sampling techniques: (i) visuals/observations of visits on blueberry flowers and (ii) pan trap triplets deployed on the ground.



Figure 2. Schematic representing the deployment of sampling stations with pan trap triplets (white, yellow, and blue), at a highbush blueberry field. Distance between stations along a given row is 10 m, the same distance separates each row.

The visual technique consisted of recording bees that entered the flower legitimately and apparently contacted the stigma [18]. A visual survey was performed on blooming sections of shrubs located in front of the pan trap triplets at standpoint view for 5 min at each sampling station, meaning 50 min observation per field per visiting round, for a total of 1800 min. We identified visiting bees on the fly by using a morphotype guide that included photos of bees present at blueberry bloom in the same region, in the previous year (i.e., 2016). Honey bees (*Apis mellifera* L.) and bumble bees (*Bombus* spp.) were identified to species on the fly. Morphotypes that were not in the photo guide, but observed foraging on blueberry flowers, were net captured. Because these crops were commercial, growers were worried about the potential negative impact of swinging a net over the shrubs during blooming season. Consequently, we only swung the net when deemed necessary in order to circumvent this issue. Collected specimens were later identified. The number of wild bees collected with this technique was described as *flower visits* while the variety of morphotypes was described as *visiting-richness*. The honey bee visits were counted but the data were not used in any statistical analysis.

Pan trapping is a standard method for sampling bees that reduces observer bias, although it may perform poorly for some taxa [17,19]. A pan trap triplet, as used in this study, was composed of three 500 mL plastic containers. Each container was painted with either fluorescent yellow or blue Krylon® paint on the interior surface or left unpainted as opaque white. Each container was filled with 250 mL of water and 1 drop of non-fragrant

liquid soap (detergent) to break surface tension [9,19]. At each sampling station, one pan trap triplet was installed (Figure 2). For the first visit, the traps were left to collect data for 24 h, while for the second round, they were kept for 48 h. As a result, 10 stations per site yielded a total of 30 sampling containers. After each sampling period, specimens were stored in 70% ethanol until pinned. The number of wild bees quantified with this technique was described as *trapped abundance* while the variety of morphotypes was described as *trapped richness*. To describe the expected general pattern, that is without distinguishing between data from the visual technique and the pan traps technique, the number of wild bees was referred to as *abundance* whereas the variety of morphotypes as *richness*.

Bees in the laboratory were identified using taxonomic classification books based on dichotomous keys such as the “Bee Genera of Eastern Canada” [20], “Bees of the World” [21], and “Bumble Bees of North America” [22]. Identification was validated by personnel from the Centre de Recherche et d’Innovation sur les Végétaux at Université Laval in Quebec City and the Entomological Collection Ouellet-Robert (QMOR) at Université de Montréal. Specimens not identified at the species level were assigned a morphotype.

2.3. Environmental Variables

Because daily fluctuations in temperature can affect the level of bee activity in blueberry fields [15], visual sampling took place between 10:00 h and 17:00 h on sunny to partially sunny days. Air temperature data were obtained from weather stations records available on Canada’s environmental and natural resources website (Government of Canada, 2017). The average minimum distance between a given sampling field and the closest weather station to that field was 8.8 km (min ~1 km; max. min ~17.8 km). Leaf temperature in the sampling sites was registered to have a more accurate indicator of how environmental temperature might affect bees’ presence. It was registered with a digital infrared thermometer Earme model GM320, within a standardized distance of 30 cm from blueberry leaves at every sampling station at the time of performing visual samplings.

2.4. Surrounding Land Cover

Five land cover types surrounding blueberry fields were identified: (1) agricultural [23], (2) forest/woodland, (3) urban, (4) water, and (5) abandoned/semi-natural areas [24], described as the remaining area in the landscape, which include spiny shrub vegetation, pasture fields, hydric herbaceous, and shrub vegetation [24]. Urban and water bodies categories were unrepresented (Supplementary Figure S1) and including them in the analysis did not add any information (data not presented here). Thus, they were not considered. Agricultural cover had the opposite effect of forest; because our objective was to study the effect of natural/seminatural cover, we also discarded agriculture from the analysis. All data were in vector format as shapefiles [25].

We extracted land cover types within radii of 500 m, 1000 m, and 2000 m (i.e., different spatial extents or scales) from the sampling sites using the buffer and clip tools in ArcGIS [25]. Then, we determined the proportional area that each landcover type occupied within the different radii. Sampling land cover at different scales has been used to characterize the surrounding landscape of focal sites in studies of crop pollination by native bees, and it has been shown that across scales, varying from 600 m to 4200 m radius, the coefficient of determination (R^2) for the positive relationship between bee flower visit and the proportion of nearby natural land cover, reaches a plateau at ca. 2000 m radius [26]. Therefore, we were interested in testing our prediction at the 2000 m radius. However, we sampled at the three scales to determine if the relationship between bee community structure and natural land cover would hold across those scales.

2.5. Statistical Analysis

The statistical analyses for the visual data and for the pan traps data were carried out separately for three reasons. First, the sampling protocol and effort differ between sampling techniques; second, the visual data allows making a more plausible connection between the

wild bee community and the pollination service bees provide to blueberry crops; third, the pan traps data in parallel with the visual data, allows visualizing that wild bee conservation in agricultural areas is possible if, at least, a given proportion of natural cover is maintained in the landscape. We predicted that flower visits (the number of individuals) and *visiting-richness* (the number of morphotypes), as well as trapped abundance and trapped richness, of wild bees, observed in blueberry fields, were positively related to the proportion of available forest habitat surrounding blueberry fields. To evaluate this prediction, we first fitted four simple regression models separately, one for each case: flower visits, *visiting-richness*, trapped abundance, and trapped richness, as a function of the proportion of forest land cover.

We then fitted multiple regressions models to evaluate potentially important factors (i.e., confounding factors) whose omission might result in biased estimations of the forest land cover effect on the wild bee communities. Four factors were initially considered: (i) shrub density (number of blueberry plants per hectare), (ii) air temperature, (iii) leaf temperature, and (iv) abandoned fields cover. However, air temperature and leaf temperature were collinear ($r = 0.52$, $p = 0.027$). Because collinear predictors can impact parameter estimates and potentially reduce the predictive accuracy of models, we retained only one of the collinear factors (see below). Each factor we modeled was retained a priori according to the rationales described below. Shrub density was considered because a higher density may represent more resources and result in higher bee abundance and richness. Leaf temperature was taken into account as ectothermic organisms (such as bees) alter their activity in response to environmental temperatures. The temperature of the sampling day could potentially affect the number of bees present in the field of focus, making it an important factor to consider. Abandoned fields were included because they are considered semi-natural habitats and have been suggested to support wild bee communities and therefore promote pollination services in agricultural fields [4]. To assess a given confounding factor while accounting for the effect of forest land cover, we added that given factor as a covariate to the initial model built on forest land cover only. We also assessed each confounding factor independently, i.e., without accounting for the effect of forest land cover (details below).

We used generalized linear models (GLMs) because our response variables were point count data, and count data often present Poisson or Negative Binomial distributions properties [27]. As there were five sites out of 18 with zero values for trapped wild bee abundance and richness, we also used Hurdle models to investigate whether the zero and positive values of the pan traps data were explained by the independent variables [28,29].

For each variable that we modeled, we reported the incidence rate ratio (IRR) estimate and its significance based on 95% confidence intervals. We did not consider the effects that multiple confounding factors at once may have on the forest land cover model, since our focus was to determine how a single confounding factor might modify the effect of forest. Furthermore, including several (>2) terms in the model might result in overfitting given our sample size ($n = 18$), causing model parameters to be heavily affected by the noise, and therefore increase the error in the model's predictions [30].

To assess the strength of evidence of the effect of each independent variable on the dependent variables, in a uni- or bi-variate model, we fitted generalized linear models (GLMs), followed by estimates of the Akaike information criteria for small samples (AICc) [31,32]. We further reported the Nagelkerke's likelihood ratio adjusted pseudo- R^2 value for each model as the goodness of fit measure. For GLMs, Nagelkerke's R^2 is equivalent to the adjusted- R^2 of multiple OLS regressions [33,34]. All GLMs were performed after testing for overdispersion in the conditional distribution of the outcome variables. We also tested for spatial autocorrelation in the models' residuals to evaluate data independence. In all cases, no spatial autocorrelation was detected ($-0.14 < \text{Moran } I < 0.09$; $p > 0.09$).

Finally, to evaluate the spatial extend-dependency of the results, we report the observed relationship between independent and dependent variables for each studied scale (500 m, 1000 m, and 2000 m radius). Poisson regressions were fitted with the function `glm` from the package `stats` v3.4.3 [35], negative binomial regressions with the function

glm.nb from the package MASS [36] and Hurdle models with the function Hurdle from the package pscl v1.5.5 [29]. Spatial autocorrelation was tested with the function testSpatialAutocorrelation from the package DHARMA [37]. All the analyses were performed in R version 3.6.3 [35].

3. Results

We sampled 39 different wild bee morphotypes, corresponding to 12 genera (Table 1). A total of 659 bees were observed visiting flowers legitimately, i.e., through visual observation, whereas 69 bees were captured with pan traps. Admittedly, the low number of bees caught with pan traps might cast doubt on our ability to accurately estimate community structure with this technique. However, wild bees seem to be caught in low numbers in berry crops [38] and orchards [39]. Nevertheless, we proceeded to test our prediction with the data collected for that purpose.

Table 1. Total number of observed (visual survey) flower visits per bee pollinator morphotypes in highbush blueberry fields in Montérégie, Quebec. * Did not take part in the statistical analysis.

Pollinator	Flower Visits	Flower Visits (%)
* <i>Apis mellifera</i>	293	-
<i>Andrena</i>	152	23.07
<i>Bombus bimaculatus</i>	4	0.61
<i>Bombus impatiens</i>	374	56.75
<i>Bombus perplexus</i>	1	0.15
<i>Bombus ternarius</i>	57	8.65
<i>Bombus terricola</i>	1	0.15
<i>Halictid green</i>	12	1.82
<i>Metallic black bee</i>	8	1.21
<i>Small black bee</i>	50	7.59

Based on the visual technique, *Bombus* spp. and *Andrena* spp. dominated the flower visits, with 66.3% and 23.07% respectively. *Bombus* spp. was represented by five distinguishable species (Table 1): *B. impatiens* was the most abundant species at most sites, comprising nearly 85.5% of all sampled bumble bees; *B. ternarius* followed in importance with approximately 13%; *B. bimaculatus*, *B. terricola*, and *B. perplexus* showed less than 1% of the total individuals observed.

In the pan traps (Table 2), *Lasioglossum* spp. and *Andrena* spp. were the most abundant bees, representing 46.38% and 20.29% of trapped abundance, respectively. *Colletes* spp. and *Ceratina* spp. were among the least represented pollinators, with less than 3% of the trapped abundance. *Bombus* spp. was not captured with this technique.

Table 2. Total number of bees morphotypes (trapped richness) and individuals (trapped abundance) captured in pan trap triplets in highbush blueberry fields in Montérégie, Quebec. * Did not take part in the statistical analysis.

Pollinator	Trapped Richness	Trapped Abundance	Relative Abundance (%)
* <i>Apis mellifera</i>	1	5	-
<i>Andrena</i>	8	14	20.29
<i>Augochlorella</i>	1	4	5.8
<i>Ceratina</i>	2	2	2.9
<i>Colletes</i>	1	2	2.9
<i>Lasioglossum</i>	11	32	46.38
<i>Nomada</i>	2	4	5.8
<i>Osmia</i>	5	6	8.7
<i>Sphecodes</i>	1	5	7.25

3.1. Surrounding Land Cover

The proportion of forest land cover (Supplementary Figure S1), mainly deciduous forests, increased from 18% to 27% with increasing spatial extent, but the proportion of abandoned fields, mostly scrublands, meadows, and pastures, decreased from 40% to 31%. Agricultural habitats, water bodies, and urban structures remained unchanged across scales, representing respectively 39, 2.5, and <1% of land cover.

3.2. The Influence of Natural Habitat

We predicted that wild bee abundance and richness would be positively related to the proportion of available forest habitat surrounding blueberry fields. Recall that we show the results from the visual and pan traps techniques separately.

Based on the GLMs for the observational data (Table 3), we found that forest land cover alone had a statistically significant and positive effect on bee flower visits at the 1000 and 2000 m radii (IRR > 1; Figure 3b,c), but not at the 500 m radius (Figure 3a). When potentially confounding factors were added to the models on bee flower visits, i.e., fitting bivariate models, the effect of forest cover remained positive and statistically significant. However, the bivariate model was not significant when leaf surface temperature was included as a covariate in the forest model. Leaf temperature, after controlling for forest effect, showed no effect either (Table 3). Overall, the confounding factors had no effect on wild bee flower visits. For visiting-richness, we did not find a correlation between forest land cover, confounding factors, and the number of morphotypes visiting blueberry flowers at the three different scales (Figure 3d–f, Table 3). This could be due to limited visual observations or a small sample size.

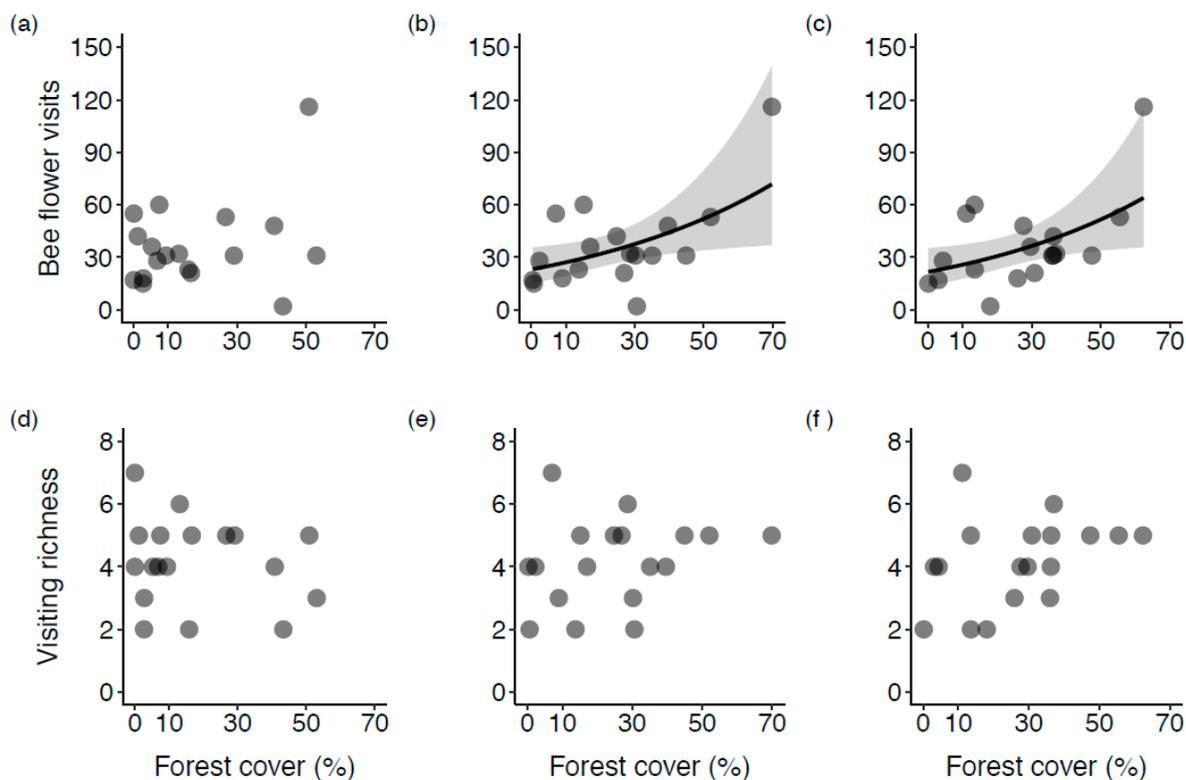


Figure 3. The relationship of wild bee flower visits (a–c) and visiting richness (d–f), as a function of the proportion of forest land cover habitat at 500 m, 1000 m, and 2000 m scales (from left to right) at the sampled highbush blueberry fields in Montréal, Canada. Models for bee flower visits are Negative Binomial regressions whereas models for visiting richness are Poisson regressions. Grey area represents confidence intervals. Only statistically significant fitted lines are plotted.

Table 3. Generalized linear models for visual data showing the relationship of wild bee flower visits and visiting richness as a function of different factors at 2000 m, 1000 m, and 500 m radii. Incidence Rate Ratios (IRR) and their 95% Confidence Intervals are presented for each variable in the models. Forest, in bold font, is the main factor to be tested whereas Covariate corresponds to potentially confounding factors. Flower visits represent Negative Binomial models; Visiting richness represents Poisson models. Statistically significant effects are shown in bold.

Radius (m)	Flower Visits	Forest		Covariate	
	Model	IRR	95% CI	IRR	95% CI
2000	Forest	1.018	1.004–1.032		
	Forest + Abandoned Fields	1.017	1.004–1.032	1.002	0.984–1.022
	Forest + Temperature	1.016	0.999–1.034	0.979	0.849–1.130
	Forest + Shrub Density	1.018	1.004–1.032	1.000	1.000–1.000
1000	Forest	1.016	1.004–1.030		
	Forest + Abandoned Fields	1.016	1.004–1.030	1.000	0.983–1.018
	Forest + Temperature	1.015	1.000–1.031	0.977	0.853–1.120
	Forest + Shrub Density	1.016	1.004–1.030	1.000	1.000–1.000
500	Forest	1.010	0.995–1.027		
	Forest + Abandoned Fields	1.010	0.995–1.026	1.006	0.991–1.021
	Forest + Temperature	1.005	0.986–1.024	0.923	0.794–1.069
	Forest + Shrub Density	1.010	0.995–1.027	1.000	1.000–1.000
Visiting Richness					
2000	Forest	1.007	0.993–1.020		
	Forest + Abandoned Fields	1.006	0.993–1.019	1.003	0.986–1.019
	Forest + Temperature	1.009	0.993–1.025	1.035	0.908–1.180
	Forest + Shrub Density	1.006	0.993–1.020	1.000	1.000–1.000
1000	Forest	1.004	0.992–1.016		
	Forest + Abandoned Fields	1.004	0.990–1.016	1.003	0.988–1.018
	Forest + Temperature	1.005	0.991–1.020	1.019	0.896–1.160
	Forest + Shrub Density	1.004	0.991–1.016	1.000	1.000–1.000
500	Forest	0.997	0.983–1.010		
	Forest + Abandoned Fields	0.997	0.983–1.010	1.003	0.991–1.013
	Forest + Temperature	0.995	0.980–1.010	0.973	0.862–1.099
	Forest + Shrub Density	0.997	0.983–1.010	1.000	1.000–1.000

The GLMs for the pan trap data (Table 4) showed that, at the 2000 m radius, the effect of forest land cover on the abundance of trapped wild bees was positive and statistically significant in both univariate (Figure 4c) and bivariate models (IRR > 1). In the bivariate models, the confounding factors showed no effect at this scale. At the 1000 m radius, forest alone (Figure 4b) or modeled together with shrub density showed a positive and significant effect on trapped abundance, but not when it was modeled together with abandoned fields, which showed a positive and significant effect (Table 4). At the 500 m radius, forest alone (Figure 4a) or modeled together with a confounding factor (Table 4) did not affect bee-trapped abundance. Instead, abandoned fields showed a positive and significant effect on trapped abundance after accounting for forest land cover. Regarding wild bee richness from pan traps (Table 4), forest land cover modeled alone (Figure 4d–f) or together with a confounding factor, showed no effect on the number of morphotypes captured in the blueberry fields; this was consistent across the three different scales. In contrast, after

accounting for forest land cover, abandoned fields showed a positive and significant effect on the wild bee trapped richness at the 1000 m and 500 m radii (Table 4).

Table 4. Generalized linear models for pan traps data showing the relationship of trapped abundance and trapped richness of wild bees as a function of different factors at 2000 m, 1000 m, and 500 m radii. Incidence Rate Ratios (IRR) and their 95% Confidence Intervals are presented for each variable in the models. Forest, in bold font, is the main factor to be tested whereas Covariate corresponds to potentially confounding factors. Both trapped abundance and richness represent Negative Binomial models. Statistically significant effects are shown in bold.

Trapped Abundance		Forest		Covariate	
Radius (m)	Model	IRR	95% CI	IRR	95% CI
2000	Forest	1.040	1.009–1.075		
	Forest + Abandoned Fields	1.037	1.008–1.070	1.028	0.986–1.078
	Forest + Temperature	1.041	1.006–1.082	1.011	0.760–1.340
	Forest + Shrub Density	1.042	1.010–1.077	1.000	1.000–1.000
1000	Forest	1.035	1.001–1.072		
	Forest + Abandoned Fields	1.021	0.991–1.054	1.044	1.002–1.091
	Forest + Temperature	1.032	0.997–1.072	0.950	0.717–1.250
	Forest + Shrub Density	1.036	1.003–1.074	1.000	1.000–1.000
500	Forest	1.006	0.966–1.050		
	Forest + Abandoned Fields	0.999	0.966–1.033	1.047	1.013–1.086
	Forest + Temperature	1.003	0.960–1.048	0.871	0.635–1.185
	Forest + Shrub Density	1.007	0.967–1.052	1.000	1.000–1.000
Trapped Richness					
2000	Forest	1.028	0.999–1.061		
	Forest + Abandoned Fields	1.026	0.999–1.055	1.029	0.992–1.072
	Forest + Temperature	1.028	0.995–1.066	0.994	0.756–1.303
	Forest + Shrub Density	1.029	1.000–1.062	1.000	1.000–1.000
1000	Forest	1.024	0.994–1.057		
	Forest + Abandoned Fields	1.012	0.985–1.041	1.040	1.004–1.081
	Forest + Temperature	1.022	0.989–1.058	0.956	0.731–1.243
	Forest + Shrub Density	1.026	0.996–1.060	1.000	1.000–1.000
500	Forest	1.001	0.966–1.038		
	Forest + Abandoned Fields	0.997	0.968–1.026	1.040	1.013–1.072
	Forest + Temperature	0.996	0.959–1.034	0.883	0.667–1.156
	Forest + Shrub Density	1.002	0.968–1.040	1.000	1.000–1.000

The Zero-Hurdle models (due to the number of sites with no bee data) showed that none of the independent variables determined a zero or a positive value of wild bee trapped abundance (Table S5) or trapped richness (Table S6) in a given blueberry field. However, the truncated or Count-Hurdle models revealed that forest land cover, but not the confounding variables, had a statistically significant effect on the positive values of trapped abundance (Figure 5b,c; Table S5) and trapped richness (Figure 5e,f; Table S6). This result was consistent at the 2000 m and 1000 m radii. Neither forest land cover nor the confounding variables showed any effect on wild bee trapped abundance or richness at the 500 m radius (Figure 5a,d).

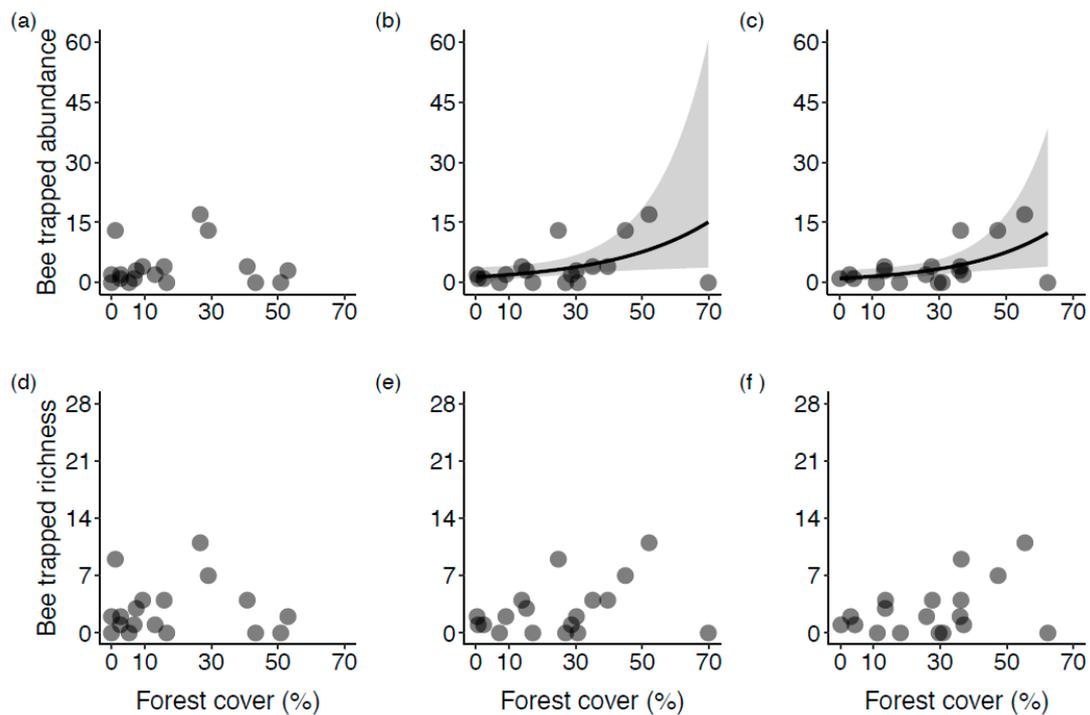


Figure 4. The relationship of wild bee trapped abundance (a–c) and trapped richness (d–f), as a function of the proportion of forest land cover habitat at 500 m, 1000 m, and 2000 m scales (from left to right) at the sampled highbush blueberry fields in Montérégie, Canada. Models for trapped abundance and trapped richness are Negative Binomial regressions. Grey area represents confidence intervals. Only statistically significant fitted lines are plotted.

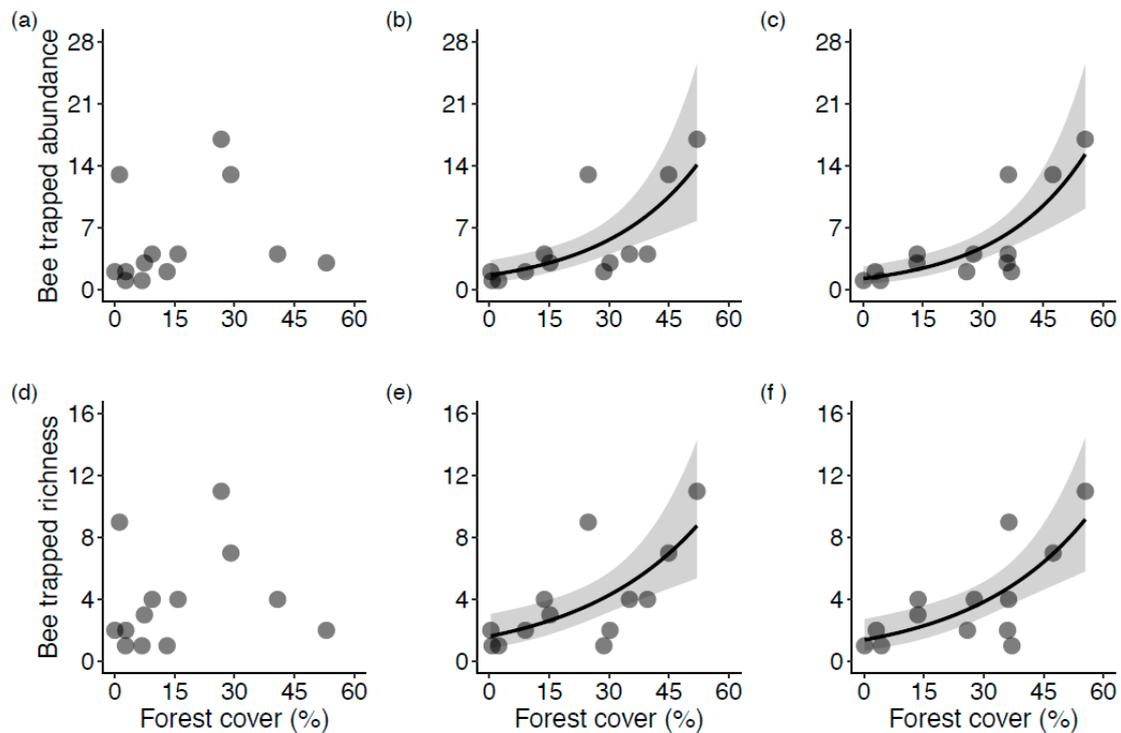


Figure 5. The relationship of wild bee trapped abundance (a–c) and trapped richness (d–f), as a function of the proportion of forest land cover habitat at 500 m, 1000 m, and 2000 m scales (from left to right) at the sampled highbush blueberry fields in Montérégie, Canada. Models for trapped abundance and trapped richness are Hurdle Negative Binomial regressions fitted on positive counts only. Grey area represents confidence intervals. Only statistically significant fitted lines are plotted.

In terms of goodness of fit (Nagelkerke's R^2) and the strength of evidence (AICc), the GLM models based on the visual technique data (Table S2) indicate that forest land cover is a predictor stronger than the confounding factors, of wild bee flower visits at the 2000 m and 1000 m scales. At the 500 m scale, however, leaf temperature was the most important predictor of flower visits, whereas forest land cover and abandoned fields came in second and third place, respectively. For the visiting richness, the result shows that plant density, forest cover, and abandoned fields were the first, second and third most important predictors respectively; this was consistent across the three scales (Table S2). The models based on pan traps data (Table S3) show that forest is the strongest predictor of wild bee trapped abundance and trapped richness observed in the blueberry fields (not visiting flowers) only at the 2000 m scale; at the 1000 m and 500 m scale, forest's importance falls much below the importance of abandoned fields, which became the main predictor (Table S3). Regarding Count-Hurdle models for the pan traps data (Table S4), the results showed that forest land cover was the most important factor in explaining the spatial variation of both trapped abundance and trapped richness in the blueberry fields, at the 2000 m and 1000 m scales (Figure 5b,c,e,f). Abandoned fields and plant density were among the second most important predictors of trapped abundance and richness at those scales (Table S4). At 500 m radius, abandoned fields and leaf temperature were the first and second most important variables, respectively, in accounting for the spatial variations of abundance and richness. Forest land cover was the third most important predictor of wild bee trapped abundance at this scale, but not of trapped richness (Table S4).

4. Discussion

The results were consistent with our predictions that higher values of wild bee abundance and richness would be associated with a larger proportion of forested land cover. This relationship at 2000 m and 1000 m scales is in accordance with earlier studies suggesting that the presence of bees in crops and thus pollination services rely on natural areas adjacent to farmlands [18,26,40,41]. At 500 m, however, this relationship was not observed. Our results indicate that forest land cover near blueberry fields can help sustain the abundance, richness, and flower visitation of wild bees in these crops.

4.1. The Effect of Forest Proportion on Wild Bee Diversity in Blueberry Fields

Blueberry fields in areas with a larger proportion of remaining forest had higher flower visits and higher number of wild bee species (Figures 3b,c, 4b,c, and 5b–d,f), which is consistent with previous similar studies. For example, Watson et al. [41] found that wild bee abundance was positively related to the proportion of forest land cover surrounding sampled apple orchards. Similarly, Benjamin et al. [18] showed that wild bee abundance decreases with agricultural land cover within 300 m and 1500 m radii. However, a study also conducted in fruit crops of southern Quebec concluded that fruit crops diversity in the region as well as the proximity to suburban areas had a positive effect on wild bee diversity (richness and abundance) at the landscape level (380–2000 m radii) [42]. As such, our study somewhat contradicts these results, but one has to consider that Martins et al. [42] also included apple orchards and raspberry fields in their study, which differ from the specific wild bee species composition from blueberry field. Other factors to consider that potentially can result in differences in abundance and richness of pollinators between studies are the differences in sampling effort, the sampling techniques, and the sampled fields' surroundings.

The higher numbers of flower visits and bees associated with a higher proportion of forest cover observed in this study are relevant from the pollination service perspective [26,40] and therefore to blueberry production [3]. Evidence shows that different types of crop production increase with the frequency of wild bee flower visits [43–45]. In blueberry fields, wild bee pollination efficiency is known to be two to four times higher than that of honey bees [11,13], but see [46]. In this study, the lack of data on yield from a larger number of farms prevented us from assessing fruit set. Nevertheless, the evidence indicates that

farmers may be able to increase the production of marketable fruits by increasing natural area near their blueberry fields.

Although the proportion of surrounding abandoned fields did not influence the number of bee flower visits and abundance in pan traps, it had a strong and positive influence on bee richness, which aligns with a previous study in the same region. Martins et al. [42] studied local- and landscape-level drivers of bee diversity and argued that wild bee abundance and richness observed in croplands (including apple orchards, raspberry and blueberry fields), respond positively to hedgerows and meadows habitats because they provide nesting and foraging resources for wild bee communities observed in those crops. Hedgerows and meadows habitats are included in the abandoned fields category in the present study.

4.2. The Role of Bumble Bees and Incidental Visitors

Our results indicate that bumble bees in southern Quebec are the most active native pollinators on highbush blueberry flowers during blooming (Table 1). Indeed, as previously stated, the genus *Bombus* spp., with five species, accounted for 66.3% of the observed wild bee abundance. Estimates for a geographic region near to our study area, show that *Bombus* spp. provide ~75% of the pollination in blueberry fields nested in landscapes dominated by woodland and ~5% in commercial fields [15]. Similarly, *Bombus* spp. would pollinate up to 6.5 flowers in the same lapse of time that honeybees would pollinate one flower [13]. Arguably, *Bombus* spp. is the most efficient pollinator in these agroecosystems due to its co-evolutionary history with *Vaccinium* spp. and its sonification pollination behaviour [15,47,48]. Conversely, bees caught in the pan traps seemed to be incidental visitors that had little part in the highbush blueberry crops' pollination. However, andrenid bees and halictid bees are among the pollinators observed to perform high rates of legitimate flower visits to blueberry flowers [15].

Although *B. impatiens* represented 85.5% of all sampled bumble bees, its presence is unlikely to be related to managed colonies; growers participating in this study reported no use of commercial *B. impatiens* to provide sufficient pollination, but its use should not be disregarded. A study over 150 years of *Bombus* records in northeastern US, indicates that 11 out of 16 species show declining trends while seven species have increased, with *B. impatiens* being the most successful wild bee [49]. Plausible reasons for population shifts in wild bees may include but are not limited to landscape changes, fragmentation of optimal bee habitat, climate change, pesticide impact, ecological displacement by competition, and the use of managed colonies of species such as *B. impatiens* [14,49,50].

4.3. Assessing the Effective Spatial Scale of Natural Habitat Preservation

The spatial extent to which preserving natural habitat patches is meaningful remains poorly explored. Here, wild bee abundance, richness, and rates of visitations are positively associated with the amount of forest habitats available in a 1- or 2-km radius around blueberry fields. However, there is no such relationship when considering forest habitat cover in a 0.5-km radius. These results are consistent with the fact that some wild bees are known to forage in a 2-km radius from their nest, while others can go as far as 11 km or more [44,45,50–52]. Further, ground-nesting bee abundance has been reported to increase in sites with higher forest cover within 2 km [53], and croplands farther than 2 km from natural areas show a decrease in visitation rate [3]. Together, these results might reflect the ability of wild bees to travel long distances, but also that the sampling distance of 500 m, at least in this study, did not capture the forested source where the bees come from.

4.4. Landscape Management and Conservation Perspectives

Our research can be used as a guide to determine how much natural habitat should be preserved around highbush blueberry crops. It is recommended that the distance considered when assessing the availability of natural habitat should be no less than 500 m, but preferably stay between 1 and 2 km. Approximately 30% of the area around farms should be dedicated to forest habitats, as this is the minimum amount of cover that should

be provided. Moreover, to guarantee optimal pollination of neighboring crops, it is recommended that forest remnants should have a minimum area of 1 km². Despite the rarity of large forest patches in the study region and in other intensively farmed areas globally, there are still various measures that could be taken to ensure these patches can provide pollinator habitats. Monitoring patch sizes in agricultural landscapes and establishing buffer zones around forest patches with native trees and shrubs are two possible ways to protect them from land use changes. Additionally, creating pollinator-friendly habitat corridors to connect larger remnant patches and educating farmers and landowners about the importance of preserving and increasing pollinator habitats are important actions that should be taken.

Developing landscape management strategies to maintain wild bee diversity in agricultural ecosystems also requires considering both natural and semi-natural habitat types. Our results suggest that abandoned fields can be an important factor for wild bee abundance and richness at the 500 m scale (Table 3). Abandoned fields, being considered as a semi-natural land cover, positively influence wild bee diversity, perhaps because they provide alternative nesting habitats, or harbor a high diversity of flowers. We suggest that this might be particularly true when forest habitats are not well represented in the landscape. Therefore, strategic landscape management that favors semi-natural habitats as well could benefit wild bee diversity in agroecosystem settings. Clearly, wild bee conservation strategies should consider the availability of natural and semi-natural habitat patches at multiple spatial scales.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d15030405/s1>, Figure S1. Boxplots showing the proportional area of different land cover types sampled within (a) 500 m, (b) 1000 m, and (c) 2000 m radii in the landscape surrounding highbush blueberry fields; Table S1: Geographic coordinates, area, and highbush shrub density; Table S2: GLM based on visual technique data; Table S3: GLM based on pan trap data; Table S4: Count-Hurdle models for pan traps data; Table S5: Zero-Hurdle models for wild bee trapped abundance; Table S6: Zero-Hurdle models for wild bee trapped richness.

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