Spring 5-11-2019

Landscape Pattern and Wild Bee Communities in Maine

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Recommended Citation

Du Clos, Brianne, "Landscape Pattern and Wild Bee Communities in Maine" (2019). *Electronic Theses and Dissertations*. 2970.
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LANDSCAPE PATTERN AND WILD BEE COMMUNITIES IN MAINE

By

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A DISSERTATION

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

May 2019

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LANDSCAPE PATTERN AND WILD BEE COMMUNITIES IN MAINE

By Brianne Elizabeth Du Clos

Dissertation Co-Advisors: Dr. Cynthia S. Loftin and Dr. Francis A. Drummond

An Abstract of the Dissertation Presented
in Partial Fulfillment of the Requirements for the
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Commercial production of lowbush blueberry (*Vaccinium angustifolium* Aiton) in Maine relies primarily on managed honeybee hives; however, naturally occurring wild bees are more efficient pollinators of the crop. Wild bees have short foraging distances and must nest near crop fields to provide pollination services. After crop bloom, the surrounding landscape must provide sufficient forage to maintain wild bee populations for the remainder of the growing season. Lowbush blueberries in Maine are produced in a mixed-use landscape with two distinct landscape contexts. Here, we document bee communities and habitat resources (nesting and floral) in power line rights-of-way and eight land cover types including and surrounding lowbush blueberry fields. We assess landscape pattern surrounding crop fields in the two contrasting contexts and determine any effect of arrangement of habitat patches on wild bee abundance or diversity. Additionally, we use our field data to inform and validate predictions of wild bee abundance from a spatial model applied to the lowbush blueberry production landscape and assess any influence of landscape pattern on prediction accuracy. Finally, we describe a collaboration with lowbush blueberry growers to develop an interactive web mapping tool that provides maps of habitat resources and predicted wild bee abundance.

We documented 168 wild bee species across 72 study sites; three bee species had not been previously recorded in Maine. Power line rights-of-way had diverse and abundant bee communities owing to high habitat quality, especially within resource-poor landscapes near lowbush blueberry fields. We observed abundant floral resources in lowbush blueberry fields, forest edges, and small towns and found ample nesting resources in lowbush blueberry fields and shrubby wetlands. Bees were less abundant and diverse in a homogeneous landscape context; however, that homogeneity led to more accurate model predictions of bee abundance in crop fields. We improved prediction accuracy in a mixed-use landscape and produced accurate predictions in non-crop land cover types in a heterogeneous landscape context; however, we found that predictions of wild bee abundance in crop fields are influenced by landscape heterogeneity. The maps we share through the web tool aid growers and other stakeholders in developing pollination management and conservation plans.

ACKNOWLEDGEMENTS

This work was supported by the U.S. Department of Agriculture National Institute of Food and Agriculture – Specialty Crops Research Initiative Contract/Grant/Agreement No. 2011-51181-30673, Northeast Sustainable Agriculture and Research Education Grant GNE14-076, a Senator George J. Mitchell Center for Sustainability Solutions – Sustainability Research Grant, the Wild Blueberry Commission of Maine, and the University of Maine and Maine Department of Inland Fisheries and Wildlife through the Cooperative Agreement with the U.S. Geological Survey Maine Cooperative Fish and Wildlife Research Unit.

My co-advisors, Cyndy Loftin and Frank Drummond, have been incredible mentors. I am grateful for the guidance, patience, and expertise they provided in the development, execution, and completion of this work. I am especially appreciative of the time and effort they put in to continue providing for me as the years dragged on; it got a bit rough at times, but we finally did it. Working for them has been the best. I am grateful for the experiences I had working with each of my additional committee members: Dana Bauer, Alison Dibble, and Sam Hanes. Their expertise enriched and improved this work.

Thank you to my student technicians for assistance in fieldwork and preparing collected specimens for identification: Jacob Eddy, Randi Jackson, Sam Kenney, Ellie McCarthy, Deanna Phipps, and Crystal Thomes. Thank you to Judy Collins and Elissa Ballman and their student technicians for assistance and collaboration in fieldwork and specimen preparation. Thank you also to the landowners for allowing me to sample bees and plants on their property.

Thank you to the taxonomic experts who taught and assisted me in bee and plant identification: Sara Bushmann, Alison Dibble, Frank Drummond, Sam Droege, Jason Gibbs, and Rob Jean. Drs. Bushmann, Dibble, and Drummond created an engaging and enriching course at the Eagle Hill Institute that provided a very strong foundation for my nascent bee identification skills. I am also grateful to Sam Droege at the U.S. Geological Survey Native Bee Identification and Monitoring Lab for allowing me to spend a few days at the lab for a crash course in identification and specimen management.

BeeMapper would not have been possible without an interdisciplinary collaborative development effort initiated and fostered by Sam Hanes. Dr. Hanes provided funding, found technical support, suggested growers to test the tool, and provided me with an incredible skill set that I am excited to take with me moving forward. Thank you so much. Rob Powell at the University of Maine underwent a herculean effort to assemble the technical infrastructure behind BeeMapper, and I am incredibly appreciative of his work. I am grateful to the University of Maine Cooperative Extension and the Advanced Computing Group for providing website space and server space for BeeMapper to live on. And finally, I am grateful to the growers who took the time to provide their input on the tool. BeeMapper would not be what it is without them.

Thank you to my lab mates, office mates, colleagues, and friends at UMaine. Thank you to the Darling Marine Center for welcoming a landlubber for a couple of years and providing me with an incredible space to work. Thank you to the administrative staff of the Department of Wildlife, Fisheries, and Conservation Biology for being so wonderful.

Most importantly, thank you to my family, for their unwavering support and unceasing encouragement as I chugged along through graduate school. You all are my ultimate motivation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

WILD BEE COMMUNITIES IN POWER LINE RIGHTS-OF-WAY IN MAINE'S LOWBUSH BLUEBERRY PRODUCTION LANDSCAPE

1.1 Introduction

Lowbush blueberry (*Vaccinium angustifolium* Aiton) is a North American native plant that is commercially harvested in Maine, U.S.A., and eastern Canada. Managed honeybees (*Apis mellifera* L.) and sometimes bumble bees (*Bombus impatiens* Cresson) are used to pollinate lowbush blueberry in late spring (Drummond 2012; Hanes et al. 2015; Asare et al. 2017), though >100 wild bee species, some of which are more efficient pollinators (Kevan et al. 1990; Javorek et al. 2002; Drummond 2016), have been observed in blooming crop fields (Bushmann and Drummond 2015). Wild bees require floral resources pre- and post-crop bloom to sustain their populations. Many of the most abundant wild bee pollinators of lowbush blueberry are small bees with short foraging distances (Bushmann and Drummond 2015; Groff et al. 2016); therefore, additional floral resources must be located near crop fields to be beneficial. Field margins and planted floral strips have been explored as floral resources for lowbush blueberry pollinators beyond crop bloom (Venturini et al. 2017a; McCallum and McLean 2017; Drummond et al. 2017a); however, off-farm habitat surrounding crop fields may also provide these resources (Groff et al. 2016; Chapter 2, this dissertation).

There are 14,500 km of high-voltage power line rights-of-way (ROW) in New England (ISO New England 2019), which are managed as open, herb and shrub-dominated early-successional habitat to prevent trees or tall shrubs from reaching power lines. Power line ROW provide nesting and floral resources for wild bees (Russell et al. 2005, 2018) and a source of bee habitat throughout New England's closed canopy forest-dominated landscape (Lanham and

Whitehead 2010; Hill and Bartomeus 2016; Eldegard et al. 2017; Steinert et al. 2018). The plant communities within ROW create novel habitat comparable to semi-natural grasslands (Hill and Bartomeus 2016; Eldegard et al. 2017), though they are sensitive to environmental context, particularly site productivity (Eldegard et al. 2017; Steinert et al. 2018). Studies on butterfly communities in ROW reveal that less intensive vegetation management promotes diverse butterfly assemblages, including endangered species such as the Karner Blue (*Lycaeides melissa samuelis* Nabokov) and Frosted Elfin (*Calloprhys irus* Godast) along with threatened plant species (Smallidge et al. 1996; Swengel 1996, Forrester et al. 2005; Collins and Foré 2009; Leston and Koper 2016). Bumble bee communities (*Bombus* spp.) also thrive within ROW (Hill and Bartomeus 2016). Although ROW have been assessed as solitary bee habitat (Russell et al. 2005, 2018; Wagner et al. 2014a,b; Sydenham et al. 2016, 2017), few studies exist of ROW as bee habitat relative to nearby crop fields.

In Maine's lowbush blueberry production landscape, the late spring mass-flowering crop provides substantial forage for wild bees over a three week period every other year (Bushmann and Drummond 2015; Yarborough 2009). Mass flowering crops can promote the density and diversity of bumble bees and solitary bees (Westphal 2003; Diekotter et al. 2013; Holzschuh et al. 2013); however, other studies have found the opposite effect (Holzschuh et al. 2011, 2016; but see Magrach et al. 2018). Early-season mass flowering crops lead to greater bee abundance in both nearby semi-natural habitat and late season flowering crops when there is more semi-natural habitat in the surrounding landscape (Diekotter et al. 2010; Riedinger et al. 2014) and enhance bee communities in the following year (Riedinger et al. 2015). The flowering crops can promote bee communities in semi-natural habitats that provide nesting habitat and floral resources beyond crop bloom (Kovács-Hostyanski et al. 2013; Holzschuh et al. 2016); therefore, both local and landscape-scale effects determine how bees use habitat near crop fields.

We sought to reveal the role of power line ROW as semi-natural bee habitat relative to nearby mass flowering lowbush blueberries in Maine. Our study asks the following questions: 1) Do bee communities differ in power line ROW near to and isolated from mass flowering crop fields? 2) Do bee communities in power line ROW vary with landscape context? We expect bee communities to be more diverse and abundant in ROW near crop fields owing to population spillover, and we expect greater bee abundance and diversity in ROW within a landscape that provides few other sources of bee habitat. We also surveyed floral resources available in power line ROW to assess local-scale effects on bee communities.

1.2 Methods

1.2.1 Study area and spatial data

The Maine lowbush blueberry production landscape covers approximately 750,000 ha of coastal Maine, U.S.A (44-45°N, 67.5-69.5°W), and consists of two major growing regions with contrasting landscape contexts (Fig. 1.1). The Downeast region contains the largest and most intensively managed lowbush blueberry fields in Maine (0.05-1800 ha, average field size 21.4 ha) in a matrix dominated by managed coniferous forest. Non-blueberry agriculture and developed land cover are scattered and comprise little of this relatively homogeneous, rural landscape. In contrast, the Midcoast region is heterogeneous, containing smaller, less intensively managed crop fields (0.05-15.6 ha, average field size 8.26 ha) interspersed with other agriculture, including pasture, orchards, and small, diversified farms. Developed land in small towns is more prevalent in the Midcoast region than the Downeast region. The matrix in the Midcoast region is deciduous forest-dominant and less intensively harvested.

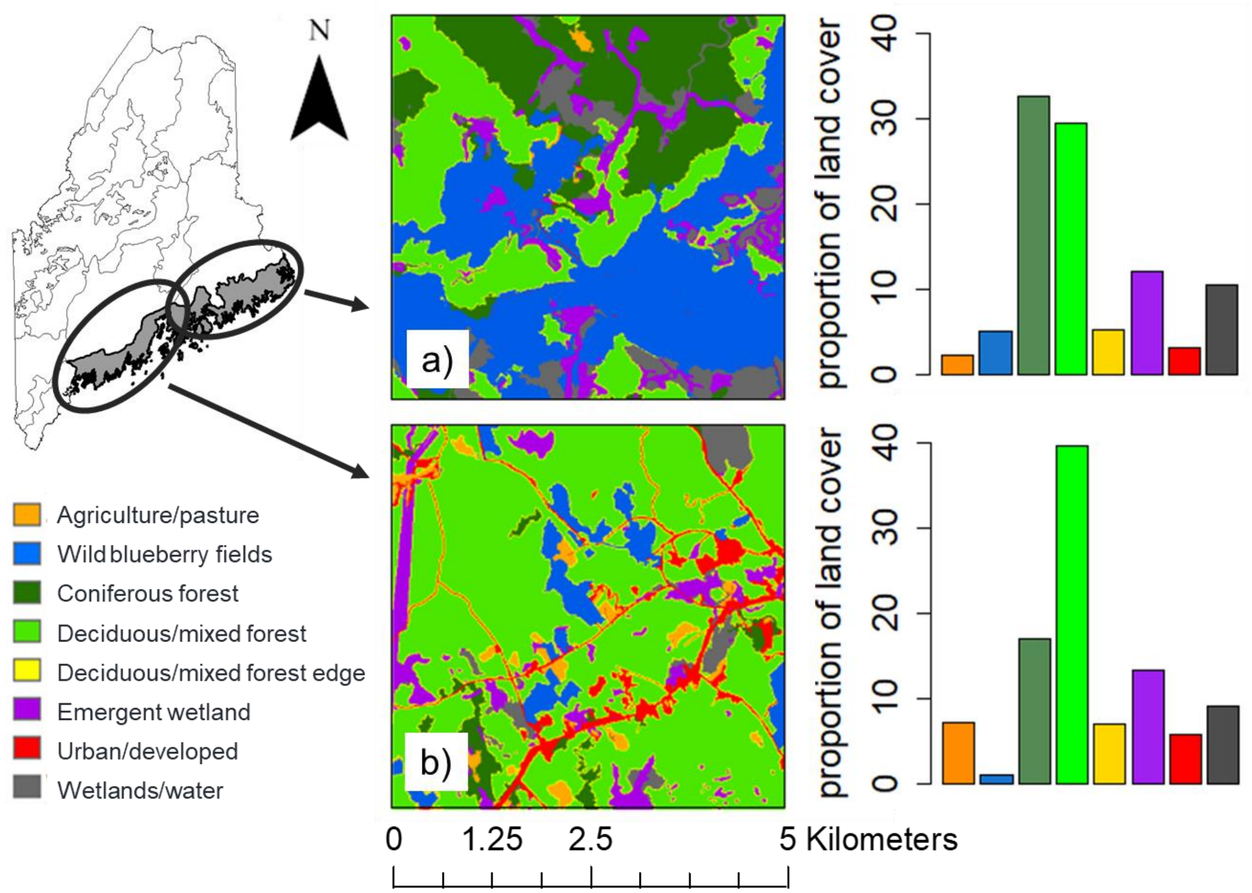

Figure 1.1. Extent of the Downeast and Midcoast growing regions within the Maine, USA, lowbush blueberry production landscape. Map insets display representative landscape contexts of the a) Downeast and b) Midcoast growing regions. Bar charts indicate proportion of eight land cover types in the Downeast (top) and Midcoast (bottom) growing regions.

We developed a land cover map of the Maine lowbush blueberry production landscape that combines the 2004 Maine Landcover Dataset (https://www.maine.gov/megis/catalog/metadata /melcd.html) with ancillary data on roads, railroads, and wetlands (Groff et al. 2016; Chapter 3; this dissertation). The prepared map has 10 m pixel size and eight land cover classes representing different floral and nesting resources (Chapters 2 and 3, this dissertation) for wild bees: agriculture/pasture, consisting of small diversified farms, orchard crops, or pasture; lowbush blueberry fields; coniferous forest; deciduous/mixed forest; deciduous/mixed forest edge; emergent wetland, an aggregation of forested wetland and scrub-shrub land cover; wetlands/water; and urban/developed areas.

1.2.2. Field sampling and site characteristics

We used our land cover map to select potential field sites, then visited each site on the ground to confirm suitability for sampling. Access to the ROW sites was granted by the power companies (Central Maine Power; Emera Maine). We conducted surveys during the 2013-2015 growing seasons. In 2013, we sampled six sites in the Downeast region; three were isolated from (≥1 km) and three were near (within 150-300 m) lowbush blueberry fields. In 2014 and 2015, we established six study sites in both growing regions (12 sites total each year) within power line ROW 30-40 m wide; in each region, three were isolated from and three were near lowbush blueberry fields. Sites were distributed within growing regions so that they could all be sampled on the same day, and all sites were at least 2.5 km apart (range 2.5-13.7 km, mean 6.1 km) to minimize overlap in bee communities. We sampled the same isolated sites in both growing regions in 2014 and 2015 and sampled different near sites if the nearby crop field was not in flower that year. We reestablished one isolated site Downeast owing to lost access between 2013 and 2014. All three near sites sampled Downeast in 2013 were resampled in 2015 (Fig. 1.2).

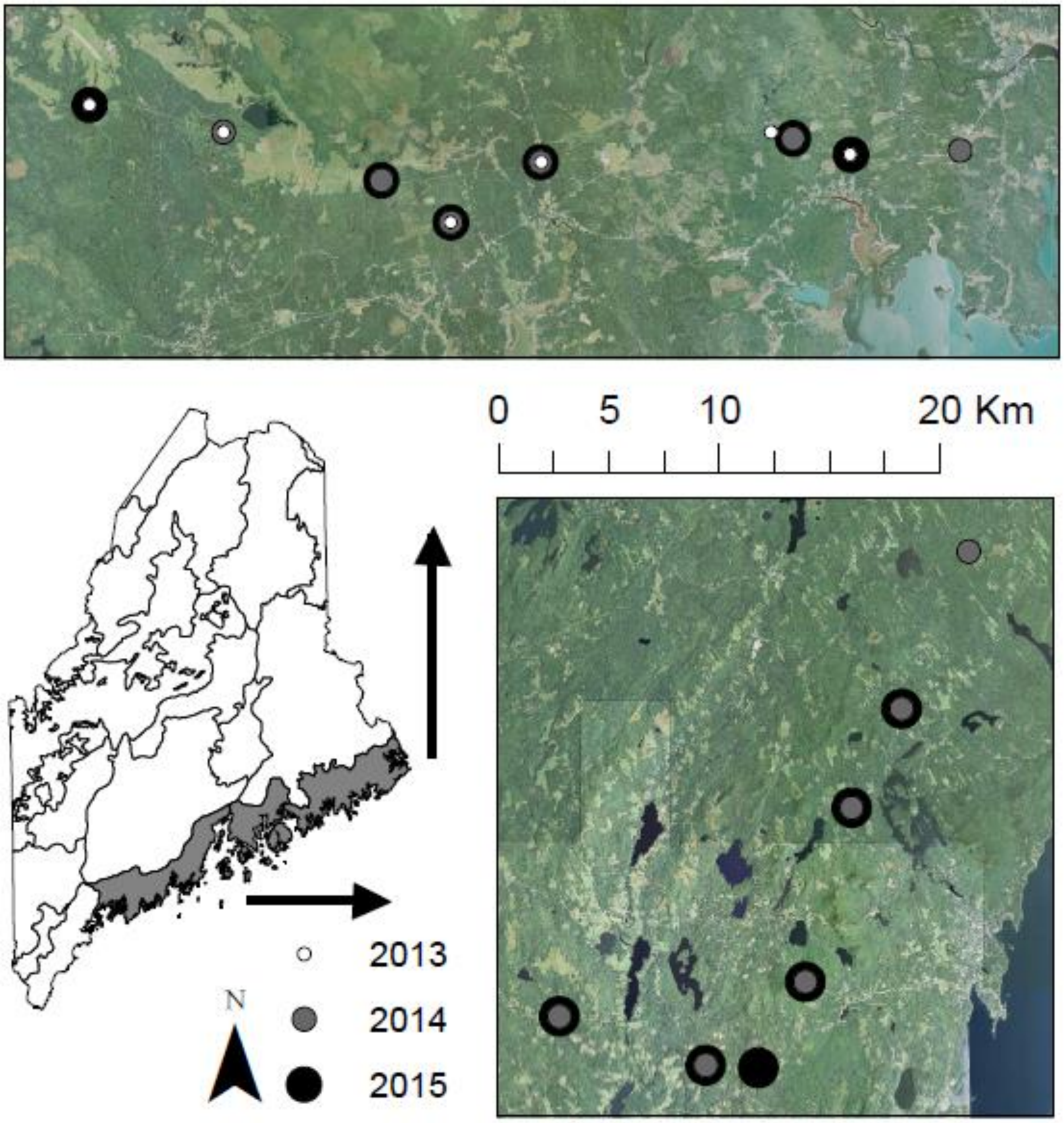

Figure 1.2. Power line ROW sampling site locations in the Downeast (top) and Midcoast (right) growing regions of the Maine, USA (left) lowbush blueberry production landscape. Many sites were sampled in multiple years from 2013-2015, as indicated by the map symbols.

We sampled sites in early (27 May-12 June), mid-(7-18 July), and late (7 Aug-21 Sept) season each year to capture seasonal variability in bee communities (Chapter 2, this dissertation). Sampling occurred on days that maximized bee activity with clear or bright cloudy skies with minimal wind and early morning temperatures >13°C (Bushmann and Drummond 2015). We surveyed bee diversity and abundance by placing a set of three cup traps (one each in fluorescent blue, yellow, and white; New Horizons Supported Services, Inc.) every 10 meters along a 150 m transect placed in the center of the ROW. Each cup contained approximately 85 ml of water and a drop of dish soap to break water tension (Droege 2015). Captured bees were collected from the bowl traps after 24 hours. We then walked along the transect for one hour, live netting foraging bees observed on flowers. We excluded honeybees from live netting owing to our interest in assessing wild bee communities, though honeybees were sometimes captured in bowl traps. Managed *Bombus impatiens* brought in for lowbush blueberry pollination could also have been present but were not differentiated; therefore, our collection may include specimens of *B. impatiens* from purchased quads. Using both bowl traps and live netting captures a more complete bee community (Wilson et al. 2008). All collected specimens were cleaned and stored in ethanol (bowl trapped) or frozen (live netted) until pinned. We identified pinned specimens to the lowest taxonomic level possible with reference to the keys of DiscoverLife.org and Haverty and Larder (1988), and obtained species-level verifications from Dr. Sara Bushmann, George Stevens Academy; Sam Droege, U.S. Geological Survey Native Bee Inventory and Monitoring Lab; Dr. Jason Gibbs, University of Manitoba; or Dr. Robert Jean, Environmental Solutions and Innovations, Inc. We gathered nesting preference, social habit, and body size of each species from the literature.

We established two 25 m long transects parallel to our bee sampling transect at 10 m and 100 m to record floral resources. We conducted floral resource surveys after collecting bowl traps during each sampling period at all sites in 2014-2015. For each blooming patch intersecting a transect up to 1 m on either side, we recorded plant species, patch size in m^2 and percent bloom. Reference specimens of each blooming plant species were collected and pressed to confirm species identification, and all identifications were confirmed by a botanist (Dr. Alison C. Dibble, University of Maine).

We calculated landscape composition surrounding our ROW transects at four spatial extents: 100, 250, 500, and 1000 m, by measuring the percentage of each land cover type present (PLAND) in Fragstats 4.2 (McGarigal et al. 2012). Landscape variables at these spatial extents influence bee abundance and species richness (Steffan-Dewenter et al. 2002; Chapter 2, this dissertation).

1.2.3. Statistical analyses

We conducted all statistical analyses in R v.3.5.0 (R Core Team 2018). Honeybees captured in bowl traps were excluded from statistical analyses. We evaluated annual and seasonal differences in bee abundance and species richness with Kruskal-Wallis tests, then determined seasonal differences post-hoc with Dunn’s test of multiple comparisons with the package dunn.test (Dinno 2017). We tested for temporal autocorrelation with the Durbin-Watson test in the package car (Fox and Weisberg 2011). We tested for spatial autocorrelation with Mantel tests on bee abundance and species richness at all focal spatial scales (100, 250, 500, and 1000 m) with the package ade4 (Dray and Dufour 2007).

We compared landscape composition and floral resource availability at our sampling sites across growing regions and site types. We compared the percentage of all eight land cover types at our four spatial scales with Mann-Whitney U tests. Floral abundance was aggregated over the entire growing season. We multiplied patch size by percent bloom for each species, then summed those values for a cumulative value. Floral species richness is the total number of blooming plant species counted over the growing season. We used simple linear regression to model floral abundance and species richness by growing region and site type, as the floral data were normally distributed and homoscedastic.

We sorted bee species into four body size classes: small (<6 mm), medium (6-9 mm), large (9-12 mm), and extra-large (>12 mm) (Russell et al. 2018). We did not include males, specimens with an undetermined sex or species identification, or queens in our body size analyses. Bees were labeled as ground or cavity nesting, though we did not include *Bombus* spp. or bees with an undetermined species identification in our nesting habit analyses. Lastly, bees were labeled as social or solitary, and we did not include bees with an undetermined species identification in our sociality analyses.

We assessed differences in bee communities across growing regions and site types with generalized linear models (GLMs) calculated with the R package MASS (Venables and Ripley 2002) and determined significant relationships with post-hoc analysis of deviance. We modeled the influence of site type, growing region, and a type x region interaction on bee abundance and species richness overall and with respect to nesting habit, sociality, and body size. Models of overall bee abundance and species richness had negative binomial error distributions owing to overdispersion, whereas, with the exception of solitary bee species richness, models of bee abundance and species richness by life history traits had Poisson error distributions. We then determined if landscape composition or floral resource availability across growing regions or site types influenced bee communities with GLMs and analysis of deviance. We targeted this series of models to explain the overall and life history-associated bee community model results, only modeling the significant relationships they revealed. We modeled bee communities with percent of each land cover type at each spatial scale; solitary bees were modeled with negative binomial error, and all other models had a Poisson error distribution.

1.3. Results

1.3.1. Bee community summary

We collected 2,121 bee specimens representing six families, 27 genera, and 125 species (Table 1.1). In 2013, we collected 225 bees representing 52 species in the Downeast growing region. Sites near lowbush blueberry fields had 147 bees representing 39 species, and isolated sites had 78 bees representing 27 species. In 2014, we collected 847 bees from 92 species across both the Midcoast and Downeast growing regions, and in 2015, we collected 1,049 bees from 95 species across both regions. Across all three sampling years, we collected 1,177 bees from 107 species in sampling sites near lowbush blueberry fields and 944 bees from 98 species in sites isolated from lowbush blueberry fields.

The most abundant bee species collected was the sweat bee *Lasioglossum cressonii* (Robertson) (535 individuals collected). Other common bees included the bumblebees *Bombus ternarius* (Say) (249) and *Bombus vagans* (Smith) (159) and the sweat bee *Augochlorella aurata* (Smith) (193). Uncommon bee genera included *Colletes* and *Osmia*, both of which contain species associated with lowbush blueberry. We collected two specimens of *Macropis nuda* (Provancher), a rare solitary bee that specializes on oils produced by *Lysimachia* spp., a plant group we found throughout our ROW sites in both growing regions. We also collected one new state record for Maine with one specimen of *Melitta americana* (Smith), a rare specialist of *Vaccinium* spp., particularly cranberry; this specimen was collected Downeast, where wild cranberry (*Vaccinium macrocarpon* Aiton) is abundant (Jones et al. 2014). A complete list of bee species, their size class, and the site types and growing regions in which they were collected is presented in Table 1.1.

We found annual differences in bee communities between 2013 and 2014 (Dunn's test abundance Z=-2.14, p=0.01) and 2013 and 2015 (abundance Z=3.44, p<0.001, species richness Z=-2.40, p=0.001), with no differences between 2014 and 2015. Bee abundance was temporally autocorrelated when 2013 data were included in analyses (Durbin-Watson test statistic=1.36, p=0.03); however, species richness was not (D-W=1.77, p=0.28). As we only sampled Downeast at different times of the growing season in 2013, we conducted all bee community data analyses on specimens collected in 2014 and 2015. Bee abundance and species richness changed throughout the sampling season (Kruskal-Wallis abundance χ^2=19.19, df=3, p<0.001, species richness χ^2=23.30, df=3, p<0.001). Bees were less abundant (538 individuals) and species rich (62 species) in the late season than early (595 individuals, 63 species) or mid-season (976 individuals, 88 species), with no significant differences in abundance or species richness between early and mid-season. We found no temporal autocorrelation in our data for bee abundance (DW=2.07, p=0.72) or species richness (DW=2.16, p=0.98) in 2014-2015. Further, we found no spatial autocorrelation within growing regions across sampling years (Mantel test: Midcoast abundance r=-0.12, p=0.79, species richness r=0.14, p=0.15; Downeast abundance r=-0.19, p=0.98, species richness r=-0.04, p=0.59).

Table 1.1. Bee species collected within power line rights-of-way in the Maine, USA lowbush blueberry production landscape, 2013-2015. Sites were located in rights-of-way near to (N) or isolated from (I) lowbush blueberry fields in the Downeast or Midcoast growing region. Species nomenclature was collected from DiscoverLife.org; introduced species are indicated with "(i)" (Dibble et al. 2017). Information on nesting habit, sociality, and body size was collected from the literature, though we did not gather this information for bees with an undetermined species identification; those specimens are marked "N/A".

	Nesting habit	**Sociality**	**Body size**	**Downeast**		**Midcoast**		**Total**
Family Andrenidae				N	I	N	I	
Andrena alleghaniensis Viereck, 1907	Ground	Solitary	Med	0	0	0	1	1
Andrena braccata Viereck, 1907	Ground	Solitary	X-Lg	3	0	1	1	5
Andrena canadensis Dalla Torre, 1896	Ground	Solitary	Med	5	0	0	0	5
Andrena carlini Cockerell, 1901	Ground	Solitary	X-Lg	2	1	6	1	10
Andrena carolina Viereck, 1909	Ground	Solitary	Med	1	6	4	1	12
Andrena crataegi Robertson, 1895	Ground	Solitary/ Communal	Lg	4	1	1	7	13
Andrena distans Provancher, 1888	Ground	Solitary	Med	0	0	1	1	2
Andrena forbesii Robertson, 1891	Ground	Solitary	Lg	0	0	0	1	1
Andrena frigida Smith, 1853	Ground	Solitary	Lg	2	0	0	0	2
Andrena hirticincta Provancher, 1888	Ground	Solitary	Lg	4	2	1	2	9
Andrena imitatrix Cresson, 1872	Ground	Solitary	Lg	3	2	0	0	5
Andrena integra Smith, 1853	Ground	Solitary	Med	1	0	0	0	1
Andrena miranda Smith, 1879	Ground	Solitary	X-Lg	1	1	1	2	5
Andrena nasonii Robertson, 1895	Ground	Solitary	Lg	0	0	0	1	1
Andrena nigrihirta Ashmead, 1890	Ground	Solitary	Lg	0	0	1	1	2
Andrena nivalis Smith, 1853	Ground	Solitary	X-Lg	9	0	1	3	13
Andrena nubecula Smith, 1853	Ground	Solitary	Med	2	0	0	0	2
Andrena nuda Robertson, 1891	Ground	Solitary	Med	0	1	1	5	7
Andrena personata Robertson, 1897	Ground	Solitary	Sm	0	0	0	1	1

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Table 1.1 Continued.

Andrena rufosignata Cockerell, 1902	Ground	Solitary	Med	6	8	0	3	17
Andrena rugosa Robertson, 1891	Ground	Solitary	Med	1	0	0	3	4
Andrena sigmundi Cockerell, 1902	Ground	Solitary	Lg	5	3	0	1	9
Andrena spiraeana Robertson, 1895	Ground	Solitary	Lg	0	0	0	1	1
Andrena thaspii Graenicher, 1903	Ground	Solitary	Lg	4	0	1	1	6
Andrena vicina Smith, 1853	Ground	Solitary	X-Lg	1	0	0	1	2
Andrena virginiana Mitchell, 1960	Ground	Solitary	Med	3	3	0	0	6
Andrena wilkella Kirby, 1802 (i)	Ground	Solitary	Med	1	1	2	1	5
Pseudopanurgus aestivalis Provancher, 1882	Ground	Solitary	N/A	0	1	0	0	1
Pseudopanurgus andrenoides Smith, 1853	Ground	Solitary	N/A	0	1	0	0	1
Pseudopanurgus sp.	N/A	N/A	N/A	3	1	0	0	4
Trachandrena sp.	N/A	N/A	N/A	1	0	1	2	4
<u>Family Apidae</u>								
Anthophora terminalis Cresson, 1869	Cavity	Solitary	X-Lg	0	1	0	0	1
Bombus bimaculatus Cresson, 1863	N/A	Eusocial	X-Lg	1	0	5	7	13
Bombus borealis Kirby, 1837	N/A	Eusocial	X-Lg	2	3	2	5	12
Bombus fernaldae Franklin, 1911	N/A	Eusocial	X-Lg	2	0	0	0	2
Bombus impatiens Cresson, 1863	N/A	Eusocial	X-Lg	3	0	22	8	33
Bombus perplexus Cresson, 1863	N/A	Eusocial	X-Lg	2	3	12	7	24
Bombus ternarius Say, 1837	N/A	Eusocial	X-Lg	45	89	66	49	249
Bombus terricola Kirby, 1837	N/A	Eusocial	X-Lg	3	0	1	7	11
Bombus vagans Smith, 1854	N/A	Eusocial	X-Lg	73	52	16	18	159
Ceratina calcarata Robertson, 1900	Cavity	Solitary	Med	3	0	7	2	12
Ceratina dupla Say, 1837	Cavity	Solitary	Med	0	1	4	3	8
Ceratina mikmaqi Rehan and Sheffield, 2011	Cavity	Solitary	Med	9	0	12	6	27

Table 1.1 Continued.

Epeolus scuttelaris Say, 1824	Kleptoparasite	Kleptoparasite	Lg	7	1	0	0	8
Eucera hamata Bradley, 1942	Ground	Solitary	X-Lg	1	0	0	0	1
Melissodes desponsa Smith, 1854	Ground	Solitary	X-Lg	3	9	0	0	12
Melissodes druriella Kirby, 1802	Ground	Solitary	Lg	6	0	2	2	10
Melissodes illata Lovell and Cockerell, 1906	Ground	Solitary	X-Lg	0	2	1	0	3
Melissodes subillata LaBerge, 1961	Ground	Solitary	N/A	0	1	0	0	1
Nomada denticulata Robertson, 1902	Kleptoparasite	Kleptoparasite	Med	2	0	0	1	3
Nomada luteoloides Robertson, 1895	Kleptoparasite	Kleptoparasite	Med	0	0	0	1	1
Nomada maculata Cresson, 1863	Kleptoparasite	Kleptoparasite	Lg	1	0	2	0	3
Nomada ovata Robertson, 1903	Kleptoparasite	Kleptoparasite	N/A	2	0	1	0	3
Nomada pygmaea Cresson, 1863	Kleptoparasite	Kleptoparasite	Med	1	0	0	2	3
Peponapis pruinosa Say, 1837	Ground	Solitary	X-Lg	0	0	5	4	9
<u>Family Colletidae</u>								
Colletes americanus Cresson, 1868	Ground	Solitary	Lg	0	1	0	0	1
Colletes consors Cresson, 1868	Ground	Solitary	Lg	1	0	0	0	1
Colletes simulans Cresson, 1868	Ground	Solitary	Lg	2	3	7	2	14
Hylaeus affinis Smith, 1853	Cavity	Solitary	Sm	7	8	7	10	32
Hylaeus annulatus Linnaeus, 1758	Cavity	Solitary	Sm	0	2	0	1	3
Hylaeus basalis Smith, 1853	Cavity	Solitary	Sm	1	1	0	0	2
Hylaeus mesillae Cockerell, 1896	Cavity	Solitary	Sm	4	3	4	3	14
Hylaeus modestus Say, 1837	Cavity	Solitary	Sm	11	11	9	9	40
Hylaeus verticalis Cresson, 1869	Cavity	Solitary	Sm	0	0	1	1	2
<u>Family Halictidae</u>								
Agapostemon texanus Cresson, 1872	Ground	Solitary	Lg	0	0	2	0	2
Agapostemon virescens Fabricius, 1775	Ground	Solitary	Lg	0	0	16	11	27

Table 1.1 Continued.

Augochlora pura Say, 1837	Cavity	Solitary	Med	0	0	1	4	5
Augochlorella aurata Smith, 1853	Ground	Eusocial*	Sm	83	37	46	27	193
Augochloropsis metallica fulgida Smith, 1853	Ground	Solitary	Med	0	0	7	2	9
Halictus confusus Smith, 1853	Ground	Eusocial	Med	0	0	2	1	3
Halictus ligatus Say, 1837	Ground	Eusocial	Med	1	0	9	3	13
Halictus rubicundus Christ, 1791	Ground	Eusocial	Lg	16	16	6	3	41
Lasioglossum abanci Crawford, 1932	Ground	Solitary	Sm	1	0	0	0	1
Lasioglossum acuminatum McGinley, 1986	Ground	Solitary	Sm	12	3	3	3	21
Lasioglossum admirandum Sandhouse, 1924	Ground	Eusocial	Sm	0	3	0	0	3
Lasioglossum albipenne Robertson, 1890	Ground	Eusocial	Med	2	2	28	3	35
Lasioglossum atwoodi Gibbs, 2010	Ground	Eusocial	Sm	2	3	3	1	9
Lasioglossum cinctipes Provancher, 1888	Ground	Eusocial	Med	3	2	1	1	7
Lasioglossum coriaceum Smith, 1853	Ground	Solitary	Med	13	7	7	6	33
Lasioglossum cressonii Robertson, 1890	Cavity	Eusocial	Med	115	111	138	171	535
Lasioglossum ephialtum Gibbs, 2010	Ground	Eusocial	Sm	1	1	0	0	2
Lasioglossum heterognathum Mitchell, 1960	Ground	Eusocial	Sm	1	0	0	0	1
Lasioglossum imitatum Smith, 1853	Ground	Eusocial	Sm	0	0	0	1	1
Lasioglossum inconditum Cockerell, 1916	Ground	Solitary	N/A	0	1	0	0	1
Lasioglossum laevissimum Smith, 1853	Ground	Eusocial	Sm	1	0	0	1	2
Lasioglossum leucocomum Lovell, 1908	Ground	Eusocial	Sm	2	0	1	0	3
Lasioglossum leucozonium Schrank, 1781 (i)	Ground	Solitary	Med	1	2	4	4	11
Lasioglossum lineatulum Crawford, 1906	Ground	Solitary	Sm	0	1	2	1	4
Lasioglossum macoupinense Robertson, 1895	Ground	Solitary	Sm	0	0	3	0	3

Table 1.1 Continued.

Lasioglossum nelumbonis Robertson, 1890	Ground	Solitary	Med	0	0	1	0	1
Lasioglossum nigroviride Graenicher, 1911	Ground	Solitary	Med	2	1	1	1	5
Lasioglossum pectorale Smith, 1853	Ground	Solitary	Sm	17	2	18	4	41
Lasioglossum pilosum Smith, 1853	Ground	Eusocial	Sm	0	0	2	0	2
Lasioglossum planatum Lovell, 1905	Ground	Eusocial	Sm	9	1	2	7	19
Lasioglossum quebecense Crawford, 1907	Ground	Solitary	Med	2	1	1	1	5
Lasioglossum smilacinae Robertson, 1897	Ground	Eusocial	Sm	1	0	2	0	3
Lasioglossum subviridatum Cockerell, 1938	Ground	Eusocial	Sm	7	1	0	1	9
Lasioglossum taylorae Gibbs, 2010	Ground	Eusocial	Sm	7	0	1	6	14
Lasioglossum tegulare Robertson, 1890	Ground	Eusocial	Sm	3	0	4	0	7
Lasioglossum truncatum Robertson, 1901	Ground	Eusocial	Med	0	0	2	0	2
Lasioglossum versans Lovell, 1905	Ground	Eusocial	Sm	5	0	1	0	6
Lasioglossum versatum Robertson, 1902	Ground	Eusocial	Sm	0	16	34	15	65
Lasioglossum viridatum Lovell, 1905	Ground	Eusocial	Sm	0	1	4	0	5
Lasioglossum zonulum Smith, 1848 (i)	Ground	Solitary	Med	5	6	4	6	21
Sphecodes cressonii Robertson, 1903	Kleptoparasite	Kleptoparasite	N/A	0	0	0	1	1
Sphecodes davisii Robertson, 1897	Kleptoparasite	Kleptoparasite	N/A	2	0	0	0	2
Sphecodes sp.	Kleptoparasite	Kleptoparasite	N/A	5	0	0	1	6
Family Megachilidae								
Coelioxys rufitarsis Smith, 1854	Kleptoparasite	Kleptoparasite	X-Lg	0	0	1	0	1
Heriades carinata Cresson, 1864	Cavity	Solitary	Med	1	0	0	0	1
Heriades variolosus/ leavitti	Cavity	Solitary	Sm	0	1	0	0	1
Hoplitis producta Cresson, 1864	Cavity	Solitary	Med	1	1	3	2	7
Hoplitis spoliata/ pilosifrons	Cavity	Solitary	Med	1	0	0	0	1
Megachile gemula Cresson, 1878	Cavity	Solitary	X-Lg	7	6	3	1	17

Table 1.1 Continued.

Megachile inermis Provancher, 1888	Cavity	Solitary	X-Lg	1	0	0	1	2
Megachile lapponica Thomson, 1872	Cavity	N/A	Lg	1	0	0	0	1
Megachile latimanus Say, 1823	Ground	Solitary	X-Lg	5	1	2	1	9
Megachile relativa Cresson, 1878	Cavity	Solitary	Lg	4	1	1	3	9
Osmia atriventris Cresson, 1864	Cavity	Solitary	Med	2	0	3	2	7
Osmia bucephala Cresson, 1864	Cavity	Solitary	Lg	0	0	0	2	2
Osmia inermis Zetterstedt, 1838	Cavity	Solitary	Lg	1	0	0	1	2
Osmia proxima Cresson, 1864	Cavity	Solitary	Med	1	0	0	1	2
Osmia pumila Cresson, 1864	Cavity	Solitary	Med	1	1	0	0	2
Osmia virga Sandhouse, 1939	Cavity	Solitary	Med	1	0	0	0	1
Family Melittidae								
Macropis nuda Provancher, 1882	Ground	Solitary	Med	0	0	1	1	2
Melitta americana Smith, 1853	Ground	Solitary	N/A	1	0	0	0	1
Total abundance				601	452	578	490	2121
Number of species				86	58	72	80	125

* *A. aurata* is partially eusocial in Maine (Packer 1990).

1.3.2. Floral resource availability

We observed 62 blooming plant species, 12 of which were non-native, in our ROW sites. Floral species richness was greater Midcoast, where we recorded 51 species, than Downeast, where we recorded 31 species ($F_{(1,22)}=13.11$, $p=0.001$). There was no significant difference in floral abundance between growing regions, and no difference in floral abundance or species richness between ROW sites near to or isolated from lowbush blueberry fields. Eleven blooming plant species were recorded exclusively Downeast, whereas 31 occurred exclusively Midcoast. Downeast-exclusive species tended to be ericaceous and bog associated, including sheep laurel (*Kalmia angustifolia* L.), Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), and Rhodora (*Rhododendron canadense* (L.) Torr.). In contrast, Midcoast-exclusive species were often weedy or disturbance associated, including chickweed (*Stellaria/Cerastium* sp.), yellow clover (*Trifolium arvense* Pollich), hawkweed (*Hieracium* spp., 2 species), and evening primrose (*Oenothera* sp.). Common species in both growing regions were meadowsweet (*Spiraea alba* var. *latifolia* (Aiton) H.E. Ahles), creeping raspberry (*Rubus* spp.), bunchberry (*Cornus canadensis* L.), and goldenrods (*Solidago* spp., 3 species; *Euthamia graminifolia* (L.) Nutt.). We also frequently observed two species of native loosestrife, *Lysimachia quadrifolia* L. and *L. terrestris* (L.) Britton, Sterns, & Poggenb., in both growing regions. These species produce oils that attract rare bees in the genus *Macropis*. Uncommon observations included gaywings (*Polygala paucifolia* Willd) and turtlehead (*Chelone glabra* L.) in the Midcoast and fireweed (*Chamerion angustifolium* (L.) Holub) Downeast. A full list of blooming plant species and the growing region(s) in which they were observed is provided in Table 1.2.

Table 1.2. Blooming plant species observed in power line rights-of-way in two growing regions of the Maine, USA, lowbush blueberry production landscape, 2014-2015. Species nomenclature and non-native status was collected from the USDA PLANTS database (plants.usda.gov); family classification was collected from the ITIS database (itis.gov).

Species	**Family**	**Downeast**	**Midcoast**	**Non-native**
Achillea millefolium L.	Asteraceae		x	x
Apocynum androsaemifolium L.	Apocynaceae	x	x	
Arisaema triphyllum (L.) Schott	Araceae	x		
Aronia melanocarpa (Michx.) Elliott	Rosaceae	x		
Brassica sp. L.	Brassicaceae		x	x
Chamerion angustifolium (L.) Holub	Onagraceae	x		
Chelone glabra L.	Plantaginaceae		x	
Clematis virginiana L.	Ranunculaceae		x	
Clintonia borealis (Aiton) Raf.	Liliaceae		x	
Cornus canadensis L.	Cornaceae	x	x	
Diervilla lonicera Mill.	Diervillaceae	x	x	
Doellingeria umbellata (Mill.) Nees	Asteraceae	x	x	
Eriophorum sp. L.	Cyperaceae	x		
Eupatorium perfoliatum L.	Asteraceae		x	
Euthamia graminifolia (L.) Nutt.	Asteraceae	x	x	
Fragaria virginiana Duchesne	Rosaceae	x	x	
Galeopsis tetrahit L.	Lamiaceae		x	x
Galium sp. L.	Rubiaceae		x	x
Hieracium aurantiacum L.	Asteraceae		x	x
Hieracium sp. L.	Asteraceae		x	
Houstonia caerulea L.	Rubiaceae	x	x	
Hypericum perforatum L.	Hypericaceae		x	x
Ilex verticillata (L.) A. Gray	Aquifoliaceae		x	
Impatiens capensis Meerb.	Balsaminaceae		x	
Kalmia angustifolia L.	Ericaceae	x		
Leucanthemum vulgare Lam.	Asteraceae		x	x
Lysimachia quadrifolia L.	Primulaceae	x	x	
Lysimachia terrestris (L.) Britton, Sterns, & Poggenb.	Primulaceae	x	x	
Maianthemum canadense Desf.	Asparagaceae	x	x	
Moehringia lateriflora (L.) Fenzl	Caryophyllaceae		x	
Oenothera sp. L.	Onagraceae		x	
Persicaria sagittata (L.) H. Gross	Polygonaceae		x	
Polygala paucifolia Willd.	Polygalaceae		x	
Potentilla simplex Michx.	Rosaceae	x	x	
Prenanthes alba L.	Asteraceae	x		

Table 1.2. Continued.

Prunella vulgaris L.	Lamiaceae		x	
Prunus virginiana L.	Rosaceae		x	
Pyrola elliptica Nutt.	Ericaceae	x	x	
Ranunculus acris L.	Ranunculaceae	x		
Rhododendron canadense (L.) Torr.	Ericaceae	x		
Rhododendron groenlandicum (Oeder) Kron & Judd	Ericaceae	x		
Rubus sp. L.	Rosaceae	x	x	
Rubus sp. L. (creeping)	Rosaceae	x	x	
Rudbeckia hirta L.	Asteraceae		x	
Scirpus sp. L.	Cyperaceae		x	
Sisyrinchium montanum Greene	Iridaceae		x	
Solidago bicolor L.	Asteraceae	x	x	
Solidago canadensis L.	Asteraceae	x	x	
Solidago sp. (*nemoralis* Aiton hybrid)	Asteraceae	x		
Spiraea alba var. *latifolia* (Aiton) H.E. Ahles	Rosaceae	x	x	
Spiraea tomentosa L.	Rosaceae	x	x	
Stellaria or *Cerastium* sp. L.	Caryophyllaceae		x	x
Symphyotrichum novi-belgii (L.) G.L. Nesom	Asteraceae	x		
Thalictrum pubescens Pursh	Ranunculaceae	x	x	x
Trientalis borealis Raf.	Primulaceae		x	
Trifolium aureum Pollich	Fabaceae		x	x
Uvularia sessilifolia L.	Colchicaceae		x	
Vaccinium angustifolium Aiton	Ericaceae	x	x	
Valeriana officinalis L.	Valerianaceae		x	x
Vicia cracca L.	Fabaceae		x	x
Viola cf. *cucullata* Aiton	Violaceae		x	
Total # of species		31	51	12
Unique species		11	31	

1.3.3. Landscape composition

We found more coniferous forest and wetland land cover at all spatial scales surrounding our ROW sites in the Downeast growing region than the Midcoast region (Appendix A, Table A.1). In contrast, we found more deciduous/mixed forest at 100, 500, and 1000 m, more urban land cover at 500 and 1000 m, and more deciduous/mixed forest edge and agriculture/pasture at all spatial scales around our ROW sites Midcoast than Downeast (Appendix A, Table A.1). Our ROW sites near lowbush blueberry fields were surrounded by more lowbush blueberry land cover at all spatial scales, and we also found more coniferous forest around our sites isolated from lowbush blueberry fields at 500 and 1000 m (Appendix A, Table A.1). We did not find a difference in the amount of lowbush blueberry surrounding our sites between growing regions.

1.3.4. Bee communities by growing region and site type

In 2014-2015, we collected 820 individual bees from 84 species in the Downeast growing region and 1,076 bees from 97 species in the Midcoast growing region. We found significant differences in both bee abundance (df=1,21, deviance=3.94, $p=0.05$) and species richness (df=1,21, deviance=16.24, $p<0.001$) between the two growing regions. We collected 1,030 bees from 98 species in sites near lowbush blueberry fields and 866 bees from 92 species in sites isolated from lowbush blueberry fields; differences in bee communities across these site types were not significant. However, we found a significant type x region interaction for bee species richness (df=1,21, deviance=5.21, $p=0.02$). Bee species richness was significantly different between sites near to and isolated from lowbush blueberry in the Downeast growing region (df=1,10, deviance=7.24, $p=0.007$); however, we found no difference in bee species richness between site types in the Midcoast growing region (Table 1.3).

Table 1.3. Bee abundance and species richness (± standard error) in power line right-of-way sites near to and isolated from lowbush blueberry fields in Downeast and Midcoast Maine, USA, 2014-2015.

Abundance	**Near lowbush blueberry**	**Isolated from lowbush blueberry**
Downeast	448 (±12.6)	372 (±6.8)
Midcoast	582 (±12.6)	494 (±8.8)
Species Richness		
Downeast **	71 (±2.3)	47 (±1.6)
Midcoast	76 (±2.6)	80 (±2.2)

** = Significantly different at p<0.01

1.3.5. Bee life history traits and ROW context across growing regions

We found significant differences in medium-bodied (df=1,21, deviance=15.10, p<0.001) and extra-large-bodied (df=1,21, deviance=14.59, p=0.008) bee species richness by growing region (Fig. 1.3). Medium-bodied bee species richness is associated with more deciduous/mixed forest edge (df=1,22, deviance=7.88, p=0.004) and less coniferous forest (df=1,22, deviance=8.65, p=0.003) surrounding ROW sites at 250 m. These relationships are also influenced by growing region, as there is less coniferous forest and more deciduous/mixed forest edge Midcoast (Fig. 1.4 a,b). In contrast, species richness of extra-large-bodied bees is associated with more agriculture/pasture (df=1,22, deviance=4.11, p=0.04) at 1000 m surrounding ROW sites with no influence of growing region (Fig. 1.5a). Additionally, we linked extra-large bee species richness to floral abundance within all ROW sites (df=1,22, deviance=17.79, p=0.04) (Fig. 1.5b).

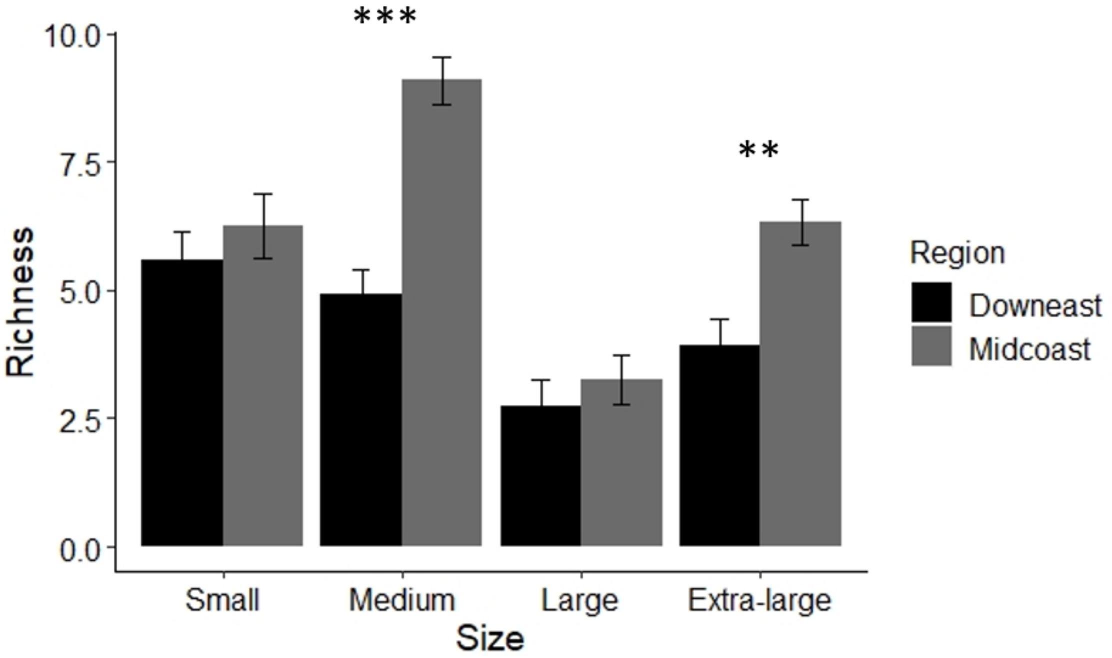


Figure 1.3. Bee species richness by body size in power line ROW sites in two Maine, USA, lowbush blueberry growing regions, 2014-2015. Size classes are: small (<6 mm), medium (6-9 mm), large (9-12 mm), and extra-large (>12 mm). ** = significant at p<0.01; *** = significant at p<0.001.

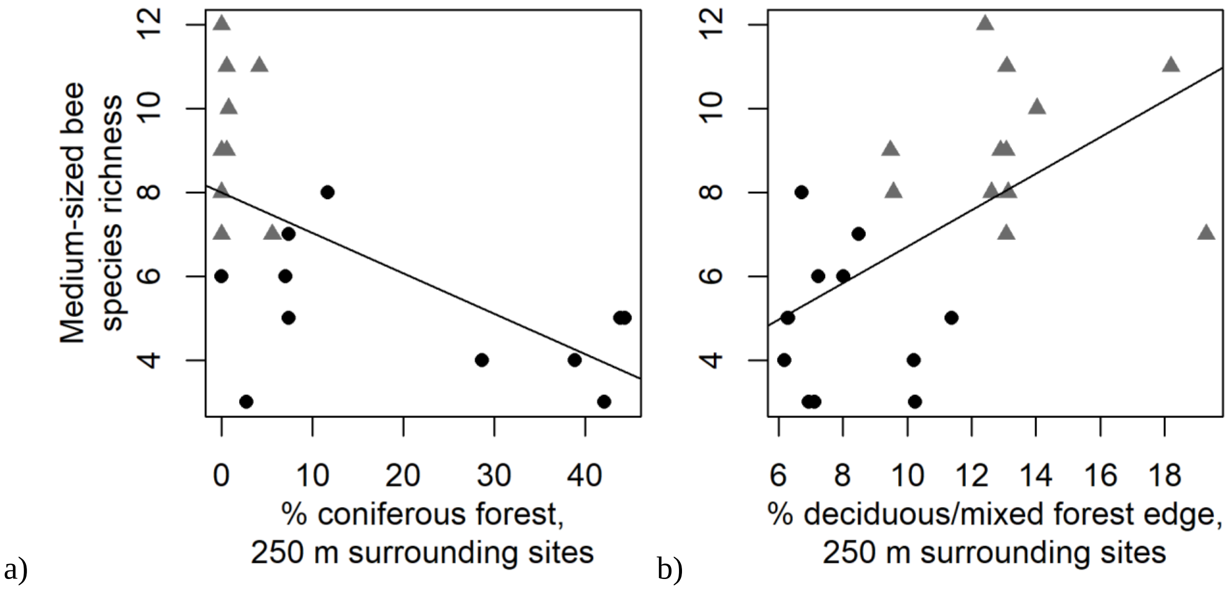


Figure 1.4. Influence of the proportion of a) coniferous forest and b) deciduous/mixed forest edge in the 250 m surrounding power line ROW sites on medium-bodied (6-9 mm) bee species richness in the Midcoast (gray triangles) and Downeast (black circles) lowbush blueberry growing regions of Maine, USA, 2014-2015.

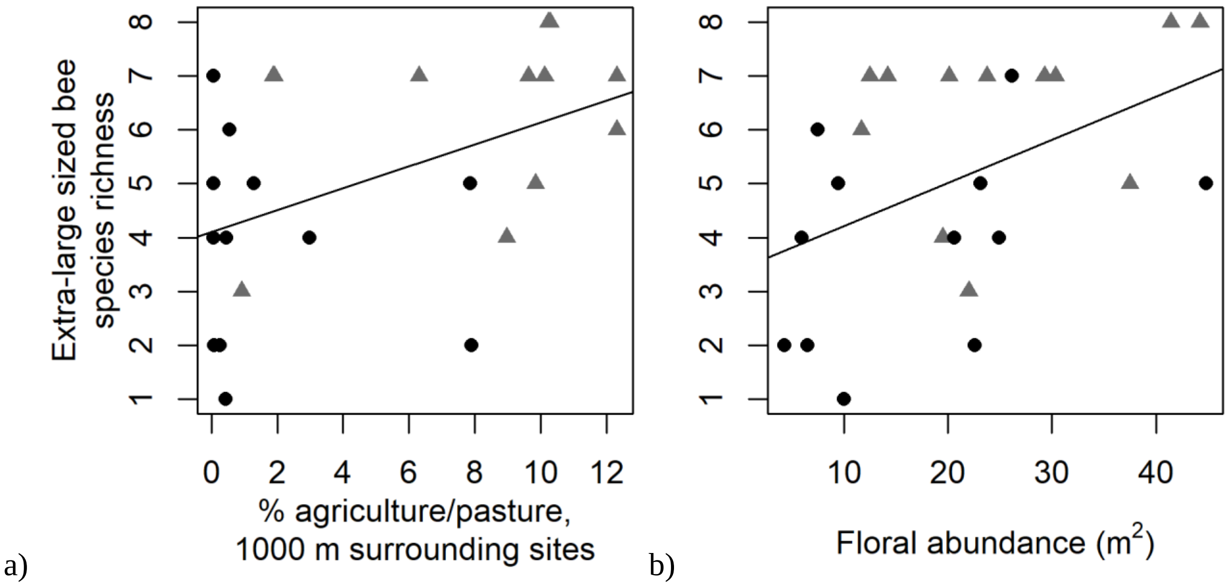


Figure 1.5. Influence of the a) proportion of agriculture/pasture in the 1000 m surrounding and b) floral abundance within power line ROW sites on extra-large-bodied (>12 mm) bee species richness in the Midcoast (gray triangles) and Downeast (black circles) lowbush blueberry growing regions of Maine, USA, 2014-2015.

We found significant differences in the species richness of social bees (df=1,21, deviance=7.12, p=0.007) and solitary bees (df=1,21, deviance=10.97, p<0.001) between growing regions. Solitary bee species richness was greater Midcoast, where it is associated with less coniferous forest and wetland and more agriculture/pasture and deciduous/mixed forest edge surrounding ROW sites (Fig. 1.6a; Appendix A, Table A.2). We found a significant site type by growing region interaction for the species richness of solitary bees (df=1,20, deviance=6.98, p=0.008) owing to an interactive effect of lowbush blueberry land cover surrounding our ROW sites at 250 (df=1,20, deviance=7.54, p=0.006), 500 (df=1,20, deviance=6.46, p=0.01), and 1000 m (df=1,20, deviance=8.68, p=0.003). Lowbush blueberry had a negative association with solitary bee species richness Midcoast and a positive association Downeast (Fig. 1.7), though as a single variable, the amount of lowbush blueberry surrounding ROW sites did not significantly influence solitary bee species richness (Appendix A, Table A.2). Furthermore, we found that greater floral abundance (m^2 per transect) in ROW sites led to greater solitary bee species richness (df=1,22, deviance=6.62, p=0.01) (Fig. 1.8a). Social bee species richness was also greater Midcoast, increasing with less coniferous forest cover and more agriculture/pasture (Fig. 1.6a; Appendix A, Table A.3) in the surrounding landscape.

Ground nesting (df=1,21, deviance=9.98, p=0.001) and cavity nesting (df=1,21, deviance=4.45, p=0.034) bee species richness was greater in Midcoast ROW (Fig. 1.6b). Less coniferous forest and more agriculture/pasture influenced ground nesting bee species richness at multiple scales surrounding ROW, whereas more deciduous/mixed forest edge and urban area and less wetland were influential at small scales surrounding ROW (Appendix A, Table A.4). Greater floral abundance in ROW sites led to greater ground nesting bee species richness (df=1,22, deviance=7.93, p=0.004) (Fig. 1.8b). We found greater cavity nesting bee species richness in ROW sites surrounded by less coniferous forest and more deciduous/mixed forest edge at small scales and more wetland at 500 m (Appendix A, Table A.5).

1.3.6. Bee life history traits and ROW context between isolated and near sites Downeast

We found significant differences in bee species richness associated with body size (df=1,10, deviance=13.00, p=0.05), sociality (df=1,10, deviance=4.85, p=0.027; Fig. 1.9), and nesting habit (df=1,10, deviance=5.43, p=0.019; Fig. 1.10) between ROW sites near to and isolated from lowbush blueberry fields in the Downeast growing region. Large-bodied (500 m scale; df=1,10, deviance=4.73, p=0.03), solitary (all spatial scales; Appendix A, Table A.6), and ground nesting (all spatial scales; Appendix A, Table A.7) bee species richness were positively associated with surrounding blueberry land cover at sites near crop fields. Coniferous forest cover at 500 and 1000 m around sites near to or isolated from crop fields reduced ground nesting bee species richness, and deciduous forest at 1000 m near crop fields reduced solitary bee species

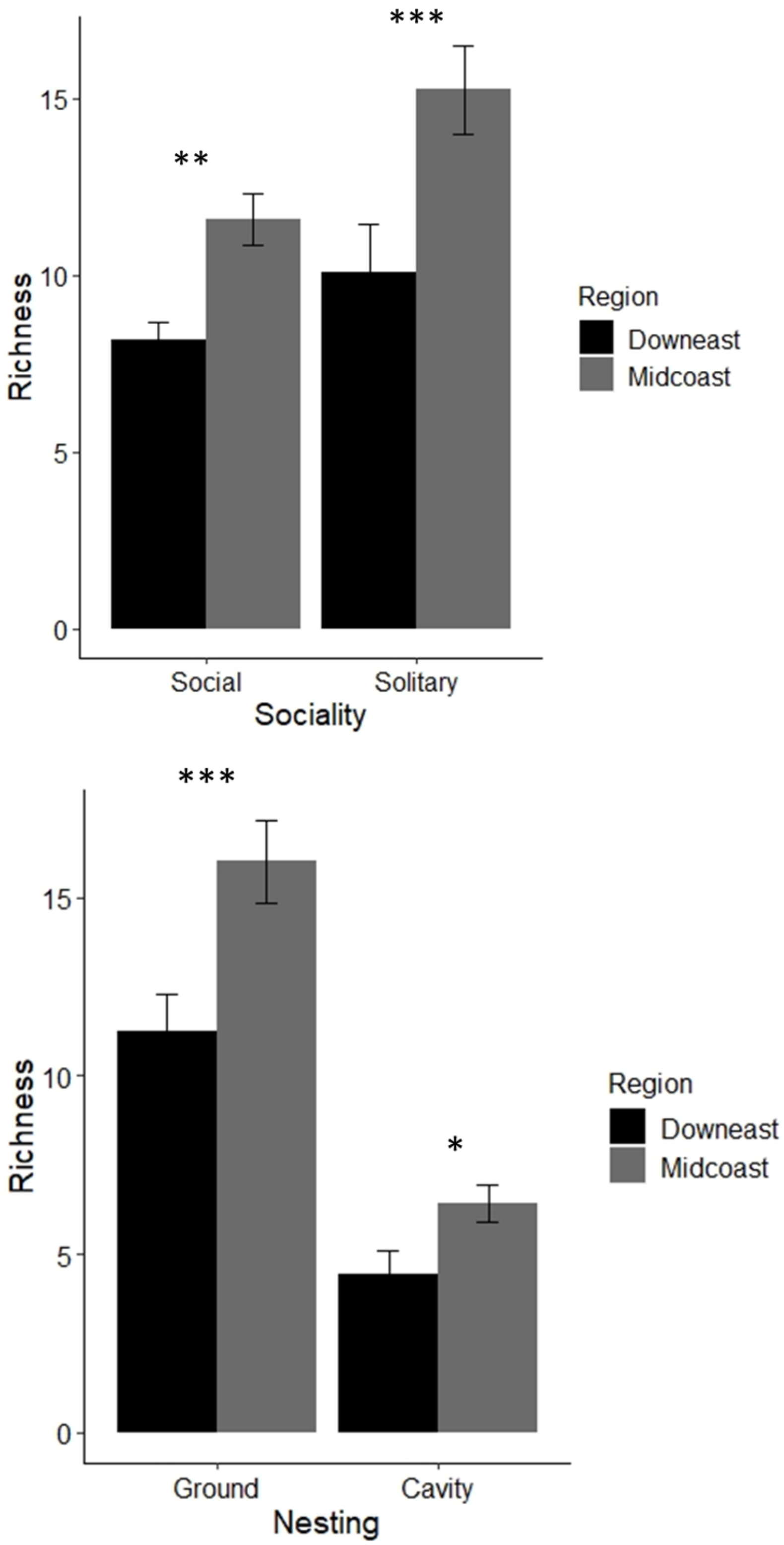


Figure 1.6. Species richness of a) social and solitary bees and b) ground and cavity nesting bees in power line ROW sites in Downeast and Midcoast Maine, USA, 2014-2015.
* = significant at p<0.05, ** = significant at p<0.01, and *** = significant at p<0.001.

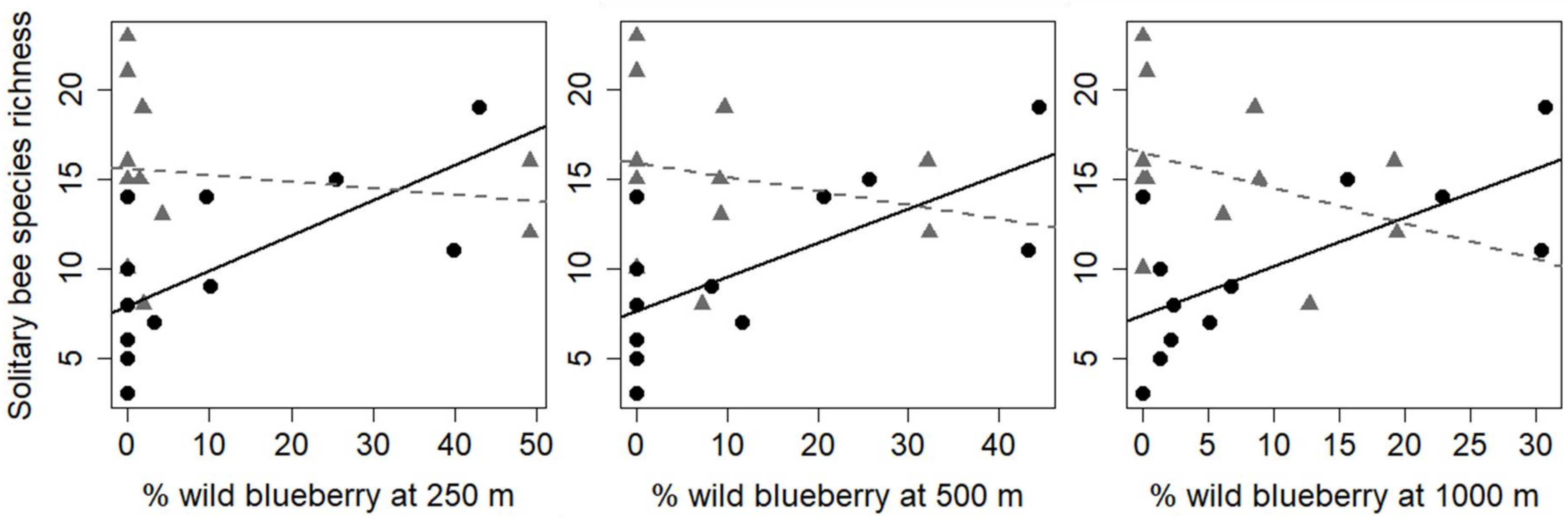


Figure 1.7: Interactive effect of percent lowbush blueberry surrounding power line ROW sites at three spatial scales on solitary bee species richness in the Midcoast (gray triangles, dashed gray line) and Downeast (black circles, solid black line) growing regions of the Maine, USA lowbush blueberry production landscape, 2014-2015.

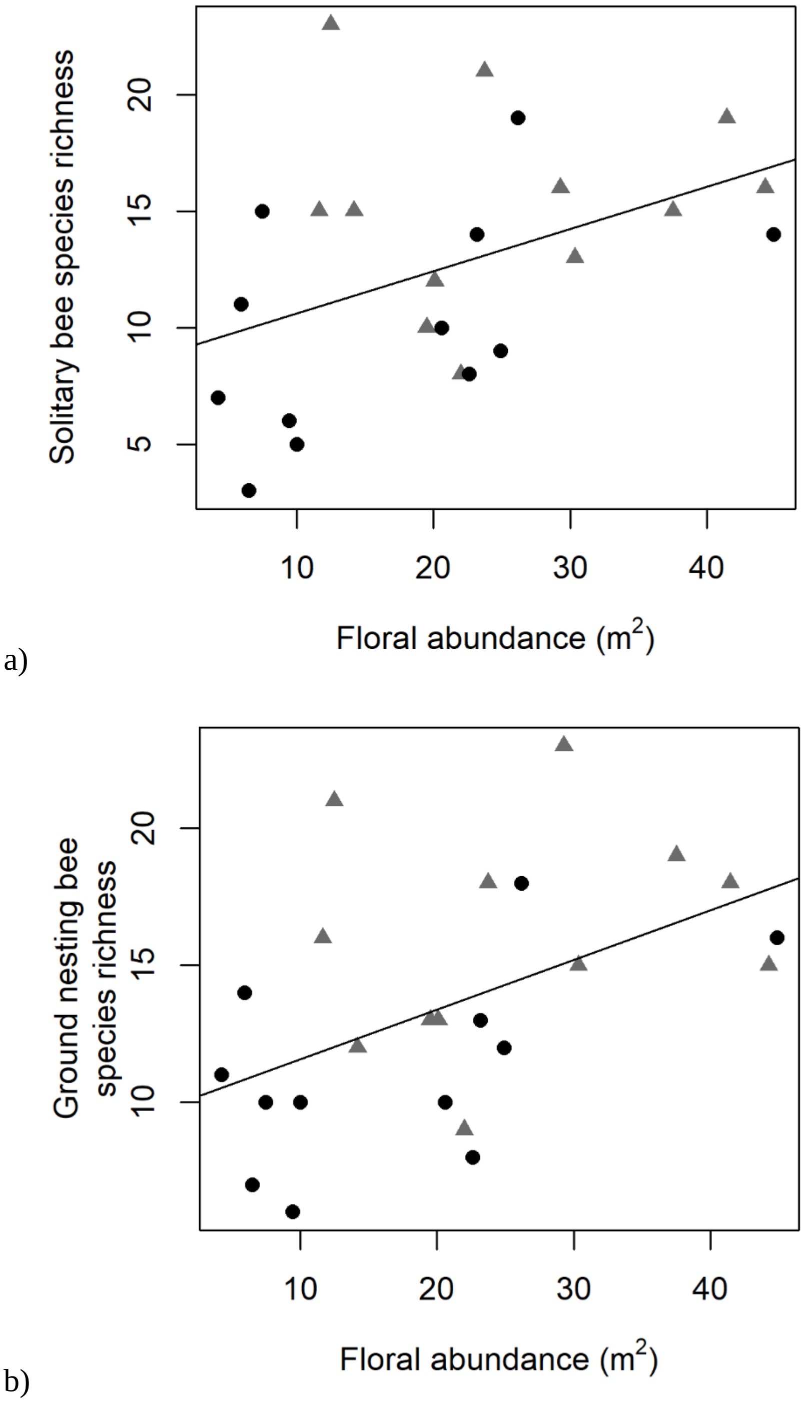


Figure 1.8. Influence of floral abundance (m^2) within power line ROW sites on a) solitary and b) ground nesting bee species richness in Downeast (gray circles) and Midcoast (black triangles) Maine, USA, 2014-2015.

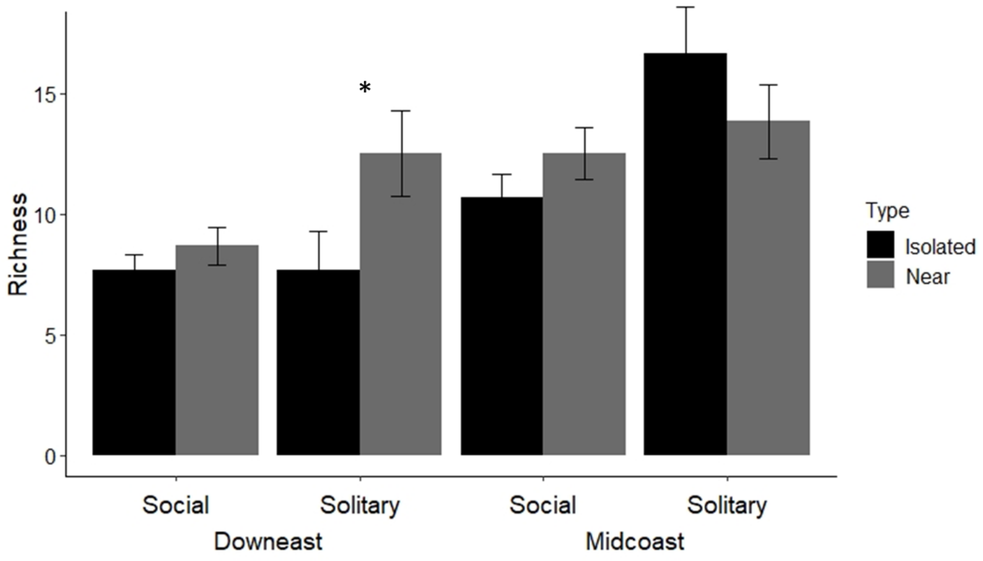


Figure 1.9. Species richness of social and solitary bees in power line ROW sites near to and isolated from lowbush blueberry fields in Downeast and Midcoast Maine, USA, 2014-2015. * = significant at p<0.05.

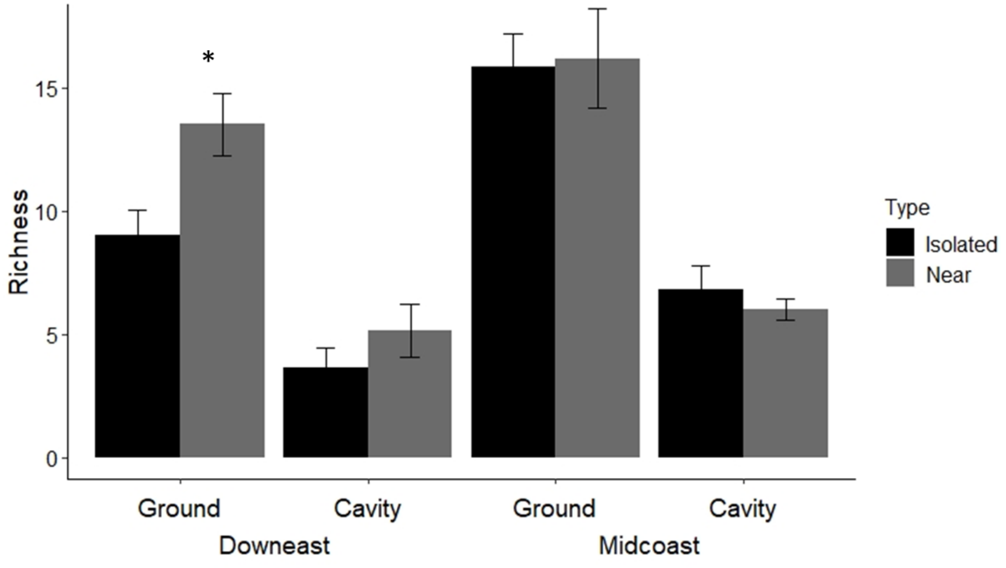


Figure 1.10. Species richness of ground and cavity nesting bees in power line ROW sites near to and isolated from lowbush blueberry fields in Downeast and Midcoast Maine, USA, 2014-2015. * = significant at p<0.05.

richness. There was no effect of coniferous land cover on bee species richness at any spatial scale surrounding near sites (Appendix A, Tables A.6, A.7). Emergent wetland land cover at 1000 m promoted ground nesting and solitary bee species richness. We found no significant differences in bee life history traits between site types in the Midcoast growing region.

1.4. Discussion

1.4.1. Bee community response to ROW

We provide evidence that bee species richness, but not bee abundance, is affected by local and landscape scale characteristics of ROW sites. In studies conducted by Russell et al. (2005, 2018), bee species richness, but not abundance, was greater in ROW habitat than in nearby grasslands in a Maryland, USA, mixed-use landscape, though both bee abundance and species richness were influenced by ROW vegetation management. The contrasting response of bee species richness in ROW by growing region in Maine may be explained by landscape context (Holzschuh et al. 2007; Sardiñas and Kremen 2015). In the Downeast region where bee habitat is relatively scarce, ROW with abundant forage may provide food for more bee species than is available in the surrounding landscape. In contrast, the diverse bee community found in Midcoast ROW may reflect surrounding landscape diversity, where bee habitat is more prevalent. Bees may selectively forage in ROW with more abundant flowers or in other habitat types with ample floral resources, including agriculture/pasture, deciduous/mixed forest edge, and urban areas. Our findings support the intermediate landscape complexity hypothesis, which states that conservation efforts will be more beneficial in structurally simple landscapes over more complex landscapes (Batáry et al. 2011; Tscharntke et al. 2012; Scheper et al. 2013), especially if the conservation activity creates quality habitat (Kleijn and vanLangevelde 2006). Power line ROW in Maine are not managed for conservation purposes; however, the habitat resulting from current management practices appears to have the same effect as conservation directed management techniques such as Integrated Vegetation Management (IVM; Russell et al. 2005, 2018) by promoting bee diversity near lowbush blueberry fields Downeast that may be surrounded by less high quality bee habitat.

1.4.2. Bee life history traits

We observed that species richness of solitary and ground nesting bees, but not social and cavity nesting bees, was influenced by floral resources and surrounding landscape composition. Our findings contrast with existing studies. When managed long term to maintain early-successional habitat, cavity nesting bees were more diverse in Maryland, USA, ROW owing to nesting resources in dead wood and woody shrubs (Russell et al. 2018). Nesting habitat assessments of similar land cover types (emergent wetland, deciduous/mixed forest edge) in Maine suggest that dead wood and woody shrubs should be plentiful in ROW and that bare ground should be sparse (Chapter 3, this dissertation); however, the bee communities we observed in this study indicate the opposite. Further assessment of nesting resources within power line ROW may provide clarity on these relationships.

Floral resources in ROW and other linear landscape features may support diverse social bee communities (Kallioniemi et al. 2017; Russell et al. 2018); however, our work links floral abundance to solitary bee species richness. Solitary bee species richness responded to more local and landscape scale habitat characteristics than all other life history traits. Social bee species vary widely in body size and therefore foraging range (Greenleaf et al. 2007), and larger social species can travel longer distances to obtain sufficient resources. In contrast, smaller solitary bees may be more dispersal-limited and thus more susceptible to limited resource availability (Sydenham et al. 2017); floral resources in ROW may be the only accessible forage after crop bloom, particularly in the coniferous forest-dominant Downeast growing region. Additionally, social bees were far more abundant (1,495 individuals), but less diverse (34 species), than solitary bees (581 individuals, 77 species). Less species richness of social bees was expected because solitary species dominate the overall bee community in Maine (Dibble et al. 2017), but the greater abundance of social species as a group was not hypothesized when we designed the study. The number of singleton solitary species occurring in our study sites may contribute to the observed effects of local and landscape resources on solitary bee species richness (McGill et al. 2007; Winfree et al. 2015). Finally, species richness as a measure of diversity overlooks potential relationships between resources and bee communities. Further analyses using functional traits (McGill et al. 2006) (e.g., tongue length; Sydenham et al. 2015, 2016, 2017) may provide more insight into how bees use our study landscape.

1.4.3. Floral resources

Power line ROW provide a consistent source of floral resources for wild bees, provisioning bee populations post-lowbush blueberry bloom through the remainder of the growing season (mid-June through October). Floral resources are often correlated with bee species richness (Potts et al. 2003; Ebeling et al. 2008). We found greater species richness of both blooming plants and bees in ROW within the Midcoast region; however, this relationship was not significant. Instead, bee species richness in our ROW sites was influenced by floral abundance in both growing regions. Available forage in ROW may be comparable to grasslands (Hill and Bartomeus 2016), though in the Maine lowbush blueberry production landscape, ROW forage is more similar to wooded or emergent wetlands (Chapter 2, this dissertation). This creates a unique habitat type that may occur in ROW throughout New England (Wagner et al. 2014a,b). Further, this unique habitat type supports rare wild bee species. We found two specimens of the native loosestrife (*Lysimachia* spp.) specialist *Macropis nuda* (Provancher). Native loosestrifes in Connecticut power line ROWs were attributed to the rediscovery of one of North America's rarest wild bees, *Epeoloides pilosula* (Cresson), which parasitizes *Macropis* spp. (Wagner and Ascher 2008).

We found more herb-dominated plant communities Midcoast and more ericaceous-dominated plant communities Downeast; a similar trend in ROW within Norway boreal forest suggests that herb-dominant communities promote wild bee diversity (Sydenham et al. 2016, 2017). However, the role of ericaceous-dominant early successional vegetation in ROW should not be overlooked. Ericaceous plant species have poricidal anthers with unique morphology that often prevents generalist bees from obtaining pollen (Bell et al. 2009). Additionally, certain suites of bee species are morphologically and behaviorally pre-adapted to extracting pollen from and pollinating ericaceous flowers (e.g., *Andrena* spp. and *Bombus* spp., Javorek et al. 2002; Drummond 2016); many of these bee species are florally constant on ericaceous flowers (Stubbs et al. 1992; Bushmann and Drummond 2015), and we collected many of these species in our ROW surveys. While our work recorded floral resources available to wild bees, quantifying all vegetation by type (trees, shrubs, herbs, grasses) and/or surveying nesting resources (tree snags, soft-pith stem resources, bare soil) would provide a more complete assessment of ROW habitat resources (Wagner et al. 2014b; Russell et al. 2018; Chapter 3, this dissertation).

1.4.4. Landscape context and mass flowering crops

In both growing regions, we found that bee species richness decreased across sociality and nesting habits in ROW surrounded by coniferous forest, which offers little forage and has low bee abundance (Groff et al. 2016; Chapter 2, this dissertation). Differences in landscape composition between the Midcoast and Downeast growing regions explain many of our results.

Bee species richness increases in landscapes with more habitat (Steffan-Dewenter 2003; Ricketts et al. 2008) and greater heterogeneity (Holzschuh et al. 2007), and landscapes with a larger bee species pool such as Midcoast Maine will have greater bee diversity within ROW sites (Tscharntke et al. 2012; Chapter 2, this dissertation). In a mixed-use, primarily forested landscape, agricultural and urban land cover promote bee species richness (Winfree et al. 2007), as they do in Midcoast Maine. Additionally, urban and agricultural land cover in Maine contain different bee species than those in the forested matrix (Chapter 2, this dissertation), contributing to the greater species richness we observed in ROW in the Midcoast growing region. Urban land cover in Maine's lowbush blueberry production landscape is generally classified as exurban along an urban-rural land use gradient (Kaminski et al., in review), meaning there is plenty of green space and natural area that provides bee habitat. Although we found more wetland land cover Downeast than Midcoast, we do not have evidence that wetlands influence Maine bee communities (Chapter 2, this dissertation). Rather, it is lowbush blueberry fields that have an important influence on bee communities in ROW Downeast, an effect that is amplified by the dominance of coniferous forest in the surrounding landscape.

We found a positive influence of surrounding lowbush blueberry land cover on bee species richness in ROW near lowbush blueberry fields in the more homogeneous Downeast but not the heterogeneous Midcoast growing region. In fact, bee species richness decreased with increasing lowbush blueberry surrounding ROW sites Midcoast. In Sweden, a similar contextual response to a mass flowering crop has been observed on plant reproductive success associated with planted floral strips; reproductive success increased near planted strips in homogeneous landscapes, whereas it decreased near planted strips in heterogeneous landscapes (Herbertsson et al. 2018). Our work supports the growing consensus that linear landscape features (e.g., floral strips, field edges, hedgerows, ROW) relative to a mass flowering crop have different bee communities based on landscape context. Previous work in California and southern England has assessed bee communities of hedgerows in agriculturally-intense landscapes (Sardiñas and Kremen 2015; Garratt et al. 2017); we reveal contextual influences in Maine on bee communities of power line ROW within heavily forested landscapes. The habitat resources provided by ROW and other linear features in homogeneous landscapes appear to be critical in supporting bee communities after the bloom of a mass flowering crop, regardless of the dominant land cover type. Further studies of other linear features, such as field edges, and more study of ROW would clarify these relationships, particularly in different crops and landscape contexts.

1.4.5. Conservation value of power line ROW in Maine

Power line ROW in Maine’s lowbush blueberry production landscape lie within a forest-dominant matrix. In the Midcoast Maine growing region, the forest is a transitional zone between the hardwood forests of southern New England and the boreal forest that dominates the Downeast Maine growing region. Our work reveals that the open habitat provided by ROW in Maine contains early-successional vegetation typical of boreal forest and transition zones, including ericaceous species that many lowbush blueberry pollinators can utilize pre- and post-crop bloom. Forest harvesting throughout the lowbush blueberry production landscape temporarily creates early-successional habitat; however, these patches eventually mature and lose their habitat value. Owing to their constancy throughout Maine’s lowbush blueberry production landscape and the variety of floral resources found within, ROW may serve as refugia for both generalist and ericaceous-specialist pollinators. When managed for an early-successional vegetation community, power line ROW may be a beneficial, but overlooked, source of wild bee habitat in forest-dominant landscapes.

CHAPTER 2

NON-CROP HABITAT USE BY WILD BEES IN A MIXED-USE AGRICULTURAL LANDSCAPE

2.1. Introduction

Insect-mediated crop pollination is a necessary ecosystem service for two-thirds of global crops and 87% of all flowering plant species (Klein et al. 2007; Ollerton et al. 2011). Bees are the dominant insect pollinator, and crop pollination requirements are generally met using commercially managed honeybees (*Apis mellifera* L.). However, naturally occurring wild bee species supplement honeybee crop pollination services and are often more efficient crop pollinators (Garibaldi et al. 2013; Asare et al. 2017). Honeybee hives are typically placed within blooming crop fields to encourage pollination, though honeybees fly an average of 1.5 km, and often much farther, to find food (Steffan-Dewenter and Kuhn 2003). In contrast, wild bee species are generally small-bodied with a limited foraging range (Greenleaf et al. 2007), meaning a large proportion of crop pollinating wild bee species are nesting nearby. Habitat types in agricultural landscapes have been used to characterize crop pollinating bee communities, with a general trend of more natural or semi-natural habitat providing greater bee diversity and abundance (Ricketts et al. 2008). Further, wild bees use different habitat types in complement to find suitable nesting sites and obtain floral resources necessary for survival (Mandelik et al. 2012).

Information on wild bee communities within non-crop habitat types remains sparse (Heinrich 1976), though such surveys are an emerging area of study (Harrison et al. 2017, 2018). A popular spatial model that predicts pollinator abundance throughout agricultural landscapes relies on expert opinion to parameterize resources available in non-crop land cover (Lonsdorf et al. 2009), and has been applied at local (Groff et al. 2016; Chapter 3, this dissertation), national

(Koh et al. 2016), and global (Kennedy et al. 2013) scales using expert opinion-informed parameters. Surveying bee communities within non-crop habitat may reduce bias and variability in expert opinion and provide a more accurate assessment of bee communities in agricultural landscapes (Groff et al. 2016). Furthermore, non-crop habitat likely has bee species not found in crop fields (Harrison et al. 2018; Neokosmidis et al. 2018). Non-crop habitat types may be scarce in a landscape with intensive agriculture and can contain rare plants and rare plant-pollinator interactions (Harrison et al. 2017; Chapter 1, this dissertation). Additionally, sampling bee communities in non-crop habitats provides baseline data for monitoring efforts in pollinator conservation (Bartomeus et al. 2013).

Landscape composition, or the proportion of different habitat types, has often been used to predict bee abundance and diversity in blooming crop fields (Ricketts et al. 2008; Garibaldi et al. 2011). Landscape configuration, or the arrangement of habitat patches, has also been assessed, but with less consistent results (Kennedy et al. 2013; Joshi et al. 2016; Nicholson et al. 2017; Neokosmidis et al. 2018). Bee response to composition and configuration changes with landscape scale, a relationship linked to varying life histories (Steffan-Dewenter et al. 2002). Landscape scales relevant to wild bees are determined by maximum foraging distance, which is estimated from the average intertegular distance, or the width between the wing bases, of individual bee species (Greenleaf et al. 2007). These foraging distances range from less than 100 m up to 3 km depending on the size of the bee. Small, solitary wild bees generally respond to landscape context at small scales, whereas large-bodied, social bees respond at large scales (Steffan-Dewenter et al. 2002; Benjamin et al. 2014). This approach has been questioned, as foraging behavior studies demonstrate that large bees can fly much farther than the calculated maximum foraging distance (Jha and Kremen 2013); however, supporting evidence has been presented for the limited spatial scales of small bees (Zurbuchen et al. 2010; Wright et al. 2015). Further, optimal foraging theory implies bees will not forage to their estimated maximum distance to obtain resources if they can gather those resources near their nest (Goulson 1999).

The landscape of the northeastern United States supports many pollinator-dependent specialty crop production systems, notably apples (*Malus domestica* Borkh.; Blitzer et al. 2016), cranberries (*Vaccinium macrocarpon* Aiton; Loose et al. 2005), and lowbush blueberries (*Vaccinium angustifolium* Aiton; Bushmann and Drummond 2015). This heterogeneous mixed-use landscape is forest dominated and interspersed with diversified agricultural, developed, and wetland land covers. Surveys in the northeastern US reveal diverse and abundant bee communities inconsistently associated with landscape context (Bartomeus et al. 2013; Bushmann and Drummond 2015; Joshi et al 2016; Tucker and Rehan 2017; Nicholson et al. 2017). These studies focus on bee communities in specialty crop habitat (but see Bartomeus et al. 2013); however, bee communities in surrounding non-crop habitat warrant further examination.

Here, we assess bee communities throughout Maine's mixed-use lowbush blueberry production landscape, in which crop fields are surrounded by natural habitat. We compare wild bee abundance and species richness across eight land cover types including and surrounding lowbush blueberry fields. We expect that each of these land cover types will offer distinct floral and nesting resources to wild bees, and we surveyed habitat resources (nesting and foraging) to confirm these relationships. We also assess the role of landscape composition and configuration in determining bee community composition by sampling in a homogeneous and a heterogeneous landscape context. We expect reduced wild bee abundance and species richness where dense, floral resource-poor coniferous forest cover predominates and more abundant and diverse bee communities where open, floral resource-rich cover types including urban areas, small diversified farms, and deciduous forest edge are common. We also hypothesize that a landscape pattern with interspersed patches of multiple cover types will support more diverse and abundant wild bee communities, and that these relationships may change from local scales to landscape scales. Understanding how mixed-use landscapes influence wild bee abundance and species richness will help inform conservation and management practices broadly and establish a baseline for wild bee use of non-crop habitat surrounding crop fields.

2.2. Methods

2.2.1. Study area and spatial data

The Maine lowbush blueberry production landscape covers approximately 750,000 ha of coastline (44-45°N, 67.5-69.5°W), and consists of two growing regions with distinct landscape contexts (Fig. 2.1). These growing regions fall into EPA Level IV ecoregions 58f (Downeast Coast; hereafter referred to as Downeast), 82h (Penobscot Lowlands), and 82b (Midcoast) (Omernik and Griffith 2014). The Downeast region contains the largest and most intensively managed lowbush blueberry fields (up to 1700 ha) in a matrix dominated by managed coniferous (spruce-fir) forest. Non-blueberry agriculture and developed land cover are scattered and comprise little of this landscape. In contrast, the Midcoast and Penobscot Lowlands (hereafter combined as Midcoast-Lowlands) region contains smaller, less intensively managed crop fields (up to 15.6 ha) interspersed with other agriculture including pastures, orchards, and small, diversified farms, and more small towns than the Downeast region. The matrix in the Midcoast-Lowlands region is deciduous forest-dominant and managed with smaller, less frequent harvesting operations than in the Downeast region (Looze 2012).

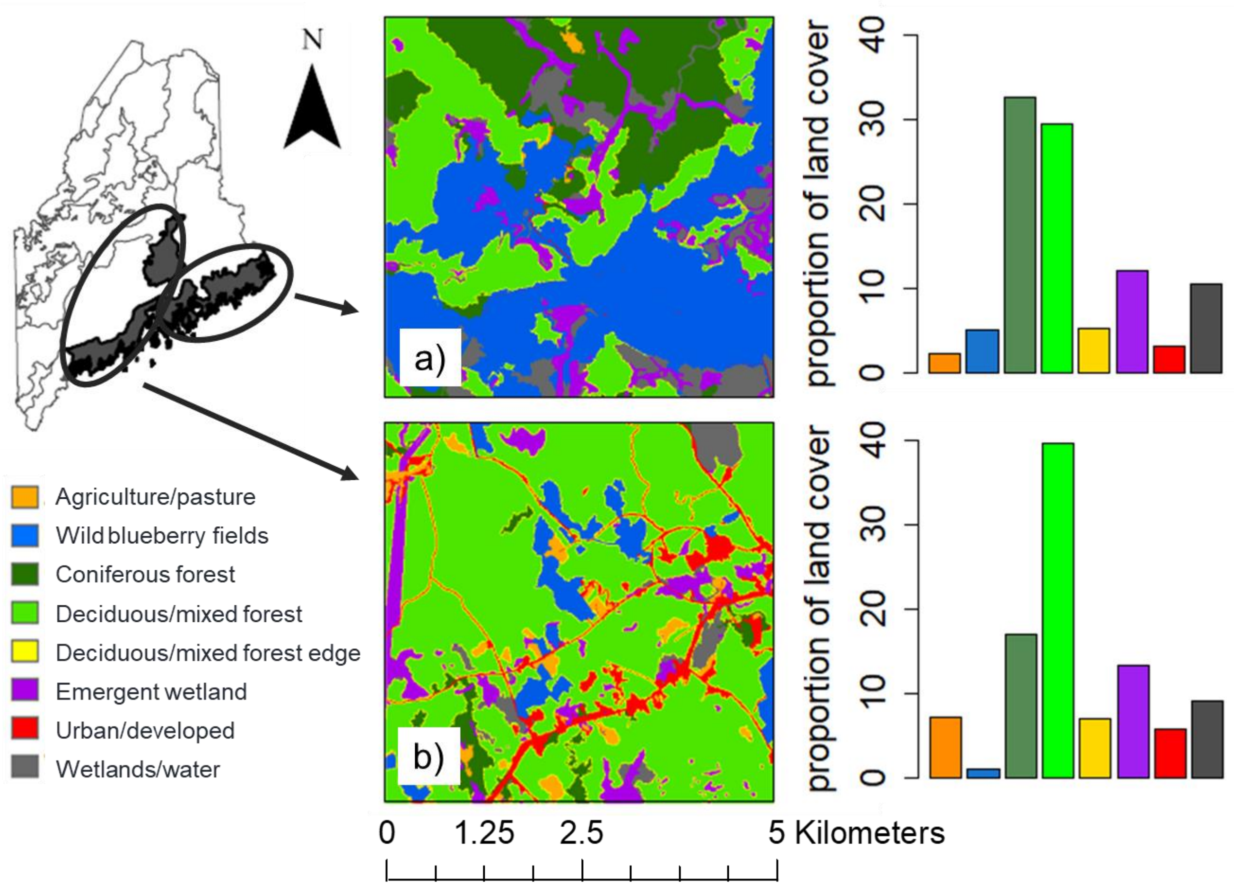


Figure 2.1. Extent of the Downeast Coast, Midcoast, and Penobscot Lowlands Level IV ecoregions in Maine, USA. Map insets display representative landscape contexts of the a) Downeast and b) Midcoast-Lowlands ecoregions. Bar charts indicate proportion of eight land cover types in the Downeast (top) and Midcoast-Lowlands (bottom) ecoregions.

A raster-based land cover map was developed for the Downeast region by Groff et al. (2016). Land cover data were derived from the Maine Landcover Dataset 2004 (MeLCD; https://www.maine.gov/megis/catalog/metadata /melcd.html) with 5 m pixel size and 42 land cover classes. Groff et al. (2016) augmented the MeLCD with ancillary datasets, then resampled and reclassified the map for computational efficiency and ecological relevance. The prepared map has 10 m pixel size and eight land cover classes representing different floral and nesting resources for wild bees: Agriculture/pasture, consisting of small diversified farms, orchard crops, or pasture; lowbush blueberry fields; coniferous forest; deciduous/mixed forest; deciduous/mixed forest edge, 10 m from deciduous/mixed forest into the neighboring land cover type; emergent wetland, an aggregation of forested wetland and scrub-shrub land cover; wetlands/open water; and urban/developed areas. Land cover data for the Midcoast-Lowlands region were prepared for this analysis following the procedure for the eastern extent in Groff et al. (2016), including unsupervised and supervised classifications of a 10 m pixel size 3600 sq km SPOT image acquired in September 2012 (Airbus Defense and Space, http://www.geo-airbusds.com) in ArcGIS® version 10.2.2 (ESRI, Redlands, CA, United States) and hand-digitizing of omitted lowbush blueberry fields revealed through the SPOT classification.

2.2.2. Field sampling

We established seven distinct blocks comprised of eight sites each (56 total sampling sites) throughout Maine’s lowbush blueberry production landscape. Each block contained one site in each focal land cover type. Sites were grouped near each other within blocks so that all eight could be sampled in one day, with fewer than 15 sites less than 500 m apart (site distance range 0.05-10.8 km; mean distance between sites 2.3 km) to minimize overlap in bee communities. We used our land cover map to select sites by land cover type, then visited each site on the ground to confirm suitability for sampling. Each site consisted of one 100 m transect placed so that the focal cover type was dominant up to 100 m surrounding the transect; however, some sites did not meet this criterion owing to land cover heterogeneity and patch size irregularity. We sampled two blocks in 2014 and five blocks in 2015. Three survey blocks were in the Midcoast region (one sampled in 2014, two sampled in 2015), two Downeast (both sampled in 2015), and two blocks were established in the Penobscot Lowlands region (one sampled in 2014, one sampled in 2015).

In each sampling year, sites were sampled in early (13 May-18 June), mid-(17-30 July), and late (30 Aug-25 Sept) season to capture variability in bee and blooming plant communities. Sampling was conducted on days that maximized bee activity with clear or bright cloudy skies, minimal wind, and early morning temperatures >13°C (Bushmann and Drummond 2015). We surveyed wild bee diversity and abundance by placing a set of three cup traps (one each in fluorescent blue, yellow, and white; New Horizons Supported Services, Inc.) every 10 meters along a 100 m transect. Each cup contained approximately 85 ml of water and a drop of dish soap to break water tension (Droege 2015). Captured bees were collected from the bowl traps after 24 hours. We then walked along the transect for 30 minutes and collected foraging bees observed on flowers with insect nets. We excluded honeybees from live netting owing to our interest in assessing wild bee communities, though honeybees were sometimes captured in bowl traps. Managed *Bombus impatiens* brought in for lowbush blueberry pollination could also have been present but were not differentiated; therefore, our collection may include specimens of *B. impatiens* from purchased quads. Using both bowl traps and live netting captures a more complete bee community (Wilson et al. 2008). All collected specimens were cleaned and stored in ethanol (bowl trapped) or frozen (netted) until pinned. We identified pinned specimens to the lowest taxonomic level possible with reference to the keys of DiscoverLife.org and Haverty and Larder (1988), and obtained species-level verifications from Dr. Sara Bushmann, George Stevens Academy; Sam Droege, U.S. Geological Survey Native Bee Inventory and Monitoring Lab; Dr. Jason Gibbs, University of Manitoba; and Dr. Robert Jean, Environmental Solutions and Innovations, Inc.. We gathered nesting and foraging habits of each species from the literature and estimated flight distance for each species with published body size measures and the logarithmic equation from Greenleaf et al. (2007).

We recorded floral abundance and species richness along the first 25 m of our bee sampling transect immediately after collecting bowl traps during each sampling period at all sites in 2015. For each blooming patch intersecting this sub-transect, we recorded plant species, patch size in m^2 and percent bloom. We identified larger blooming shrubs or trees within 25 m from the floral transect by visual assessment. Reference specimens of each blooming plant species were collected and pressed to confirm species identification, and all identifications were confirmed by a botanist (Dr. Alison C. Dibble, University of Maine).

2.2.3. Landscape pattern analysis

We calculated metrics of landscape pattern using Fragstats 4.2 (McGarigal et al. 2012) at four spatial extents (250, 500, 1000, and 2000 m) around each study site. Landscape variables at these spatial extents influence bee abundance and species richness (Steffan-Dewenter et al. 2002). Fragstats metrics that are not empirically or functionally redundant may still be correlated (Neel et al. 2004; Cushman et al. 2008). We assessed correlation among potential metrics using correlation matrices and chose the most biologically relevant metrics for further analysis when correlation coefficients *(r)* exceeded ± 0.7 (Li and Wu 2004).

We selected four configuration metrics that are independent and measure unique components of landscape pattern; three of these metrics have previously been linked to bee community composition (Kennedy et al. 2013; Joshi et al. 2016). The mean proximity index (PROX_MN) measures the distance between two patches of the same land cover type and has a positive relationship with bee abundance in apple orchards (Joshi et al. 2016). The mean perimeter-area ratio (PARA_MN) is a measure of shape complexity, and the interspersion-juxtaposition index (IJI) measures patch mixing; both were used in a global meta-analysis that assessed the interactive effects of landscape pattern and composition on bee communities (Kennedy et al. 2013). We also measured the aggregation index (AI) to assess the influence of the large, aggregate patches that commonly occur throughout our study landscape. The AI was used only at the 1000 and 2000 m scales, as percolation theory dictates that aggregation is not detectable at small landscape scales (Gardner et al. 1987). We assessed landscape composition with the percentage of landscape metric (PLAND) of each cover type surrounding each site.

2.2.4 Statistical analyses

We conducted all statistical analyses in R v.3.5.0 (R Core Team 2018). Honeybees captured in bowl traps were excluded from statistical analyses. We evaluated annual and seasonal differences in bee and floral abundance and species richness with Kruskal-Wallis tests, then determined seasonal differences post-hoc with Dunn’s test of multiple comparisons in package dunn.test (Dinno 2017). We tested for spatial autocorrelation with Mantel tests on bee abundance and species richness at all focal spatial scales (250, 500, 1000, and 2000 m) with the ade4 package (Dray and Dufour 2007).

We aggregated floral resources over the growing season for analysis. We sampled floral resources in only one of our study years, visiting each site just once per time period of the growing season. While this provides an initial data set to explore the floral resources unique to each of the eight land cover types we sampled, our experimental design does not have sufficient replication for powerful statistical analyses of seasonal effects of floral resources. We multiplied patch size by percent bloom for each species observed along our floral resource sub-transect, then summed those values across all sampling periods for an index of cumulative floral abundance. Floral species richness is the total number of blooming plant species observed over the growing season. We compared the influence of local-scale resources on bee communities by modeling the influence of floral abundance and species richness on bee abundance and species richness. We further modeled the influence of land cover type on floral communities by adding land cover as an interaction term. Models were generalized linear models with a negative binomial error distribution calculated in the package lme4 (Bates et al. 2015). We interpreted interactive effects of floral resources with regression plots using the package car (Fox and Weisberg 2011).

We determined differences in bee community composition among land cover types and growing regions with non-metric multidimensional scaling (NMDS), then identified significant differences with permutation testing in the package vegan (Wilson et al. 2016; Oksanen et al. 2017). We evaluated differences in bee abundance and richness across land cover type and growing region with generalized linear models. Models had a negative binomial error distribution owing to overdispersed data. We ran models with cover type, region, and their additive and multiplicative interaction terms and chose the best fitting model with AIC. We tested for significance of interaction terms, if included in the best fitting model, with likelihood ratio tests. We assessed the main effects of the best fitting models with analysis of deviance, and then conducted post-hoc comparisons of means with Bonferroni corrected Tukey contrasts with the packages MASS and multcomp (Venables and Ripley 2002; Hothorn et al. 2008). These tests were conducted separately for bee abundance and species richness on land cover type by growing region, as these tests cannot reliably account for interaction terms (Hothorn et al. 2008).

We assessed the influence of the eight land cover types on bee abundance and species richness with generalized linear mixed models (GLMMs) calculated in lme4. We modeled the proportion of each land cover type at each spatial scale (250, 500, 1000, and 2000 m), and we repeated this analysis by season (early, mid-, or late) and by bee body size (small; 4-10 mm, or large; >10 mm). Models had a negative binomial error distribution with the proportion of each land cover type as the fixed effect and cover type of the site sampled as a random effect. Initial models of bee abundance and species richness by proportion of land cover in the surrounding landscape revealed a strong influence of two sampling sites in the Downeast growing region with large sample sizes. At one of these sites, a lowbush blueberry field, we collected 168 bees of 35 species. We collected 188 bees of 38 species at the other site, located in deciduous/mixed forest edge. Standard deviation of bee abundance including these sites was 37.4; removing them reduced the standard deviation to 26.1. Standard deviation of bee species richness including these sites was 9.1; after exclusion it was 8.1. Therefore, we removed these sites for final analyses.

We also determined the influence of landscape pattern on bee abundance and species richness with GLMMs. Growing region, landscape metrics, and region x metric interactions were fixed effects, and cover type of the survey site was a random effect; models had a negative binomial error distribution. Initial models also revealed a strong influence of the two sampling sites with large samples (described above), therefore they were removed for final analyses. We selected the best model for each combination of scale and community metric with Akaike

Information Criteria corrected for small sample sizes (AICc) and AICc weights from the R package AICcmodavg (Mazerolle 2017). For models with AICc weights >2, we measured the variance explained by both the fixed and random effects with the R package piecewiseSEM (Lefcheck 2015), obtained confidence intervals with Wald tests, and assessed variance inflation factors (VIFs) of correlated interaction effects. Interaction effects in GLMMs are expected to be highly correlated; however, if the VIF is >10, the term can be retained in the model without influencing the output (Jaeger and Kuperman 2009). All of our interaction terms met this criterion and were therefore retained in the final models.

2.3. Results

2.3.1. Bee community summary

We collected 2,094 bee specimens representing five families, 26 genera, and 135 species (Table 2.1). Lowbush blueberry fields had the greatest abundance of bees (484 total, mean 60.5 ± 43.6 (se)), whereas deciduous/mixed forest edge had the most species rich bee communities (71 total species, mean 13.6 ± 17.4). We found few bees in either coniferous or deciduous/mixed forest. We collected more bees in the Midcoast-Lowlands growing region (1,223) than the Downeast growing region (871); however, on average, we collected more bees per site Downeast (mean 54.3 ± 7.4) than in the Midcoast-Lowlands (mean 24.2 ± 4.9). The most abundant bee species collected was the orange-banded bumble bee, *Bombus ternarius* (Say) (379 total individuals collected). Other common bees included the sweat bees *Agapostemon virescens* (Fabricius) (153), *Augochlorella aurata* (Smith) (126), and *Lasioglossum cressonii* (Robertson) (116), and the bumble bee *Bombus impatiens* (Cresson) (91). *Bombus ternarius* was the most abundant species Downeast (248), and *A. virescens* was most abundant in the Midcoast-Lowlands (144). The abundance of the genera *Andrena* and *Lasioglossum* led to capturing a number of kleptoparasitic species, including *Andrena*-associated *Nomada* spp. and *Lasioglossum*-associated *Sphecodes* spp. We also collected one kleptoparasite of *Colletes* spp., *Epeolus scutellaris* (Say). We collected two new state records, *Andrena personata* (Robertson) and *Lasioglossum platyparium* (Robertson), both of which occur in the Mid-Atlantic US. These records are the farthest north either of these species has been recorded. A complete list of bee species, their size class, and the cover types and growing regions in which they were collected is shown in Table 2.1.

We found no spatial autocorrelation of bee abundance (r=-0.074, p>0.91) or species richness (r=-0.065, p>0.88) at any of the four spatial scales. Over all cover types, bee abundance and species richness did not vary between sampling years, but did differ between sampling periods in the growing season (abundance χ^2=12.89, df=2, p=0.001, richness χ^2=12.77, df=2, p=0.001). Bee communities were more abundant (mean 22.5 bees/site ± 4.7) and species rich (mean 8.08 species/ site ± 2.24) mid-season, with no significant differences between the early (mean 13.01 bees/site ± 3.96; mean 6.6 species/site ± 2.37) or late season (mean 8.26 bees/site ±2.42; mean 4.52 species/site ±1.66).

2.3.2. Floral resources and bee communities

We observed 86 blooming plant species, 26 of which were non-native, along the first 25 m of the survey transects (Table 2.2). Common species were often either disturbance or forest-associated, including bunchberry (*Cornus canadensis* L.), Canada mayflower (*Maianthemum canadense* Desf.), goldenrod (*Solidago* spp., 3 species), and clover (*Trifolium* spp., 4 species). We found the greatest blooming plant species richness in deciduous/mixed forest edge (28), emergent wetland (29), and wetland (31). Wetland land cover had the greatest number of unique species (16), including Bur marigold (*Bidens* sp.), blue flag iris (*Iris versicolor* L.), water

Table 2.1. Bee species and size class collected from eight land cover types and two lowbush blueberry growing regions of Maine, USA, 2013-2015. Class indicates bee estimated maximum foraging distance: A (<250 m), B (250-500 m), C (500-1000 m), and D (>1000 m). Land cover types are abbreviated: Ag=agriculture/pasture, Blue=lowbush blueberry field, Con=coniferous forest, Dec= deciduous/mixed forest, Edge=deciduous/mixed forest edge, Emg=emergent wetland, Wet=wetlands/water, and Urb= urban/ developed. Growing regions are abbreviated: DE=Downeast, MC-L=Midcoast-Lowlands.

	Class	**Ag**	**Blue**	**Con**	**Dec**	**Edge**	**Emg**	**Wet**	**Urb**	**Total**	**DE**	**MC-L**
Family Andrenidae												
Andrena alleghaniensis Viereck, 1907	B								1	1		1
Andrena bradleyi Viereck, 1907	B		1							1	1	
Andrena canadensis Dalla Torre, 1896	B						6			6		6
Andrena carlini Cockerell, 1901	C	5	12		2	2	3		4	28	7	21
Andrena carolina Viereck, 1909	B	1	4			2	3	1		11	9	2
Andrena crataegi Robertson, 1895	B					2				2		2
Andrena cressonii Robertson, 1891	B					1			2	3		3
Andrena hippotes Robertson, 1895	B								1	1		1
Andrena hirticincta Provancher, 1888	C					2		2	1	5	3	2
Andrena milwaukeensis Graenicher, 1903	B					1				1		1
Andrena miranda Smith, 1879	C							1		1		1
Andrena miserabilis Cresson, 1872	B								17	17	2	15
Andrena nasonii Robertson, 1895	B		4						9	13	2	11

Table 2.1 Continued.

Andrena nigrihirta Ashmead, 1890	B				3					3		3
Andrena nivalis Smith, 1853	C	2	5	6	6	4	5	1	1	30	11	19
Andrena personata Robertson, 1897	A		1							1		1
Andrena placate Mitchell, 1960	B					1	6			7	1	6
Andrena regularis Malloch, 1917	C		1							1		1
Andrena rufosignata Cockerell, 1902	B		2							2	2	
Andrena rugose Robertson, 1891	B				1	1				2	1	1
Andrena spireana Robertson, 1895	B					1				1		1
Andrena thaspii Graenicher, 1903	B						1			1		1
Andrena vicina Smith, 1853	C						1		2	3	1	2
Andrena virginiana Mitchell, 1960	B		1				1			2		2
Andrena wheeleri Graenicher, 1904	B	1								1		1
Andrena wilkella Kirby, 1802	C	4				1			19	24	12	12
Anthidium manicatum Linneaus, 1758	C					1				1		1
Anthidium oblongatum Illiger, 1806	C					8			7	15		15
Calliopsis andreniformis Smith, 1853	A								7	7	1	6
Pseudopanurgus sp.	A					2				2	2	
Trachandrena sp.	A				1					1		1

Table 2.1 Continued.

Family Apidae

Anthophora terminalis Cresson, 1869	C							1		1		1
Bombus bimaculatus Cresson, 1863	D	6	4		1	24	4	15	7	61	48	13
Bombus borealis Kirby, 1837	D	2	1			5	7	1	5	21	2	19
Bombus griseocollis De Geer, 1773	D								1	1		1
Bombus impatiens Cresson, 1863	D	24	14		6	18	9	8	12	91	11	80
Bombus perplexus Cresson, 1863	D	3			4	3	4	1	1	16	5	11
Bombus sandersoni Franklin, 1913	D	1					1			2	1	1
Bombus ternarius Say, 1837	D	62	48		2	45	57	25	140	379	248	131
Bombus terricola Kirby, 1837	D	3	3		1	2	3	1	2	15	6	9
Bombus vagans Smith, 1854	D	11	15	1	2	27	13	7	9	85	29	56
Ceratina calcarata Robertson, 1900	A		1			1				2	1	1
Ceratina mikmaqi Rehan and Sheffield, 2011	A	3	3			3	1		2	12	7	5
Epeolus scutellaris Say, 1824	B		1							1		1
Melissodes apicata Lovell and Cockerell, 1906	C	1					1			2	1	1
Melissodes desponsa Smith, 1854	C		2			1	1		1	5	3	2
Melissodes druriella Kirby, 1802	B		1				2		3	6	1	5
Melissodes illata Lovell and Cockerell, 1906	C	1	1							2		2

Table 2.1 Continued.

Nomada articulata Smith, 1854	B		1							1		1
Nomada bidentate group	B		1							1		1
Nomada cressonii Robertson, 1893	B		2				1	1	5	9	6	3
Nomada denticulata Robertson, 1902	B								2	2	1	1
Nomada depressa Cresson, 1863	B				1					1	1	
Nomada illinoensis/sayi	A								1	1		1
Nomada inepta Mitchell, 1962	A					1				1	1	
Nomada luteoloides Robertson, 1895	B		1						4	5	1	4
Nomada maculata Cresson, 1863	B		2						2	4	1	3
Nomada nr. *imbricata* Smith, 1854	C								1	1		1
Nomada perplexa Cresson, 1863	B								1	1		1
Nomada sayi Robertson, 1893	C								1	1		1
Peponapis pruinosa Say, 1837	C	2				1	2	4	7	16		16
<u>Family Colletidae</u>												
Colletes americanus Cresson, 1868	C		1							1		1
Colletes simulans Cresson, 1868	C	1	1			4	1			7	5	2
Hylaeus affinis Smith, 1853	A	3	6			1	2	2		14	7	7
Hylaeus annulatus Linnaeus, 1758	A				1	1	1	2		5	3	2
Hylaeus mesillae Cockerell, 1896	A					3	1	1		5		5

Table 2.1 Continued.

Hylaeus modestus Say, 1837	A	3	3		1		11	1	4	23	14	9
Family Halictidae												
Agapostemon texanus Cresson, 1872	B		3			1				4	1	3
Agapostemon virescens Fabricius, 1775	B	20	13		1	5	3	11	100	153	9	144
Augochlora pura Say, 1837	B				1		1	3		5		5
Augochlorella aurata Smith, 1853	A	9	58		2	42	9	4	2	126	75	51
Augochloropsis metallica fulgida Smith, 1853	B		1		1	1	1			4		4
Dialictus sp.	A		1							1	1	
Halictus confusus Smith, 1853	A	5	8		1	3			21	38	11	27
Halictus ligatus Say, 1837	A	9	7		1	5	1	1	14	38	4	34
Halictus rubicundus Christ, 1791	A	9	7			4	11	7		38	13	25
Lasioglossum abanci Crawford, 1932	A							1		1		1
Lasioglossum acuminatum McGinley, 1986	A	2	7			3	2	1		15	5	10
Lasioglossum admirandum Sandhouse, 1924	A	12	6		1		1	2	1	23	8	15
Lasioglossum albipenne Robertson, 1890	A		3					1		4	1	3
Lasioglossum anomalum Robertson, 1892	A		1							1		1
Lasioglossum cinctipes Provancher, 1888	A					1	1	1	1	4	1	3
Lasioglossum coriaceum Smith, 1853	A		2	1	2	1	2	1	2	11	3	8

Table 2.1 Continued.

Lasioglossum cressonii Robertson, 1890	A	13	28		4	24	15	19	13	116	58	58
Lasioglossum ellisiae Sandhouse, 1924	A		4			1				5	4	1
Lasioglossum ephialtum Gibbs, 2010	A		1		3	1	1			6	1	5
Lasioglossum foxii Robertson, 1895	A							1		1		1
Lasioglossum heterognathum Mitchell, 1960	A		3							3		3
Lasioglossum hitchensi Gibbs, 2012	A		2						4	6	2	4
Lasioglossum imitatum Smith, 1853	A								2	2		2
Lasioglossum katherineae Gibbs, 2011	A		1							1	1	
Lasioglossum laevissimum Smith, 1853	A								1	1	1	
Lasioglossum leucocomum Lovell, 1908	A	1	62			6	2		1	72	45	27
Lasioglossum leucozonium Schrank, 1781	A	5	3			5	4		10	27	8	19
Lasioglossum lineatulum Crawford, 1906	A					2			2	4		4
Lasioglossum macoupinense Robertson, 1895	A				2	1	1		1	5	3	2
Lasioglossum nigroviride Graenicher, 1911	A	1				2		1		4	1	3
Lasioglossum nymphaearum Cockerell, 1916	A	2						1		3		3
Lasioglossum oblongum Lovell, 1905	A		1	1	2	1	2	2		9	3	6
Lasioglossum paradmirandum Knerer and Atwood, 1966	A							1		1	1	

Table 2.1 Continued.

Lasioglossum pectorale Smith, 1853	A		20			15		1	1	37	33	4
Lasioglossum perpunctatum Ellis, 1913	A		6			2				8	8	
Lasioglossum pilosum Smith, 1853	A		2							2		2
Lasioglossum planatum Lovell, 1905	A	1	4	2	5	11	8	23		54	24	30
Lasioglossum platyparium Robertson, 1895	A					1				1		1
Lasioglossum quebecense Crawford, 1907	A				1	1		1		3		3
Lasioglossum smilacinae Robertson, 1897	A		3							3	3	
Lasioglossum subversans Mitchell, 1960	A		3							3	3	
Lasioglossum subviridatum Cockerell, 1938	A				2	1	2	3		8	1	7
Lasioglossum tegulare Robertson, 1890	A		16			1			2	19	7	12
Lasioglossum timothyi Gibbs, 2010	A		4			2				6	6	
Lasioglossum trigeminium Gibbs, 2011	A						2			2		2
Lasioglossum truncatum Robertson, 1901	A		4			2		4		10	2	8
Lasioglossum versans Lovell, 1905	A	1			5	5		1		12	3	9
Lasioglossum versatum Robertson, 1902	A	7	37			12	26	2	1	85	27	58
Lasioglossum weemsi Mitchell, 1960	A	1					1	2	2	6		6
Lasioglossum zonulum Smith, 1848	A	7				2	3	15	8	35	9	26
Sphecodes cressonii/atlantis	A					1				1		1

Table 2.1 Continued.

Sphecodes davisii Robertson, 1897	A		2			3				5	4	1
Sphecodes sp.	A	1	6		1		2		3	13	5	8
<u>Family Megachilidae</u>												
Heriades carinata Cresson, 1864	A						1			1		1
Hoplitis producta Cresson, 1864	A					2	1	1		4	2	2
Megachile gemula Cresson, 1878	C		1			6	1		1	9	4	5
Megachile inermis Provancher, 1888	C					4				4		4
Megachile latimanus Say, 1823	C	2	8				1	1		12	3	9
Megachile melanophaea Smith, 1853	C		1							1	1	
Megachile relative Cresson, 1878	C					3	1	1	2	7	2	5
Megachile rotundata Cresson, 1878	B					3				3		3
Osmia atriventris Cresson, 1864	B	1				2	1	1		5	3	2
Osmia bucephala Cresson, 1864	C						2			2	1	1
Osmia inermis Zetterstedt, 1838	C		1							1	1	
Osmia inspergens Lovell and Cockerell, 1907	B		1							1		1
Osmia lignaria Say, 1837	C					1				1	1	
Osmia pumila Cresson, 1864	C					1	1			2		2
Osmia virga Sandhouse, 1939	B						1			1		1
Total abundance		248	484	11	67	359	259	189	477	2094	871	1223
Number of species		40	69	5	31	71	61	56	46	135	83	120
Number of unique species		1	17	0	3	11	6	5	10		14	51

hemlock (*Cicuta maculata* L.), and water plantain (*Alisma subcordatum* Raf.). Lowbush blueberry is associated with a number of plant species found within and bordering crop fields, including wood lily (*Lilium philadelphicum* L.), St. John's Wort (*Hypericum perforatum* L.), and red sorrel (*Rumex acetosella* L.); we observed these and 20 other blooming plant species in crop fields over the growing season. A full list of blooming plant species and the cover type in which they were observed is provided in Table 2.2.

Over all cover types, floral abundance did not vary across the growing season in 2015. However, floral species richness was significantly greater in the mid-season (χ^2=10.05, df=2, p=0.01; mean 3.17 blooming species/site ± 0.34 (se)) with no significant differences between the early (mean 1.77 blooming species/site ± 0.31) or late season (mean 2.31 blooming species/site ± 0.38). An increase in floral abundance resulted in a significant increase in bee abundance (z=2.27, p=0.023, r^2=0.09); however, there was no effect on bee species richness (z=1.809, p=0.07, r^2=0.06). Likewise, bee species richness (z=3.01, p=0.002, r^2=0.15), but not abundance (z=1.81, p=0.07, r^2=0.06) increased with floral species richness. We found significant interactive effects of deciduous/mixed forest edge and floral abundance on bee abundance (z=4.88, p<0.001, r^2=0.79) and bee species richness (z=4.09, p<0.001, r^2=0.77). The slopes of these relationships were much steeper for forest edge than the other cover types owing to a forest edge site in the Downeast region, where we found high bee abundance and species richness as well as high floral abundance and species richness (Fig. 2.2).

Table 2.2. Blooming plant species observed in eight land cover types in the Maine, USA, lowbush blueberry production landscape, 2015. Column labels are abbreviations: Ag=agriculture/pasture, Blue=lowbush blueberry field, Con=coniferous forest, Dec= deciduous/mixed forest, Edge=deciduous/mixed forest edge, Emg=emergent wetland, Wet=wetlands/water, and Urb=urban/ developed. Species nomenclature and non-native status was collected from the USDA PLANTS database (plants.usda.gov); family classification was collected from the ITIS database (itis.gov).

Species	**Family**	**Ag**	**Blue**	**Con**	**Dec**	**Edge**	**Emg**	**Wet**	**Urb**	**Non-native**
Achillea millefolium L.	Asteraceae							x		x
Agalinis sp. Raf.	Orobanchaceae							x		
Alisma subcordatum Raf.	Alismataceae							x		
Anaphalis margaritacea (L.) Benth.	Asteraceae					x				
Aronia melanocarpa (Michx.) Elliott	Rosaceae		x				x	x		
Bidens sp. L.	Asteraceae							x		
Calla sp.	Araceae							x		
Cephalanthus occidentalis L.	Rubiaceae							x		
Cicuta maculata L.	Apiaceae							x		
Comptonia peregrina (L.) J.M. Coult.	Myricaceae		x							
Cornus canadensis L.	Cornaceae		x	x	x	x	x	x		
Cypripedium acaule Aiton	Orchidaceae			x						
Daucus carota L.	Apiaceae	x			x	x			x	x
Doellingeria umbellata (Mill.) Nees	Asteraceae		x			x	x	x		
Erigeron annuus (L.) Pers.	Asteraceae	x								
Eupatorium perfoliatum L.	Asteraceae					x				
Galeopsis sp. L.	Lamiaceae							x		x
Galium mollugo L.	Rubiaceae	x				x				
Hieracium aurantiacum L.	Asteraceae	x								x
Hieracium venosum L.	Asteraceae	x				x				
Hosta sp. Tratt.	Asparagaceae								x	x

Table 2.2 Continued.

Houstonia caerulea L.	Rubiaceae	x				x				
Hudsonia ericoides L.	Cistaceae		x					x		
Hypericum perforatum L.	Hypericaceae		x			x				x
Impatiens capensis Meerb.	Balsaminaceae						x			
Iris versicolor L.	Iridaceae							x		
Leucanthemum vulgare Lam.	Asteraceae	x				x	x			x
Lilium sp. L. (ornamental)	Liliaceae								x	
Lilium philadelphicum L.	Liliaceae		x							
Linum catharticum L.	Linaceae							x		x
Lotus corniculatus L.	Fabaceae					x	x			x
Lupinus polyphyllus Lindl.	Fabaceae	x					x			x
Lysimachia quadrifolia L.	Primulaceae					x				
Lysimachia terrestris (L.) Britton, Sterns, & Poggenb.	Primulaceae						x	x		
Lysimachia thyrsiflora L.	Primulaceae						x			
Maianthemum canadense Desf.	Asparagaceae		x	x	x	x		x		
Matricaria discoidea DC.	Asteraceae								x	x
Monotropa uniflora L.	Ericaceae				x	x				
Nuttallanthus canadensis (L.) D.A. Sutton	Plantaginaceae		x							
Oenothera biennis L.	Onagraceae	x			x		x			
Pisum sativum L.	Fabaceae							x		x
Plantago major L.	Plantaginaceae	x								x
Polygala sanguinea L.	Polygalaceae							x		
Persicaria pensylvanica (L.) M. Gómez	Polygonaceae							x		
Persicaria sagittata (L.) H. Gross	Polygonaceae						x	x		
Potentilla simplex Michx.	Rosaceae	x	x		x		x			

Table 2.2 Continued.

Prenanthes alba L.	Asteraceae						x			
Prunella vulgaris L.	Lamiaceae				x	x			x	
Ranunculus sp. L.	Ranunculaceae	x					x	x		
Rhamnus cathartica L.	Rhamnaceae							x		x
Rhinanthus minor L.	Orobanchaceae	x								
Rhododendron canadense (L.) Torr.	Ericaceae							x		
Rosa sp. L.	Rosaceae						x			?
Rubus spp. L.	Rosaceae				x	x	x			
Rudbeckia hirta L.	Asteraceae		x							x
Rumex acetosella L.	Polygonaceae		x							x
Rumex crispus L.	Polygonaceae	x								x
Sambucus sp. L.	Adoxaceae						x			x
Silene vulgaris (Moench) Garcke	Caryophyllaceae		x							x
Sisyrinchium angustifolium Mill.	Iridaceae		x			x				
Solanum dulcamara L.	Solanaceae							x		x
Solidago bicolor L.	Asteraceae		x				x			
Solidago canadensis L.	Asteraceae					x	x	x		
Solidago hispida Muhl. ex Willd.	Asteraceae		x			x	x			
Solidago sp. L.	Asteraceae	x	x		x	x	x	x		
Spiraea alba var. *latifolia* (Aiton) H.E. Ahles	Rosaceae		x			x	x	x		
Spiraea tomentosa L.	Rosaceae						x			
Stellaria media (L.) Vill.	Caryophyllaceae	x	x		x				x	x
Symphyotrichum novi-belgii (L.) G.L. Nesom	Asteraceae					x	x	x		
Symphyotrichum lateriflorum (L.) Á. Löve & D. Löve	Asteraceae	x			x					

Table 2.2 Continued.

Taraxacum officinale F.H. Wigg	Asteraceae	x							x	
Trifolium arvense L.	Fabaceae		x							x
Trifolium aureum Pollich	Fabaceae								x	x
Trifolium pratense L.	Fabaceae	x				x				x
Trifolium repens L.	Fabaceae	x				x	x	x	x	x
Unknown species 1		x								?
Unknown species 2			x							?
Vaccinium angustifolium Aiton	Ericaceae		x	x		x				
Verbena hastata L.	Verbenaceae						x			
Viburnum nudum L.	Adoxaceae						x			
Vicia cracca L.	Fabaceae	x	x			x		x		x
TOTAL # of species		21	23	3	11	26	26	29	10	26
Unique species		6	8	1	0	3	8	16	4	

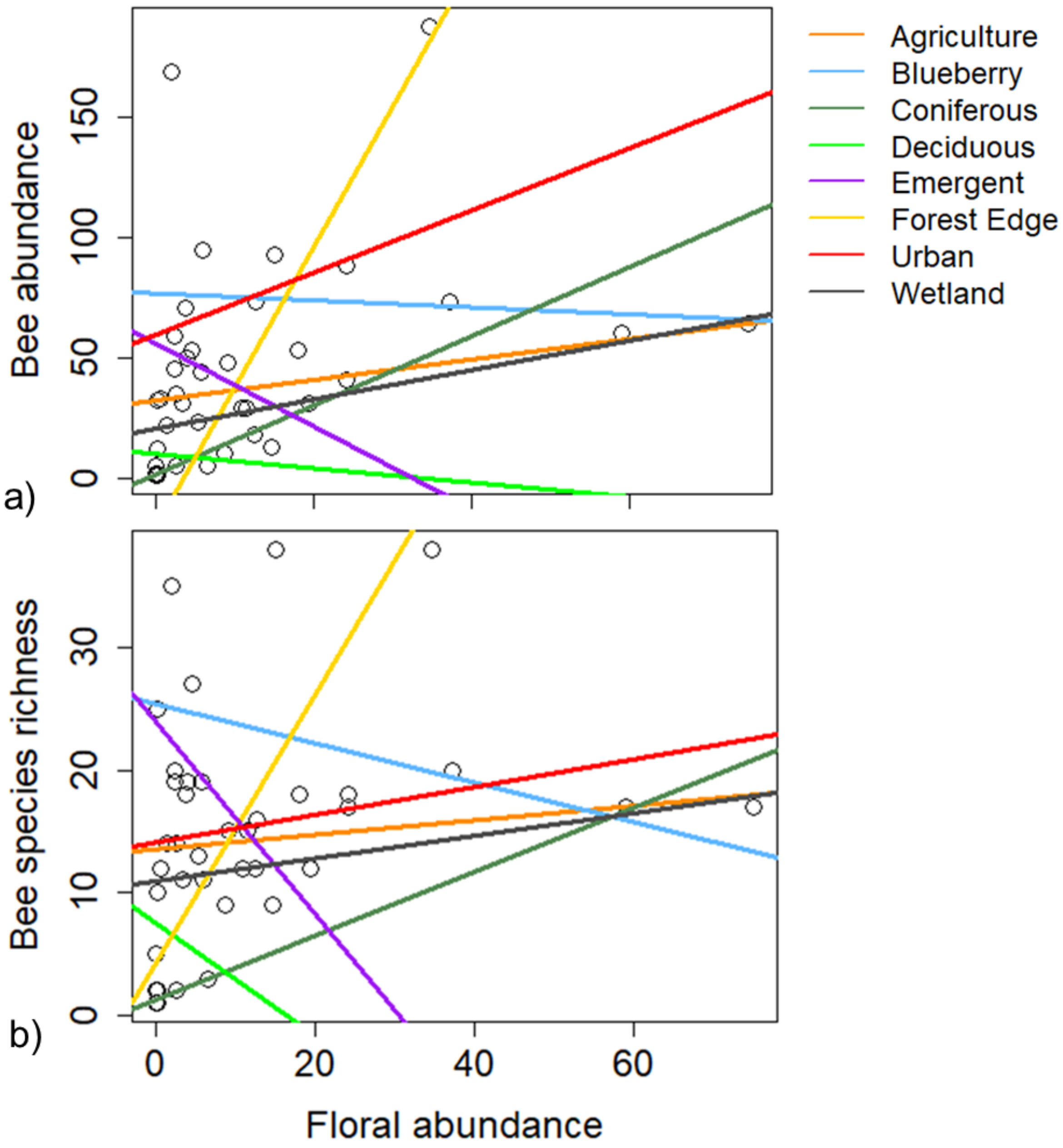


Figure 2.2. Regression relationships between floral abundance and a) bee abundance and b) bee species richness in eight land cover types of the Maine, USA, lowbush blueberry production landscape. Dots represent sites; colored lines indicate slope for each of eight land cover types.

2.3.3. Bee communities by growing region and land cover type

We found significantly different bee communities among land cover types (p=0.001, r^2=0.48) and between growing regions (p=0.008, r^2=0.10) (NMDS stress=0.19). Urban and agricultural cover types had different bee species from forested cover types, while wetland associated bees were found in nearly all other cover types (Fig. 2.3a). The sand bee *Andrena miserabilis* (Cresson) (17 total individuals collected) was collected only in urban areas, whereas the congener *A. nivalis* (Smith) was one of two species collected in all eight land cover types (30). *Bombus vagans* (85) was also collected in all eight cover types, whereas most *Bombus* spp. were found in >4 cover types. Most specimens (62 of 72 and 16 of 19, respectively) of the important lowbush blueberry pollinators *Lasioglossum leucocomum* (Lovell) and *L. tegulare* (Robertson) (Bushmann and Drummond 2015) were collected within crop fields. All species that were unique to either wetland type (emergent or open water) were spatially rare or singletons. There was substantial overlap in bee communities between the two growing regions (Fig. 2.3b). Most common species were abundant in both growing regions, though abundance typically was greater in the Midcoast-Lowlands. We collected <5 individuals of many of the 51 species unique to the Midcoast-Lowlands, with one exception, the squash specialist *Peponapis pruinosa* (Say) (16), which is likely associated with small farms and urban gardens more common in that region.

We found a significant difference in bee abundance (df=1,55, deviance=4.13, p=0.04), but not species richness (df=1,55, deviance=0.434, p=0.51), between growing regions. When pooled across growing regions, we found significant differences in both abundance (df=7,49, deviance=52.79, p<0.001) and species richness (df=7,49, deviance=41.99, p<0.001) among our eight land cover types. There was a significant interaction between land cover type and growing region on bee abundance (χ^2=17.97, df=8,39, p=0.021), but not species richness (χ^2=10.5,

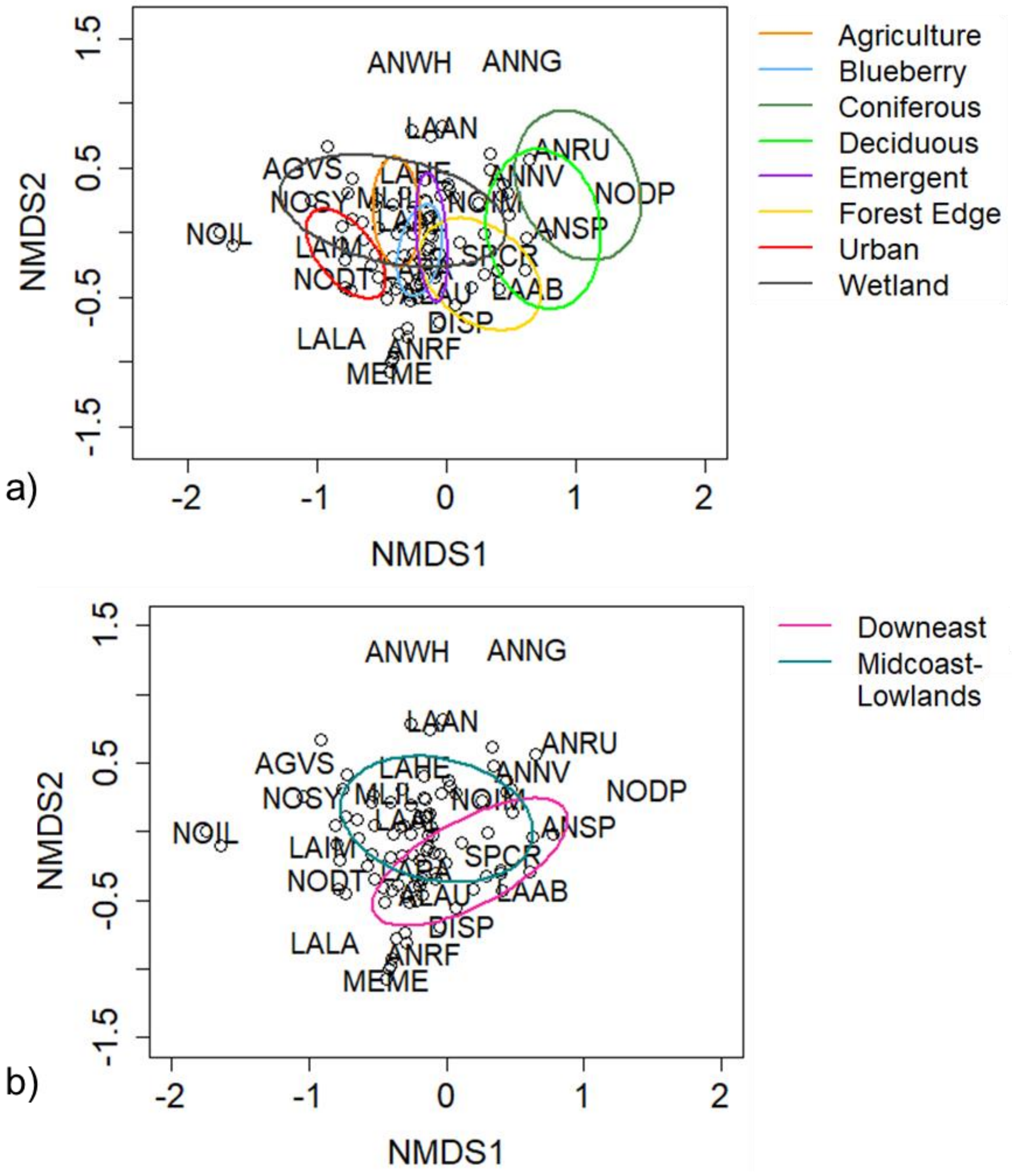


Figure 2.3. Maine wild bee species by a) land cover type and b) growing region represented in an NMDS ordination. Labels are four letter species codes (Appendix B); dots occur where multiple species codes overlap. Ellipses are 95% confidence intervals characterizing bee communities in each land cover type surveyed. Permutation testing revealed these differences were significant (cover r^2=0.48, p=0.001, region r^2=0.1, p=0.008).

df=8,39, p=0.23). Post-hoc multiple comparisons indicated that the relationships between bee communities and land cover type varied between the growing regions. In the Downeast growing region, bee abundance was significantly greater in all other cover types (group B) than coniferous and deciduous forest (group A) (Fig. 2.4, top left). Species richness Downeast was greater in all cover types than coniferous forest (group A) except in deciduous/mixed forest (group C), and greater in lowbush blueberry, deciduous/mixed forest edge, and urban/developed areas (group C) than deciduous/mixed forest (group B) (Fig. 2.4, top right). Differences in bee abundance or species richness between non-forested cover types were obscured by two sites Downeast (described in Methods). In the Midcoast-Lowlands, bees were significantly more abundant in all cover types except deciduous forest and wetland (group C) than coniferous forest (group A) and in lowbush blueberry fields and urban/developed areas (group C) than deciduous/mixed forest (group B) (Fig. 2.4, bottom left). Bee species richness was greater in blueberry fields, emergent wetland, and urban areas (group B) than coniferous forest (group A) (Fig. 2.4, bottom right).

2.3.4. Bee size and proportion of land cover in the surrounding landscape

For small-bodied bees, coniferous forest was associated with low abundance (model parameter estimate=-0.436, p=0.031) and species richness (-0.423, p=0.01) at the 250 m scale in the early season. Abundance of small-bodied bees was also low in deciduous/mixed forest (-0.413, p=0.03) and deciduous/mixed forest edge (-0.374, p=0.016) at the 250 m scale mid-season, but was high in agriculture/pasture (0.40, p=0.037) at the same scale and time. We found no significant effects of proportion of any land cover type on communities of small-bodied bees in the late season or over the growing season as a whole. Full results of these analyses are presented in Appendix C, Table C.1a.

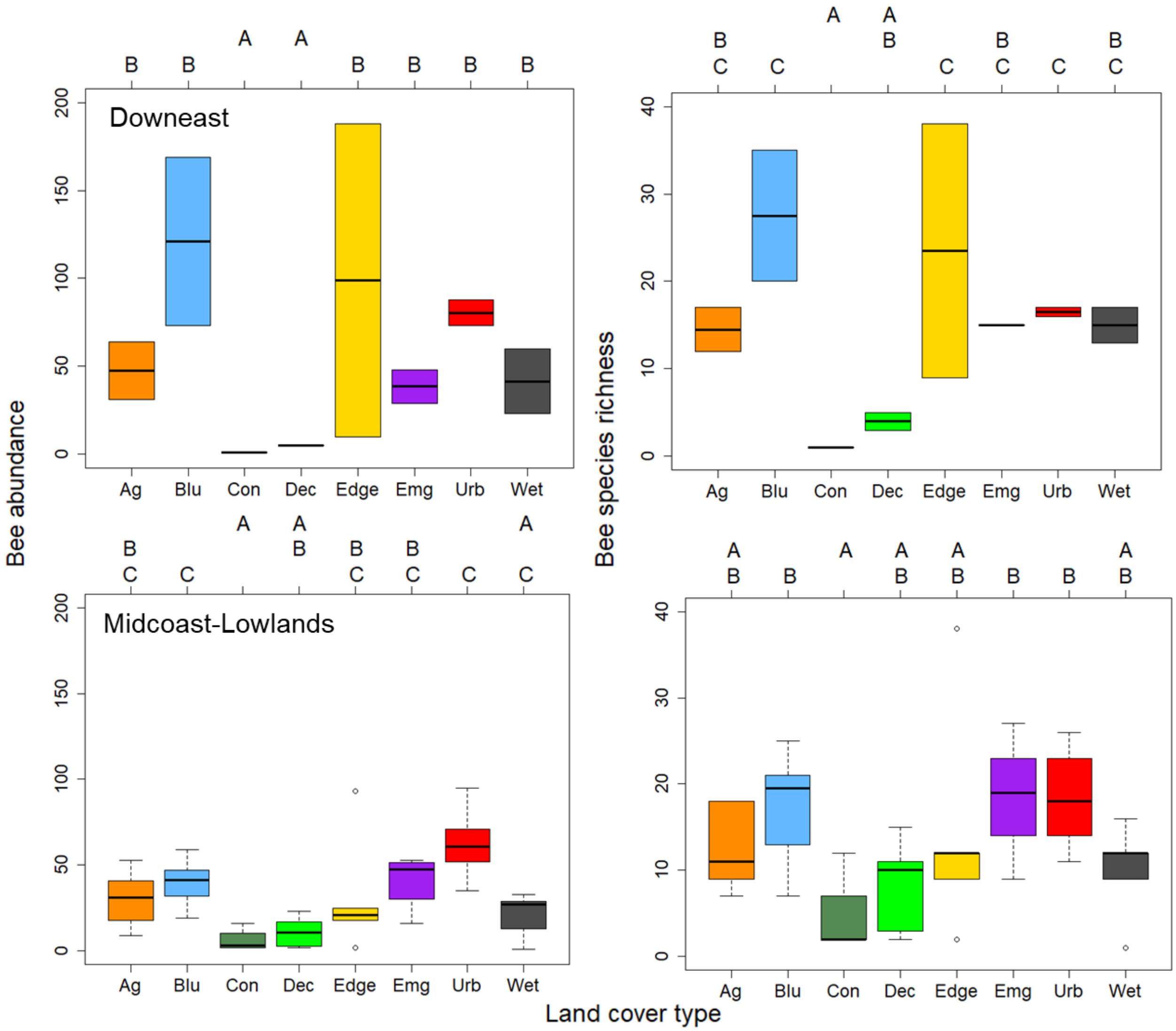


Figure 2.4. Bee abundance and species richness by land cover type in the Downeast (top row) and Midcoast-Lowlands (bottom row) growing regions of the Maine, USA, lowbush blueberry production landscape, 2014-2015. X-axis labels are abbreviated land cover types: Ag=agriculture/pasture, Blue=lowbush blueberry field, Con=coniferous forest, Dec=deciduous/mixed forest, Edge=deciduous/mixed forest edge, Emg=emergent wetland, Urb=urban/developed, and Wet=wetlands/water. Letters above each plot indicate significant differences in bee communities between land cover types in each growing region after multiple comparisons.

Urban/developed area increased species richness of large-bodied bees at the 1000 m scale (0.217, p=0.02) over the entire growing season. In contrast, emergent wetland had low abundance and species richness of large-bodied bees at the 1000 (abundance -0.554, p=0.001; richness -0.298, p=0.007) and 2000 m (abundance -0.482, p=0.005; richness -0.275, p=0.013) scales over the entire growing season. Emergent wetland was negatively associated with large-bodied bee abundance at the 1000 (-0.658, p=0.013) and 2000 m (-0.624, p=0.026) scales in mid-season, and only at the 1000 m (-0.467, p=0.033) scale in the late season. The negative relationship between emergent wetland and abundance and species richness of large-bodied bees appears to be driven by two sites: one with an abundance of large-bodied bees but little emergent wetland in the surrounding landscape at 1000 and 2000 m, and one with few large-bodied bees but dominated by emergent wetland at 1000 and 2000 m. We found no seasonal effect of urban/developed area in the mid- or late season and no effect of the proportion of any land cover type on communities of large-bodied wild bees in the early season. Full results of these analyses are in Appendix C, Table C.1b.

2.3.5. Influence of landscape pattern metrics on bee communities

We found no significant effects of landscape pattern on bee abundance or species richness at the 250 m or 500 m scales. Most of the variance explained in these models came from the cover type of the survey site; variance explained by the landscape pattern metrics was ≤10% for all final models (Table 2.3). At larger scales (1000 and 2000 m), patch mixing (IJI) and the patch mixing by growing region interaction significantly influenced bee abundance and species richness (Table 2.3). Variance explained by the landscape metrics was greater at larger scales than smaller scales. Correlations were high between the main effects and interaction terms; however, the variance inflation factors were less than 10, which is the threshold for variable retention. Average patch mixing values were greater Downeast (range 60-79, average 70.5) than in the Midcoast-Lowlands (range 52-75, average 66.5) at larger scales, contributing to the interactive effect.

2.4. Discussion

2.4.1. Local scale resources

We observed a strong influence of local scale resource heterogeneity on bee abundance and species richness from different land cover types in the mixed-use lowbush blueberry production landscape. For example, there were few floral resources at our forested sites where we captured fewer bees and bee species. In contrast, though we did not find abundant or diverse floral resources in urban survey sites, these sites had greater bee abundance in the Midcoast-Lowlands region. In urban areas, small, diverse patches of floral resources distributed across the landscape support diverse and abundant wild bee communities (Lowenstein et al. 2014, Davis et al. 2017, Simao et al. 2017); our visual assessments of additional floral resources surrounding sampled transects at our urban sites revealed diverse patches that likely support bee populations. Lowbush blueberry fields are associated with a variety of other plant species (Bushmann and Drummond 2015) that support abundant bee communities (Drummond et al. 2017a). The floral resources we observed along our sampled transects in crop fields likely contributed to the high bee abundance at these sites throughout the growing season.

We sampled small, diversified farms to represent agriculture/pasture land cover and found abundant, but not diverse, floral resources at our sampling sites. Further, the bee communities we observed on small farms did not differ from those observed in large, mass-flowering lowbush blueberry fields. This contrasts with other small, diversified farming systems, such as organic farming, where bee abundance and diversity are greater than in conventional

Table 2.3: Influence of landscape pattern metrics on bee abundance and species richness by body size and spatial scale. Landscape metrics: PARA_MN = mean perimeter area ratio; IJI = interspersion/juxtaposition index. Body size: Sm = small-bodied (4-10 mm), can fly up to 500 m; Lg = large-bodied (>10 mm); can fly up to 2000 m. Models with the smallest AICc are listed, as are variance explained by the pattern metrics (fixed effects; marginal r^2) and pattern metrics + cover type (fixed+random effects; conditional r^2) Variation inflation factors (VIF; <10) indicate all interaction terms can be retained in final models.

Body size	**Landscape size**	**Predictors**	**AICc**	**Marginal r^2**	**Conditional r^2**	**Significant variables**
Abundance						
Sm	250 m	Region*PARA_MN	429.7	0.04	0.91	N/A
Sm	500 m	Region*PARA_MN	424.7	0.09	0.93	N/A
Lg	1000 m	Region*IJI	394.7	0.29	0.86	IJI (p=0.014, confint: 0.17-1.54, VIF=6.02) Region:IJI (p=0.002, confint: -1.824--0.374,VIF=5.44)
Lg	2000 m	Region*IJI	393.3	0.28	0.86	IJI (p=0.001, confint: 0.302-1.258, VIF=3.56) Region:IJI (p=0.001, confint:-1.469--0.362, VIF=3.12)
Species richness						
Sm	250 m	Region*PARA_MN	343.0	0.03	0.68	N/A
Sm	500 m	Region*PARA_MN	338.9	0.1	0.74	N/A
Lg	1000 m	Region*IJI	276.4	0.13	0.49	IJI (p=0.053, confint:-0.007-0.951, VIF=8.08) Region:IJI (p=0.013, confint: -1.149--0.134, VIF=6.99)
Lg	2000 m	Region*IJI	277.2	0.13	0.47	IJI (p=0.023, confint: 0.059-0.801, VIF=4.89) Region:IJI (p=0.015, confint: -0.939--0.099, VIF=4.09)

farming systems owing to diverse floral resources (Kremen et al 2007; Kennedy et al. 2013). We suspect this results from a) the diversity of floral resources at the landscape scale in Maine's mixed-use landscape (urban areas, forest edges) and b) the diversity of floral resources within and bordering lowbush blueberry fields (Drummond et al. 2017a).

In emergent wetland, we attribute the inverse relationship we found between floral abundance and bee abundance and species richness to regional differences in landscape-scale resources. We observed greater floral abundance and lower bee abundance and species richness Downeast, whereas we saw lower floral abundance and greater bee abundance and species richness in the Midcoast-Lowlands. Emergent wetland may provide one of few sources of bee habitat Downeast (Chapter 1, this dissertation); however, the larger plant species pool in the Midcoast-Lowlands owing to greater overall resource availability (Tscharntke et al. 2012) leads to a larger bee species pool throughout that region. Wetlands had high floral abundance and the greatest floral diversity of any cover type; however, we found no strong association between these resources and bee communities. This is especially intriguing as we also found ample cavity nesting resources in wetlands (Chapter 3, this dissertation). There are few published examples of relationships between habitat resources and bee communities in wetlands (Moroń et al. 2008; O'Neill and O'Neill 2010, but see Vickruck et al. 2019); more research may reveal relationships between wetland habitat resources and wild bee communities.

2.4.2. Landscape composition and configuration

Our study differs from previously reported studies in that our survey sites were primarily located in non-crop habitat. However, our limited number of survey sites in each growing region may not have captured the landscape variation occurring around our focal non-crop habitats. For example, we found strong negative local scale effects of both coniferous and deciduous/mixed forest on bee abundance and species richness; however, we were not able to corroborate the landscape scale findings of Groff et al. (2016). They found that the proportion of deciduous/mixed forest, deciduous/mixed forest edge, and urban areas were positively correlated with bee abundance in 40 Downeast lowbush blueberry fields, whereas the proportion of coniferous forest was negatively correlated with bee abundance in those crop fields (Groff et al. 2016). The interplay between local and landscape scales has been extensively explored; however, this generally has been studied within agriculturally-intensive landscapes and with an emphasis on landscape composition over configuration (Ricketts et al. 2008; Garibaldi et al. 2011; but see Kennedy et al. 2013). Our study adds to a growing body of work on wild bee communities in mixed-use landscapes, which indicates that local scale habitat influences community composition; however, the influence of landscape scale habitat is inconsistent. Effects of landscape composition are similar across northeastern US crop systems. Isolation from natural areas reduces bee visitation in multiple northeast specialty crops (Connelly et al. 2015; Joshi et al. 2016; Nicholson et al. 2017); however, crop systems are not always isolated from natural areas (Winfree et al. 2008; this study).

We found that patch mixing of non-crop cover types in the lowbush blueberry production landscape promoted communities of large-bodied bees, a group dominated by bumble bees (*Bombus* spp.) but also including solitary species such as *Anthidium* spp. *Anthophora terminalis* (Cresson), some *Colletes* spp., a few *Megachile* spp., a few *Osmia* spp., and some *Andrena* spp. These bees can fly longer distances and therefore may use the landscape differently than small-bodied wild bee species (Steffan-Dewenter et al. 2002). The Downeast growing region, where the influence of patch mixing was significant, contains more coniferous forest, which is poor bee habitat; therefore patches of consistent, high quality bee habitat such as urban areas or power line rights-of-way (Chapter 1, this dissertation) interspersed in this landscape play a strong role in maintaining wild bee communities. Our results contradict those of a global meta-analysis that found no effect of patch mixing in temperate biomes (Kennedy et al. 2013). Other studies of landscape configuration in northeastern US crop systems also reveal inconsistent influences on wild bee communities. For example, solitary bees respond positively to the mean proximity index at the 500 m scale surrounding apple orchards in Pennsylvania (Joshi et al. 2016); however, we found no effect of this metric on bees in Maine landscapes. Landscape configuration metrics of edge density and mean patch size did not affect bee communities in the Vermont highbush blueberry landscape (Nicholson et al. 2017), which resembles the Midcoast-Lowlands region of Maine. More study of complex regional landscapes may lead to increased consistency of trends in effects of landscape pattern on bee communities. Further, using a common set of metrics to measure across systems, such as variation of nearest neighbor distance, mean perimeter area ratio, and patch mixing (Kennedy et al. 2013), may aid in detection of consistent effects of landscape configuration on bee communities. We evaluated these metrics, although we substituted the mean proximity index, a similar measure used by Joshi et al. (2016), as the nearest neighbor distance cannot be measured at small scales in complex landscapes.

2.4.3. Habitat resources in non-crop cover types

Recent studies in mixed-use landscapes indicates that forests have bee communities distinct from urban or agriculturally-dominant landscapes and are critical for supporting rare bee species that depend on resources found only in forests (Harrison et al. 2017, 2018). Forests offer floral and nesting resources along a vertical gradient from ground level herbaceous vegetation to canopy level blooming trees, though the amount of these resources and their associated bee communities are not well studied (Ulyshen et al. 2010). Forest covers 89% of Maine’s land area

(Huff et al. 2016). Maple (*Acer* spp.)/beech (*Fagus grandifolia* Ehrh.)/birch (*Betula* spp.) forest is dominant throughout the Midcoast-Lowlands region, whereas spruce (*Picea* spp.)/fir (*Abies balsamea* (L.) Mill) is more prevalent Downeast; typical forest harvesting patterns also differ between these regions (Looze 2012). The Downeast forest is a working forest, with harvests consisting of partial removal or patch cutting methods over large areas that leave many trees intact and lead to the dominance of mixed age stands; similar harvesting patterns occur less frequently and over smaller areas in the Midcoast-Lowlands forest (Noone 2010; Looze 2012). Spruce-fir forest contains ruderal plant species that provide pollen and especially nectar for wild bees (Kevan et al. 1993). Clearcutting practices in Sweden's spruce-fir forest increased bee abundance 3-5 years post-harvest (Rubene et al. 2015); however, clearcutting is much less common in Maine owing to state legislation that restricts the maximum area of clearcut stands (114th Maine Legislature 1989; Legaard et al. 2015). The association between Maine forest harvesting patterns and wild bee communities warrants further exploration.

In western Maine, Heinrich (1976) found that blooming plants in highly-disturbed hayfields, including clovers (*Trifolium* spp.) and wild carrot (*Daucus carota* L.), provide large amounts of nectar to bumble bees late in the growing season. Our study in coastal and central Maine revealed the strongest association of non-blueberry agriculture, which included hayfield sites, on small-bodied bees in mid-summer, perhaps providing floral resources between early summer specialty crops and late summer goldenrods and asters. The positive association of agriculture on abundance of small-bodied bees at the 500 m scale is driven by sites in the Midcoast-Lowlands growing region, where non-blueberry agriculture is more prevalent and is interspersed with small towns and lowbush blueberry fields. This is consistent with Öckinger et al. (2012), who found that bee species richness increased with area of arable land in a forest/agricultural landscape, though this effect was reduced in sites surrounded by a greater amount of forest land cover.

Emergent wetland sites in more heterogeneous landscapes contained more large-bodied bees. This suggests that bees may not seek out wetland shrubs for feeding and nesting when the surrounding landscape offers few resources; however, they may find such habitat suitable when there are complementary resources nearby. Bumble bee foraging habits through pastures, bogs, and woodlands in western Maine revealed bogs to be the most important habitat type, providing bloom throughout the growing season (Heinrich 1976). Wetlands similar to the Great Heath, a large wetland associated with lowbush blueberry fields in the Downeast growing region are interspersed with lowbush blueberry fields throughout Maine and may provide forage resources for bees following crop bloom. In fact, Downeast lowbush blueberry fields near the Great Heath have some of the highest bee species richness in the region (Drummond, pers. comm.).

2.4.4. Conservation value of non-crop habitat in mixed-use landscapes

In a mixed-use, forest-dominant landscape, wild bee communities are diverse and abundant in non-forested cover types, including diversified agriculture, shrubby wetland, and small towns. Surprisingly, they are comparably diverse and abundant in lowbush blueberry fields, indicating that bees in this agroecosystem are similarly supported by both crop and non-crop habitat. These cover types together provide nesting and floral resources for wild bees that may or may not contribute to crop pollination. This supports the call to study bees and the landscapes they occupy for their conservation value, not solely for their well-recognized ecosystem service contribution (Kleijn et al. 2015). Global trends of the influence of landscape pattern on bee communities are contradictory at regional scales (Kennedy et al. 2013; Neokosmidis et al. 2018); this contradiction also occurs with the influence of bee diversity on ecosystem service delivery (Kleijn et al. 2015; Winfree et al. 2018). More regional scale study, particularly in mixed-use landscapes such as those of the northeastern US, may inform management practices to conserve existing wild bee populations and inform predictive landscape modeling, which has been limited owing to complex landscape pattern and variability in expert opinion (Lonsdorf et al. 2009; Groff et al. 2016). This may lead to local strategies for wild bee conservation, which are important for implementation by land managers and would provide maximum benefit to bee communities.

CHAPTER 3

INFLUENCE OF FIELD-BASED PARAMETER VALUES AND LANDSCAPE CONTEXT ON PERFORMANCE OF A SPATIALLY-EXPLICIT PREDICTIVE WILD BEE ABUNDANCE MODEL

3.1. Introduction

Maine is the largest producer of lowbush blueberries (*Vaccinium angustifolium* Aiton) in the United States, harvesting 40-47 million kilograms annually since 2012 (Yarborough 2016). Lowbush blueberry is reliant on insect pollination to set fruit, and the most effective insect pollinators are naturally occurring wild bees (Drummond 2016; Yarborough et al. 2017). Despite the effectiveness of wild bees, most lowbush blueberry growers invest heavily in commercially managed honeybee (*Apis mellifera* L.) hives (Hanes et al 2015; Asare et al. 2017); depending on anticipated crop yield, the number of hives entering the state each May ranges from fewer than 30,000 to more than 70,000 (J. Lund, Maine State Apiarist, pers. comm.). Rising demand for and increased risk in managing commercial honeybee hives (Aizen and Harder 2009; Kulhanek et al. 2017) has led to greater interest in wild bee pollinators to provide pollination services for lowbush blueberry (Hanes et al. 2015). Crop growers can use on-farm habitat management techniques to enhance and promote wild pollination services (Venturini et al. 2017a,b); however, understanding the resources available to wild bees in the natural habitat surrounding crop fields allows growers to be more strategic when incorporating wild pollination services into their pollination management plans.

Wild bee habitat requirements consist of pollen and nectar from flowers, nesting substrate, and mating sites (Stubbs and Drummond 2001). Bees either nest underground in loose, sandy soil (Cane 1991) or in cavities found in hollow twigs or soft wood (O’Toole and Raw

1991). Foraging preferences vary widely; however, wild bees typically are central place foragers and therefore need access to sufficient forage within their physiological flight limit from their nests in order to feed themselves and provision their young (Goulson 1999). The location of wild bee nesting habitat determines a crop field's potential wild pollination force; any nest within the flight limit to a crop field could provide pollination services to that field (Kremen and Chaplin-Kramer 2007; Lonsdorf et al. 2009). However, bee habitat availability varies across landscapes and land cover types (Garibaldi et al. 2011; Kennedy et al. 2013; Dibble et al. 2018).

Habitat resources and bee communities vary within mixed-use landscapes (Chapter 2, this dissertation), which may lead to difficulty determining consistent pollination services at landscape scales (Kennedy et al. 2013). Crop fields surrounded by natural habitat contain diverse and abundant bee communities and are pollinated more effectively, while simple, agriculturally-dominant landscapes are associated with depauperate bee communities with lower pollination efficiency (Ricketts et al. 2008). For example, the intensively farmed Central Valley of California (Kremen et al. 2002) provides much less natural habitat for wild bees than is available in mixed-use landscapes such as the Maine lowbush blueberry production landscape (Groff et al. 2016).

The InVEST Crop Pollination Model (Lonsdorf et al. 2009; hereafter referred to as the Lonsdorf model) is a spatially-explicit predictive model that estimates pollinator abundance across agricultural landscapes. The model combines parameter values describing nesting substrate suitability, floral resource availability, and bee life history traits with land cover data to predict relative pollinator abundance within each cell of an input land cover map. The model has been applied at global (Kennedy et al. 2013), national (Koh et al. 2016), and regional (Olsson et al. 2015; Groff et al. 2016; Kammerer et al. 2016; Graham et al. 2017) scales. Model output can be used to assess potential wild pollination services in crop fields in terms of bee abundance, or with additional data, in terms of crop yield. The Lonsdorf model is also a powerful landscape conservation tool that can identify effective pollinator conservation or management sites (Davis et al. 2017; Nicholson et al. 2019).

When applied to simple, agriculturally-dominant landscapes, the model describes up to 80% of the variance in pollinator abundance in crop fields (Lonsdorf et al. 2009). However, the Lonsdorf model does not perform consistently in heterogeneous, mixed-use landscapes (Lonsdorf et al. 2009; Kennedy et al. 2013). Indeed, previous application of the Lonsdorf model to one of Maine's two lowbush blueberry growing regions resulted in low prediction accuracy of bee abundance within crop fields (Groff et al. 2016). This was attributed to variation in model parameter values derived from differing expert opinions. Lonsdorf model parameter values typically are informed by expert opinion, as empirical estimation is labor-intensive (Lonsdorf et al. 2009; Kennedy et al. 2013; Koh et al. 2016). However, expert-based parameter values may not accurately account for the variation in nesting and foraging resources in mixed-use landscapes (Groff et al. 2016).

Field sampling potentially provides a more accurate assessment of pollinator habitat resource availability than expert opinion. Although labor intensive, sampling pollinator communities and habitat resources in mixed-use landscapes surrounding crop fields may lead to more accurate predictive parameter values for the Lonsdorf model while also providing field-based assessments of how pollinators and their habitats vary across these landscapes. Providing accurate, field-based predictions of pollinator abundance may increase the likelihood that crop growers adopt new conservation or management practices that benefit pollinators (Hanes et al.

2018). Improving Lonsdorf model performance can also inform pollinator conservation and management efforts beyond agricultural applications.

Our primary aim for this study is to improve Lonsdorf model prediction accuracy within Maine lowbush blueberry fields by creating parameter values informed by field assessments. We sampled eight land cover types across coastal Maine lowbush blueberry growing regions, assessing bee abundance and diversity, floral resource availability, and nesting suitability; full methods and results of this work are described in Chapter 2 of this dissertation. We then created and tested multiple sets of field data-based model parameter values and compared model predictions to those from expert opinion-based parameter values. We also assessed Lonsdorf model prediction accuracy outside of lowbush blueberry fields with a validation data set collected in non-crop cover types. Finally, by applying the Lonsdorf model to a second Maine lowbush blueberry growing region, we assessed model performance and any influence of landscape pattern on prediction accuracy in a more heterogeneous landscape context.

3.2. Methods

3.2.1 Study area

The Maine lowbush blueberry production landscape covers approximately 750,000 ha of coastline (44-45°N, 67.5-69.5°W), and consists of two growing regions with contrasting landscape contexts (Fig. 3.1). The Downeast region contains the largest and most intensively managed lowbush blueberry fields (0.05 -1800 ha, average field size 21.4 ha) in a matrix dominated by coniferous forest managed for timber harvest. Non-blueberry agriculture and developed land cover are scattered and comprise little of this relatively homogeneous landscape. In contrast, the Midcoast region is heterogeneous, containing smaller, less intensively managed crop fields (0.05-15.6 ha, average field size 8.26 ha) interspersed with other agriculture, including pasture, orchards, and small, diversified farms. Developed land in small towns is more prevalent in the Midcoast region than the Downeast region; however, in both growing regions, towns are classified as rural or exurban development along the common urban-rural development gradient (Kaminski et al., in review). The matrix in the Midcoast region is deciduous forest-dominant and less intensively harvested.

3.2.2. Lonsdorf model

The Lonsdorf model is freely available as the crop pollination model of the Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) model suite (https://naturalcapitalproject.stanford.edu/invest/). Our analyses were conducted with InVEST version 3.3.3 (Sharp et al. 2016). The model requires three pieces of input: 1) a cell-based land cover map; 2) a table of bee species and their respective life history trait parameter values, including active flight season, estimated maximum foraging distance, and preferred nesting substrate; and 3) a table of nesting suitability and floral resource availability parameter values for each land cover type within the study area. Parameter values can be populated with values generated from field data, expert opinion, or a combination of both (Lonsdorf et al. 2009). Model output is a map of relative pollinator abundance, with a predicted value in each cell of the input land cover map. Model predictions are based on the nesting and floral resources available in surrounding land cover to the extent of maximum foraging distance for all modeled bee species.

3.2.3. Spatial data

We used the land cover map developed by Groff et al. (2016) as one of the required inputs for the Lonsdorf model. This map covers the Downeast Maine lowbush blueberry growing region with 10 m spatial resolution and eight land cover classes representing different floral and nesting resources for bees: agriculture/pasture, consisting of small diversified farms, orchard

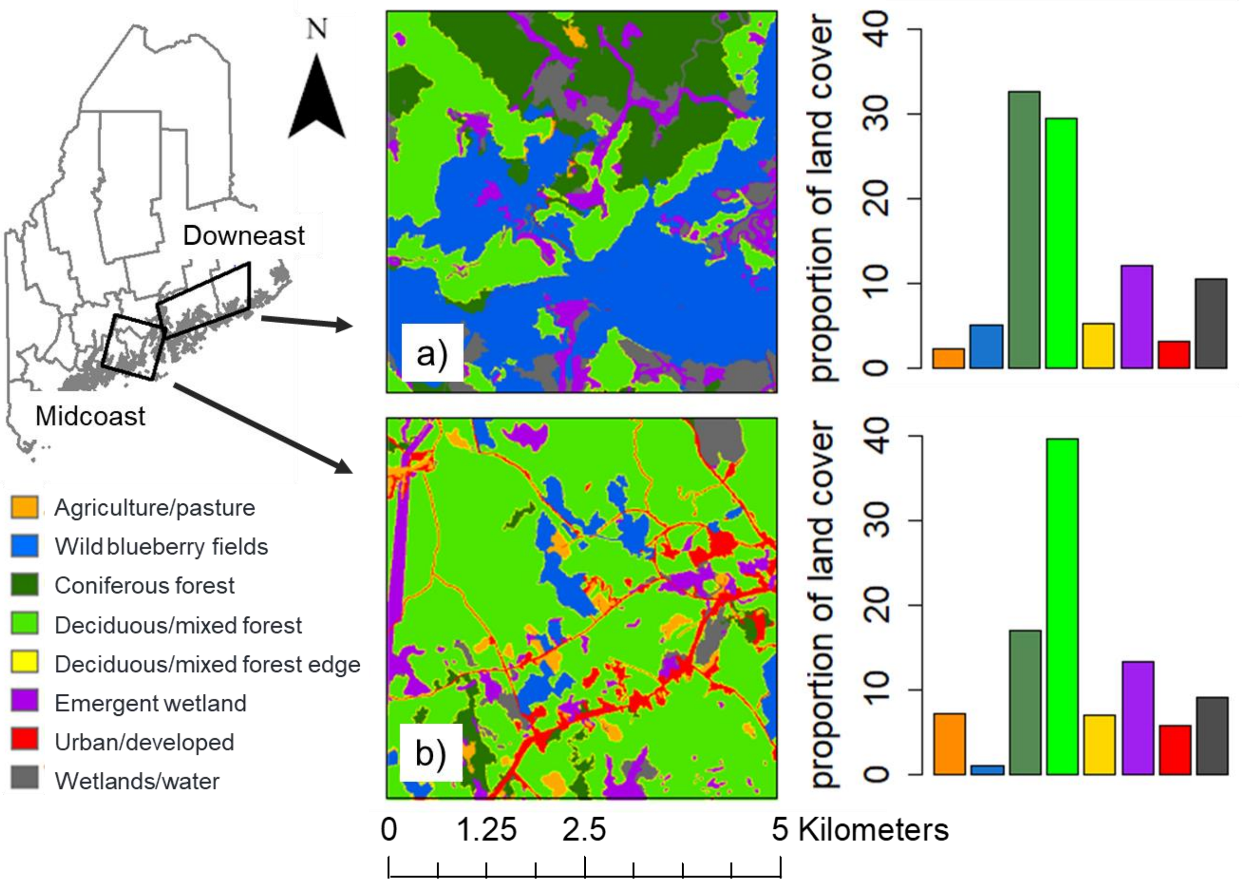


Figure 3.1. Extent of the Downeast and Midcoast lowbush blueberry growing regions in Maine, USA. Map insets display representative landscape contexts of the a) Downeast and b) Midcoast regions. Bar charts indicate proportion of eight land cover types in the Downeast (top) and Midcoast (bottom) regions.

crops, or pasture; lowbush blueberry fields; coniferous forest; deciduous/mixed forest; deciduous/mixed forest edge; emergent wetland, an aggregation of forested wetland and scrub-shrub land cover; wetlands/water; and urban/developed areas (Fig. 3.1). We prepared a similar land cover map for the Midcoast region (Chapter 2, this dissertation) following the same procedures used by Groff et al. (2016).

3.2.4. Field data collection

We visually assessed ground and cavity nesting suitability for bees at 40 sites (16 Downeast, 24 Midcoast) distributed across Maine's lowbush blueberry production landscape at the beginning of the growing season in May 2015. We surveyed five sites in each of the eight land cover types by ranking the amount and condition of standing dead wood, fallen dead wood, shrubs, and bare soil on a 1-5 scale (1=very little, poor condition to 5=very much, excellent condition). We determined the condition of standing and fallen dead wood as poor for cavity nesting if it was soft and mostly decomposed and excellent if it was recently dead, dried, and mostly intact. We assessed the condition of shrubs as poor for cavity nesting if they were alive with wet, green twigs and as excellent if they were mostly dead with dried hollow or soft pithy twigs. Lastly, we found bare soil in poor condition for ground nesting if it contained mostly clay and in excellent condition if it contained mostly sand. One surveyor conducted all nesting suitability assessments.

We collected bee community and floral resource data in early (13 May-18 June), mid-(17-30 July), and late (30 Aug-25 Sept) season to capture variability in bee and blooming plant communities. We captured bees along a 100 m transect with bowl traps and nets then recorded species and patch size of blooming plants along the first 25 m of the bee bowl transect at each site; full details are in Chapter 2 of this dissertation.

3.2.5. Generating field-based model parameter values

A full set of Lonsdorf model parameter values includes: 1) bee life history traits for each modeled bee species, 2) nesting suitability rankings for each nesting substrate within each land cover type, and 3) floral resource availability rankings for each time period of the growing season within each land cover type. We generated 11 subsets of field-based parameter values in three categories: 1) five subsets directly informed by field survey data; 2) four subsets indirectly informed by bee community proxies; and 3) two subsets informed by potential sources of additional variation attributed to a) time periods in the growing season or b) land cover types (Fig. 3.2). We generated field-based bee life history parameter values describing active flight season (bee species presence during each sampling period); however, we used expert-based parameter values describing preferred nesting substrate and estimated maximum flight distance for 14 bee species found in our study area (Groff et al. 2016). These species are known to be effective and abundant pollinators of lowbush blueberry (Bushmann and Drummond 2015); our field survey data collected outside of lowbush blueberry fields throughout the growing season expands our knowledge of these species' habitat associations and flight activity (Chapter 2, this dissertation).

We generated nesting suitability parameter values describing ground and cavity nesting resources in each land cover type by averaging ranks over all sites from the visual assessments in each cover type. We rescaled averaged ranks from 1-5 to 0-1 to meet Lonsdorf model requirements. Bare soil was the sole ranked ground nesting parameter; averaged cavity nesting parameters included ranks for standing dead wood, fallen dead wood, and woody shrubs. We first assigned field-based nesting suitability parameter values for the Lonsdorf model following the top down method used by Groff et al. (2016), in which the land cover type with the greatest

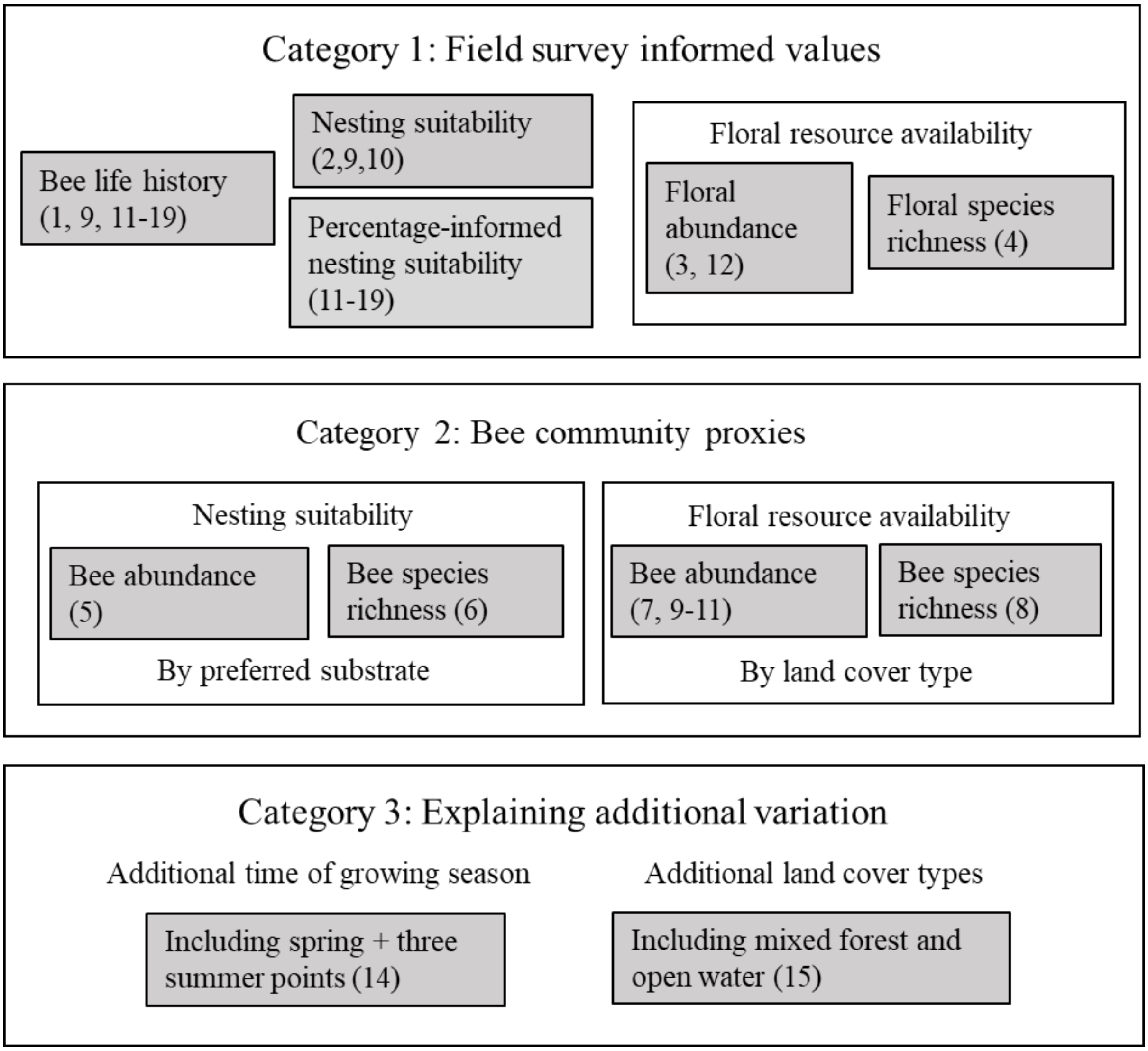


Figure 3.2: Lonsdorf model parameterization and application approach to improve prediction accuracy in the Maine, USA lowbush blueberry production landscape. We generated 11 subsets of field-based parameter values (in gray boxes) in three categories and applied them individually and in combination (corresponding model scenarios listed in parentheses) to improve prediction accuracy over solely expert-based parameter values. All 19 model scenarios and their validation data sources are listed in Table 3.1.

averaged suitability rank was given a parameter value of 1.0 and all other land cover types were assigned parameter values relative to each subsequent rank's relationship to the highest rank. We then assigned field-based nesting suitability parameter values reflecting the percentage of each cover type offering each nesting resource instead of a rank (Lonsdorf et al. 2009) based on our nesting suitability assessments. We tested for differences in field-based nesting suitability parameter values among land cover types with pairwise comparisons using Wilcoxon rank sum tests in R v.3.5.0 (R Core Team 2018).

We used field data to create proportional indices of floral resources, assigning parameter values following the top down approach of Groff et al. (2016). We generated field-based floral resource parameter values by aggregating field-collected floral abundance and blooming plant species richness data in each land cover type at each time period of the growing season. We combined patch size measurements of observed blooming plant species over all sites in each land cover type, then divided by the total area of bloom over all sites to create field-based, floral abundance informed floral resource parameter values. We created field-based, floral species richness informed floral resource parameter values by adding all blooming plant species present in each land cover type then dividing by the total number of blooming plant species observed.

Nesting suitability and floral resource availability have been found to be correlated with bee abundance and species richness in general (Potts et al. 2003, 2005) and also in lowbush blueberry landscapes (Drummond et al. 2017a,b; Venturini et al. 2017b); therefore we used these bee community metrics to create proxy nesting suitability and floral resource availability parameter values for each land cover type. We developed bee community proxy nesting suitability parameter values by counting the abundance and species richness of bees that nest in the ground or in cavities collected in each land cover type and dividing those values by the total collected abundance or species richness of ground or cavity nesting bees. We developed bee community proxy floral resource parameter values by counting the abundance and species richness of bees collected in each land cover type and dividing those values by the total abundance and species richness of collected bees. We compared all subsets of field-based parameter values to corresponding expert-based parameter values provided by Groff et al. (2016) with Spearman's rank correlation coefficients and calculated percent difference between pairs of parameter values in R v.3.5.0.

Lastly, we created two subsets of parameter values describing potential sources of additional variation in our study system that had not been incorporated into our applications of the Lonsdorf model. The first subset added a time period to the beginning of the growing season to account for early season resource availability. We assigned floral resource parameter values for the additional time period between the early summer and late summer based on author experience (Appendix D, Table D.1) and distributed bee life history scores across the time periods based on their collection in field surveys (Chapter 2, this dissertation; Appendix D, Table D.2). The second subset included two new land cover types: mixed forest, which separated the existing deciduous/mixed forest cover type into separate classes of deciduous and mixed forest, and open water, which separated the existing wetlands/water cover type into water bodies and wetlands. Parameter values for these cover types were informed by the authors' expertise and field-collected data. Parameter values for open water were all 0, as this cover type offers neither floral nor nesting resources to bees. Mixed forest nesting suitability parameter values were the same as coniferous and deciduous forest; however, we assigned floral resource parameter values between those of coniferous and deciduous forest (Appendix D, Table D.3).

3.2.6 Model application and validation

We tested whether field-based parameter values would lead to more accurate model predictions than expert-based parameter values with a forward stepwise selection process to replace expert-based values with their field-based counterparts. We first ran model scenarios (1-4; Table 3.1) with field-based parameter values informed by 1) bee life history, 2) nesting suitability, 3) floral abundance, and 4) floral species richness field data to compare expert-based bee life history, nesting suitability, or floral resource (abundance and species richness) parameter values used by Groff et al. (2016). We followed these with seven scenarios (5-11; Table 3.1) using bee community proxy parameter values for nesting suitability and floral resource availability. Scenarios 5-8 featured substitutions of expert-based parameter values with field-based values; scenarios 9-11 incorporated combinations of field-based parameter values for bee life history, floral resources, and nesting suitability to obtain the greatest predictive accuracy. We ran three scenarios (11-13; Table 3.1) with percentage-informed field survey based nesting suitability parameter values to find the floral resource values with the greatest predictive accuracy. We then determined if model predictions were improved by adding greater detail with two additional scenarios: scenario 14 added one time period to the growing season, and scenario 15 added two additional cover types to the land cover map (Table 3.1). Model scenarios 1-15 were applied to the Downeast growing region (Figure 3.1); resulting predictions were validated with simple linear regression and Pearson's product moment correlation coefficients using data collected in 40 Downeast Maine lowbush blueberry fields from 2010-2012 by Bushmann and Drummond (2015) (Table 3.1).

Table 3.1. Lonsdorf model scenarios assessed for prediction accuracy of wild bee abundance in the Maine, USA, lowbush blueberry production landscape. Output from scenarios 1-19 were compared to output from two scenarios from Groff et al (2016), which are listed in the top two rows. Validation data sources are A) Bushmann and Drummond (2015) or B) Chapter 2, this dissertation.

		Source of parameter value				
	Scenario	**Bee life history**	**Floral resource**	**Nesting suitability**	**Validation data source**	**Pearson's r (p)**
	Expert-based model (Groff et al 2016)	Expert	Expert	Expert	A	0.34 (0.03)
	Informed optimization (Groff et al 2016)	Expert	Expert, optimized	Expert, optimized	A	0.48 (0.001)
1	Bee life history	Field	Expert	Expert	A	0.45 (0.003)
2	Nesting suitability	Expert	Expert	Field (survey)	A	0.42 (0.006)
3	Floral resource abundance	Expert	Field (floral abundance survey)	Expert	A	0.16
4	Floral resource richness	Expert	Field (floral diversity survey)	Expert	A	0.2
5	Nesting suitability: abundance proxy	Expert	Expert	Field (bee abundance proxy)	A	0.08
6	Nesting suitability: richness proxy	Expert	Expert	Field (bee diversity proxy)	A	0.18
7	Floral resources: abundance proxy	Expert	Field (bee abundance proxy)	Expert	A	0.03
8	Floral resources: richness proxy	Expert	Field (bee diversity proxy)	Expert	A	0.06
9	All field-based, floral bee abundance proxy	Field	Field (bee abundance proxy)	Field (survey)	A	0.01
10	Scenario 9, with expert-based bee life history values	Expert	Field (bee abundance proxy)	Field (survey)	A	0.02
11	Scenario 9, with percentage-informed nesting parameter values	Field	Field (bee abundance proxy)	Field (survey, %-informed)	A	0.06
12	Scenario 11, with floral abundance field survey values	Field	Field (floral abundance survey)	Field (survey, %-informed)	A	0.23

Table 3.1 Continued.

13	Percentage-informed nesting parameters, final	Field	Expert	Field (survey, %-informed)	A	0.43 (0.005)
14	Add'l time of growing season	Field, four seasons	Expert, modified for four seasons	Field (survey, %-informed)	A	0.42 (0.006)
15	Add'l land cover types	Field	Expert, modified for 2 more land cover types	Field (survey, %-informed)	A	0.28
16	Midcoast, crop fields 2014-2015	Field	Expert	Field (survey, %-informed)	B, 14 crop fields 2014-2015	0.16
17	Midcoast, crop fields 2015	Field	Expert	Field (survey, %-informed)	B, 8 crop fields 2015	0.3
18	Midcoast, non-crop sites only	Field	Expert	Field (survey, %-informed)	B, 17 non-crop field sites	0.65 (0.005)
19	Midcoast, crop fields and non-crop sites	Field	Expert	Field (survey, %-informed)	B, 31 field sites	0.32

We applied the best performing set of parameter values from the Downeast growing region to the Midcoast growing region. We validated model predictions in the Midcoast region with simple linear regression and Pearson's product moment correlation coefficients. Each Midcoast model scenario featured a different validation data set derived from bee community survey data collected in: 16) 14 crop fields during 2014-2015, 17) eight crop fields in 2015, 18) 17 non-crop land cover sites during 2014-2015, and 19) a full set of all 31 crop and non-crop Midcoast sites (Table 3.1).

Lonsdorf et al. (2009) used the variance to mean^2 ratio (Arnold and Wade 1984) to measure model performance in a complex heterogeneous landscape. This ratio standardizes variance and allows comparisons of groups that differ in mean values. Small standardized variance values indicate a lack of variance to explain in a system, i.e., pollinator communities vary too little to be accurately predicted by the Lonsdorf model. We applied this ratio to field-collected bee abundance and species richness in 40 Downeast crop fields, 14 Midcoast crop fields, and 17 Midcoast non-crop sites.

3.2.7. Landscape pattern assessment

We measured four landscape metrics (location of validation site within each crop field, field size, perimeter area ratio, and the proportion of lowbush blueberry in the surrounding landscape) at four scales (250, 500, 1000, and 2000 m) surrounding all 54 crop field validation sites to assess the influence of landscape pattern on Lonsdorf model predictions. Metrics were measured in Fragstats version 4.2 (McGarigal et al. 2012). We used general linear models (ANOVA for site location, simple linear regression for the others) and Pearson product moment correlation analysis to describe relationships. We conducted these assessments separately by growing region to compare effects of landscape context. All data met assumptions of linear models except the perimeter-area ratio Downeast, which was log-transformed to achieve normality.

We further assessed the influence of proportion of non-blueberry land cover types surrounding the 14 Midcoast lowbush blueberry fields following a similar assessment by Groff et al. (2016) of the 40 Downeast crop fields. We assessed the influence of land cover type on field-collected bee abundance, bee species richness, and Lonsdorf model predictions. All assessments were made with simple linear regression and Pearson product moment correlation analysis in R v.3.5.0. All assumptions underpinning these statistical models were met by our data.

3.3. Results

3.3.1. Nesting suitability survey

Ground nesting suitability varied among the eight land cover types. Lowbush blueberry fields had more bare soil than in all cover types except urban/developed areas; additionally, soil in lowbush blueberry fields was more suitable for nesting than soil in agriculture/pasture, coniferous forest, and both wetland cover types. Wetlands had less bare soil than agriculture/pasture, lowbush blueberry fields, and urban/developed areas; further, there was less soil suitable for nesting in wetland land cover than in all other cover types except emergent wetland, deciduous/mixed forest edge, and coniferous forest. Urban/developed ground nesting resources were ranked second greatest overall, with more bare soil than in both wetland cover types and more soil in suitable condition than found in agriculture/pasture, coniferous forest and both wetland types. Availability and suitability of ground nesting resources in agriculture/pasture and forest cover types did not significantly differ from most other cover types (Table 3.2; Appendix D, Table D.4).

Table 3.2. Average (±standard deviation) rank from 1 to 5 of nesting resources available in eight land cover types of the Maine, USA, lowbush blueberry production landscape. Condition of resources was ranked from poor to most suitable: wet, clay soils to dry, sandy soils; live, green twigs to hollow, dead twigs; fully decayed to intact but soft enough for cavities; and falling/disintegrating to upright with hollow cavities.

	Bare soil		Woody shrubs		Fallen dead wood		Standing dead wood	
Land cover	Amount	Condition	Amount	Condition	Amount	Condition	Amount	Condition
Deciduous/mixed forest edge	2.4 (1.3)	2.8 (1.0)	2.8 (1.3)	2.0 (0.7)	**3.6 (0.8)***	2.2 (0.4)	**3.0 (0.6)***	2.6 (0.5)
Urban/developed	**3.2 (0.7)***	**3.8 (0.5)***	1.4 (0.5)	1.0 (0)	1.0 (0)	**1.0 (0)***	1.0 (0)	**1.0 (0)***
Coniferous forest	2.4 (1.0)	1.8 (0.4)	1.8 (0.7)	1.6 (0.8)	**4.0 (0.6)***	2.6 (0.8)	**3.0 (0.9)***	2.2 (0.7)
Deciduous/mixed forest	2.6 (1.2)	2.8 (0.7)	1.6 (0.5)	1.4 (0.5)	**5.0 (0)***	3.0 (1.1)	**3.4 (1.3)***	2.2 (0.7)
Emergent wetlands	1.5 (0.5)	1.5 (0.5)	**4.0 (1.0)***	**3.0 (1.0)***	1.8 (0.4)	2.8 (1.3)	2.0 (1.0)	1.8 (0.4)
Wetlands/water	**1.4 (0.5)***	**1.4 (0.5)***	**4.0 (0.9)***	**2.8 (1.0)***	2.4 (1.0)	3.4 (1.0)	2.4 (1.2)	2.6 (1.3)
Agriculture/pasture	2.8 (0.4)	2.4 (0.5)	1.6 (0.8)	1.3 (0.4)	1.2 (0.4)	**1.0 (0)***	1.2 (0.4)	**1.0 (0)***
Lowbush blueberry fields	**4.4 (0.8)***	**4.0 (0.7)***	1.8 (0.7)	1.8 (0.8)	2.3 (0.4)	2.4 (0.5)	1.4 (0.5)	1.8 (0.7)

* indicates significant difference(s) with other land cover types ($p \leq 0.05$); for a more detailed assessment of results see Appendix D, Table D.4.

Similarly, cavity nesting suitability also varied among land cover types. Wetlands and emergent wetlands had significantly more woody shrubs than all other cover types with more hollow or soft pithy twigs suitable for nesting cavities than observed in agriculture/pasture, deciduous forest, and urban/developed areas. Coniferous and deciduous/mixed forest provided more fallen dead wood than in nearly all other cover types, and fallen dead wood was in poor condition for nesting in agriculture/pasture and urban/developed areas. Standing dead wood was more prevalent in forested cover types than in lowbush blueberry, agriculture/pasture, and urban/developed areas; further, the condition of standing dead wood was unsuitable for nesting in agriculture/pasture and urban/developed areas (Table 3.2, Appendix D, Table D.4).

3.3.2. Comparison of field-based and expert-based model parameter values

3.3.2.1. Bee life history parameter values

Field-based life history parameter values describing bee active flight season were more evenly distributed over the growing season than expert-based parameter values (Table 3.3). Field-based parameter values were not correlated with expert-based parameter values in the early summer or mid-summer; however, they were correlated in the late summer (Spearman's rho=0.72, p=0.003). Field-based values for bee active flight season in the late summer were less than expert-based values (Table 3.3, Appendix D, Table D.5). Bee species that are abundant in early lowbush blueberry bloom, including *Osmia inspergens* (Lovell and Cockerell) and *O. atriventris* (Cresson) (Bushmann and Drummond 2015) were also abundant in our non-crop field surveys in the early summer period but not later.

Table 3.3. Lonsdorf model field-based bee life history parameter values of 14 important bee species in the Maine, USA lowbush blueberry production landscape. Field data was collected for Chapter 2 of this dissertation. Percent difference from expert-based bee life history parameter values from Groff et al. (2016) (Appendix D, Table D.5) is in parentheses. Bold text indicates field-based parameter values are significantly correlated ($p \leq 0.05$) with expert-based parameter values.

	Preferred nesting substrate		Active flight season			
Species	Ground	Cavity	Early summer	Mid-summer	Late summer	Maximum foraging distance (m)
Andrena carlini	1	0	0.33 (0)	0.33 (0)	**0.33 (0)**	598
Andrena carolina	1	0	0.5 (100)	0.5 (0)	**0 (-100)**	246
Andrena vicina	1	0	0.33 (0)	0.33 (0)	**0.33 (0)**	569
Augochlorella aurata	1	0	0.33 (94)	0.33 (0)	**0.33 (-34)**	60
Colletes inaequalis	1	0	0.33 (0)	0.33 (0)	**0.33 (0)**	1091
Halictus ligatus	1	0	0.33 (-23)	0.33 (14)	**0.33 (-13)**	148
Lasioglossum acuminatum	1	0	0.33 (94)	0.33 (0)	**0.33 (-34)**	186
Lasioglossum cressonii	0	1	0.33 (14)	0.33 (14)	**0.33 (-23)**	63
Lasioglossum heterognathum	1	0	0.33 (94)	0.33 (0)	**0.33 (-34)**	16
Lasioglossum leucocomum	1	0	0.33 (14)	0.33 (14)	**0.33 (-23)**	31
Lasioglossum pectorale	1	0	0.33 (14)	0.33 (14)	**0.33 (-23)**	81
Lasioglossum versatum	1	0	0.33 (14)	0.33 (14)	**0.33 (-23)**	79
Osmia atriventris	0	1	0.5 (100)	0.5 (0)	**0 (-100)**	186
Osmia inspergens	0	1	1 (100)	0 (-100)	**0 (0)**	495

3.3.2.2. Floral resource availability parameter values

3.3.2.2.1. Field-based floral resource availability parameter values

Floral resource availability parameter values directly informed by field surveys were generally less than expert-based values, and parameter values informed by floral abundance field data were less than those informed by field data on floral species richness (Table 3.4). Parameter values informed by early season floral species richness were significantly correlated with early season expert-based floral resource parameter values (rho=0.74, p=0.04); no other field-based parameters informed by floral abundance or species richness data were correlated with their expert-based counterparts. Field-based floral resource parameter values for lowbush blueberry fields differed from expert-based values owing to a seasonal offset in field surveys and expert opinion; that is, field surveys were conducted in June, July, and August, whereas expert opinion estimated floral resources in April/May, June/July, and August/September (Table 3.4).

3.3.2.2.2. Field-based bee community proxies, floral resource availability parameter values

Floral resource availability parameter values indirectly informed by field-collected bee abundance or species richness data had two consistent trends. First, lowbush blueberry and deciduous/mixed forest edge had larger parameter values resulting from greater field-collected bee abundance and species richness. Second, coniferous forest and deciduous/mixed forest had smaller parameter values associated with lower field-collected bee abundance and species richness throughout the growing season. In the mid-season, parameter values informed by field-collected bee species richness were significantly correlated with their corresponding expert-based parameter values (rho=0.909, p=0.001). Bee species richness proxy values were less than expert-based floral resource values in urban/developed areas and greater in wetlands, with no difference in valuation in lowbush blueberry fields and emergent wetlands (Table 3.4).

Table 3.4. Sets of field-based Lonsdorf model floral resource availability parameter values for application to the Maine, USA lowbush blueberry production landscape. Percent difference from expert-based values (Groff et al. 2016) is in parentheses. Bold text indicates the set of field-based parameter values is significantly correlated ($p \leq 0.05$) with the corresponding set of expert-based parameter values.

	Expert-based			Floral abundance			Floral species richness			Floral abundance proxy			Floral species richness proxy		
	Spring	Early summer	Late summer	Early summer	Mid-summer	Late summer	Early summer	Mid-summer	Late summer	Early summer	Mid-summer	Late summer	Early summer	Mid-summer	Late summer
Deciduous/mixed forest edge	0.9	0.9	1.0	0.5 (-44)	0.1 (-89)	0.5 (-50)	**0.7** **(-22)**	0.5 (-44)	0.6 (-40)	0.97 (8)	0.76 (-16)	0.91 (-9)	0.74 (-18)	**0.92** **(2)**	0.75 (-25)
Urban/developed	1.0	0.9	1.0	0.1 (-90)	1 (11)	0.1 (-90)	**0.7** **(-30)**	0.8 (-11)	0.6 (-40)	0.34 (-66)	1.0 (11)	0.36 (-64)	0.7 (-30)	**0.48** **(-47)**	0.58 (-42)
Coniferous forest	0.1	0.1	0.1	0.1 (0)	0.1 (0)	0.1 (0)	**0.2** **(100)**	0.1 (0)	0.1 (0)	0.03 (-70)	0.01 (-90)	0.01 (-90)	0.07 (-30)	**0.01** **(-90)**	0.01 (-90)
Deciduous/mixed forest	0.7	0.5	0.4	0.2 (-71)	0.1 (-80)	0.1 (-75)	**0.4** **(-43)**	0.2 (-60)	0.1 (-75)	0.07 (-90)	0.04 (-92)	0.06 (-85)	0.11 (-84)	**0.16** **(-68)**	0.08 (-80)
Emergent wetlands	0.7	0.6	0.6	0.2 (-71)	0.2 (-67)	0.5 (-17)	**0.5** **(-29)**	0.9 (50)	1.0 (67)	0.21 (-70)	0.34 (-43)	0.91 (52)	0.37 (-47)	**0.68** **(13)**	0.5 (-17)
Wetlands/water	0.3	0.2	0.5	0.6 (100)	0.2 (0)	1.0 (100)	**0.6** **(100)**	1.0 (400)	0.7 (40)	0.12 (-60)	0.43 (115)	0.96 (92)	0.26 (-13)	**0.76** **(280)**	0.67 (34)
Agriculture/ pasture	0.9	0.7	0.9	1.0 (11)	1.0 (43)	0.1 (-89)	**1.0** **(11)**	0.7 (0)	0.4 (-56)	0.21 (-77)	0.46 (-34)	1.0 (11)	0.37 (-59)	**0.6** **(-14)**	0.33 (-63)
Lowbush blueberry fields	0.4	1.0	0.5	0.6 (50)	0.3 (-70)	0.2 (-60)	**0.5** **(25)**	0.8 (-20)	0.5 (0)	1.0 (150)	1.0 (0)	0.96 (92)	1.0 (150)	**1.0** **(0)**	1.0 (100)

3.3.2.3. Nesting suitability parameter values

3.3.2.3.1. Field-based nesting suitability parameter values

Field-based ground nesting suitability parameters assigned using the top-down method from Groff et al. (2016) were significantly correlated with their expert-based counterparts (rho=0.95, p>0.001). Field-based, percentage-informed nesting suitability parameter values, which reflected the percentage of each cover type offering each nesting resource, decreased lowbush blueberry ground nesting suitability from the expert-based value of 1.0 (100% of lowbush blueberry fields provided ground nesting habitat) to 0.5 (50%). The field-based parameter value for ground nesting suitability in emergent wetland was greater than its expert-based counterpart, while the field-based parameter value for wetlands was less than its expert-based counterpart. Cavity nesting suitability for lowbush blueberry, agriculture/pasture, and deciduous forest and both ground and cavity nesting parameter values for forest cover types decreased to reflect the percentage of nesting habitat provided by these cover types (Table 3.5). Field-based, percentage-informed ground nesting suitability parameter values remained significantly correlated with expert-based parameter values (rho=0.72, p=0.04).

3.3.2.3.2. Field-based bee community proxies for nesting suitability parameter values

Ground nesting suitability parameter values indirectly informed by field-collected bee abundance and species richness data were not different from expert-based parameter values, whereas cavity nesting parameter values for lowbush blueberry were greater (Table 3.5). Proxy values informed by the species richness of ground nesting bees were significantly correlated with expert-based ground nesting suitability parameters (rho=0.79, p=0.01), owing to similarities in values for lowbush blueberry fields and deciduous/mixed forest edge (Table 3.5).

Table 3.5. Sets of field-based Lonsdorf model nesting suitability parameter values for application to the Maine, USA lowbush blueberry production landscape. Percent difference from expert-based values (Groff et al. 2016) is in parentheses. Bold text indicates the set of field-based parameter values is significantly correlated ($p \leq 0.05$) with the corresponding set of expert-based parameter values.

	Expert opinion		Nesting assessment		Nesting abundance proxy		Nesting species richness proxy		Nesting assessment %-informed	
	Ground nesting	Cavity nesting	Ground nesting	Cavity nesting	Ground nesting	Cavity nesting	Ground nesting	Cavity nesting	Ground nesting	Cavity nesting
Deciduous/mixed forest edge	0.9	1.0	**0.7** **(-22)**	0.8 (-20)	0.54 (-40)	1.0 (0)	**0.9** **(0)**	0.88 (-12)	**0.4** **(-56)**	0.8 (-20)
Urban/developed	0.9	0.6	**0.7** **(-22)**	0.5 (-17)	0.16 (-82)	0.39 (-35)	**0.48** **(-47)**	0.5 (-17)	**0.7** **(-22)**	0.5 (17)
Coniferous forest	0.5	0.6	**0.4** **(-20)**	0.8 (33)	0.01 (-98)	0.01 (-98)	**0.06** **(-88)**	0.01 (-98)	**0.3** **(-40)**	0.6 (0)
Deciduous mixed forest	0.6	0.9	**0.6** **(0)**	1.0 (11)	0.04 (-93)	0.01 (-99)	**0.16** **(-73)**	0.01 (-99)	**0.3** **(-50)**	0.6 (-33)
Emergent wetlands	0.2	0.4	**0.3** **(50)**	0.8 (100)	0.13 (-35)	0.71 (78)	**0.35** **(75)**	1.0 (150)	**0.4** **(100)**	0.8 (100)
Wetlands/water	0.1	0.1	**0.4** **(300)**	0.8 (700)	0.15 (50)	0.43 (330)	**0.35** **(250)**	0.88 (780)	**0.2** **(100)**	0.8 (700)
Agriculture/pasture	0.7	0.2	**0.6** **(-14)**	0.4 (100)	0.13 (-82)	0.29 (45)	**0.39** **(-44)**	0.5 (150)	**0.6** **(-14)**	0.2 (0)
Lowbush blueberry fields	1.0	0.4	**1.0** **(0)**	0.5 (25)	1.0 (0)	1.0 (150)	**1.0** **(0)**	0.75 (88)	**0.5** **(-50)**	0.2 (-50)

3.3.3. Model runs and validation

The Lonsdorf model prediction accuracy of bee abundance in 40 Downeast lowbush blueberry fields increased with field-based bee life history parameter values (observed v. predicted bee abundance Pearson's r=0.45, p=0.003); therefore, we used field-based values in all model scenarios. Field-based nesting suitability parameter values (r=0.42, p=0.006) also increased prediction accuracy compared to expert-based results (r=0.34, p=0.03) (Table 3.1). Model scenario 13, which used field-based, percentage-informed nesting parameter values and expert-based floral resource parameter values, performed best (r=0.43, p=0.005). Incorporating floral abundance field survey or bee abundance proxy-informed floral resource parameter values led to loss of predictive capability (Table 3.1, Scenarios 11-13). Therefore, we retained the field-based, percentage-informed nesting suitability parameter values and expert-based floral resource availability parameter values to predict bee abundance. Scenarios that incorporated additional sources of variation (i.e., two additional land cover classes and an early time period of the growing season) had mixed results. Dividing the growing season into four time periods resulted in nearly the same predictive accuracy as three time periods; therefore, for simplicity, we retained three periods of the growing season. Adding two land cover types (mixed forest and open water) did not improve prediction accuracy over expert-based results (Table 3.1, Scenarios 14-15). Our best-performing model run for the Downeast growing region (scenario 13), with field-based bee life history parameter values, field-based, percentage-informed nesting suitability parameter values, and expert-based floral resource parameter values, was a 26% improvement over models parameterized solely with expert-based values (Fig. 3.3).

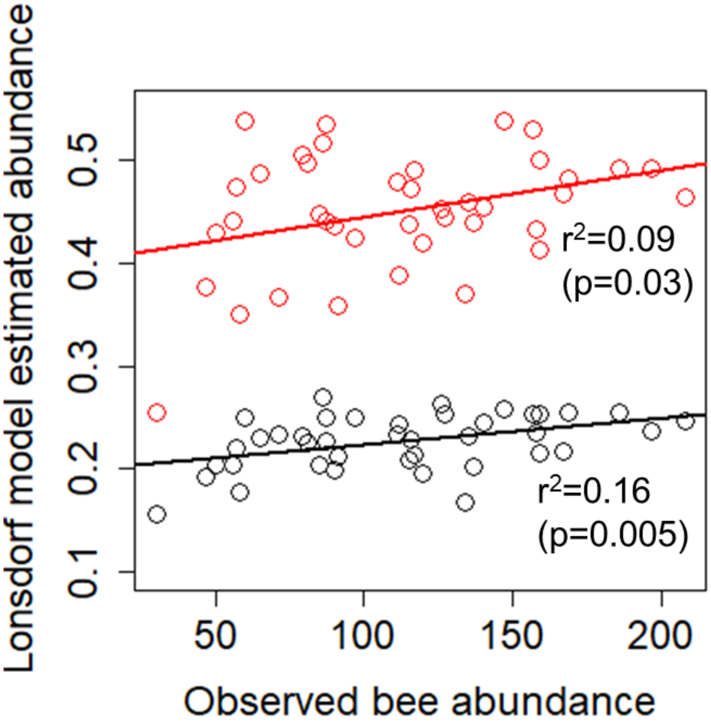


Figure 3.3. Lonsdorf model predictions for 40 Downeast Maine, USA, lowbush blueberry fields with expert-based (top line, in red) and field-based, percentage-informed nesting suitability parameter values (bottom line, in black) validated with simple linear regression.

When we applied the best performing set of parameter values from the Downeast growing region to the Midcoast growing region, the model was unable to accurately predict bee abundance in lowbush blueberry fields in three of our four Midcoast scenarios (Table 3.1, Scenarios 16-19; Fig. 3.4). Validating model predictions with 14 crop fields surveyed in 2014-2015 (Scenario 16), eight crop fields surveyed in 2015 (Scenario 17), and 31 crop and non-crop field sites (Scenario 19) did not lead to predictive capability. However, the Lonsdorf model was able to accurately predict wild bee abundance in 17 non-crop field sites (Table 3.1, Scenario 18). Midcoast model predictions were not significantly correlated with bee species richness within or outside of lowbush blueberry fields.

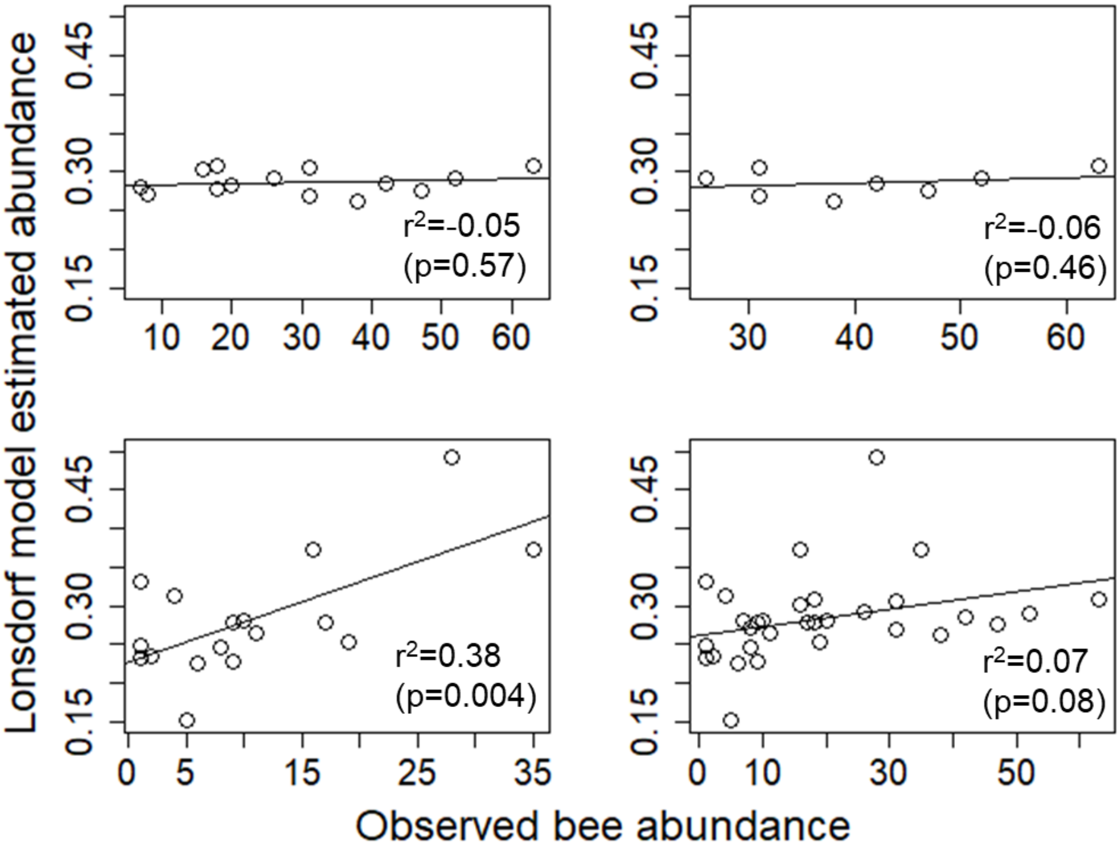


Figure 3.4. Lonsdorf model predictions for four Midcoast Maine, USA, application scenarios validated with simple linear regression. Scenarios are: a) 14 lowbush blueberry fields sampled in 2014-2015, b) eight lowbush blueberry fields sampled in 2015, c) 17 non-crop land cover sites sampled in 2014-2015, and d) 31 crop and non-crop sites sampled in 2014-2015.

3.3.4. Landscape pattern assessment

We found no significant relationship between field size, perimeter-area ratio, survey site location (center, edge, or midfield) within the crop field, or proportion of blueberry in the surrounding landscape (at 250, 500, 1000, and 2000 m) and model predictions of bee abundance within 40 crop fields in the Downeast growing region. In the Midcoast growing region, we found no significant influence of field size or proportion of lowbush blueberry in the surrounding landscape. However, we found a significant influence of perimeter-area ratio (r^2=0.24, p=0.04, $F_{(1,12)}$=5.16, Fig. 3.5) and survey site location (r^2=0.59, p=0.002, $F_{(2,11)}$=10.53, Fig. 3.6). Model predictions of bee abundance were greater in fields with a greater perimeter-area ratio and greater along field edges than they are in the field center.

Assessment of the influence of non-crop land cover surrounding Midcoast crop fields revealed significant correlations between model predictions of bee abundance and the amount of agriculture/pasture (250 m, Pearson's r=0.64, p=0.01; 500 m, r=0.67, p=0.007) and deciduous/mixed forest edge (250 m, r=0.65, p=0.01; 500 m, r=0.62, p=0.01) at small scales (Table 3.6). The amount of emergent wetland at the 2000m scale was also significantly correlated with model predicted bee abundance (r=0.53, p=0.05). This does not corroborate with field-collected data, as observed bee abundance was positively correlated with the amount of coniferous forest at 2000 m (r=0.55, p=0.04) and emergent wetland at 1000 m (r=0.53 p=0.05), and observed bee species richness was correlated with the amount of urban/developed land cover at 250m (r=0.61, p=0.02, Table 3.6).

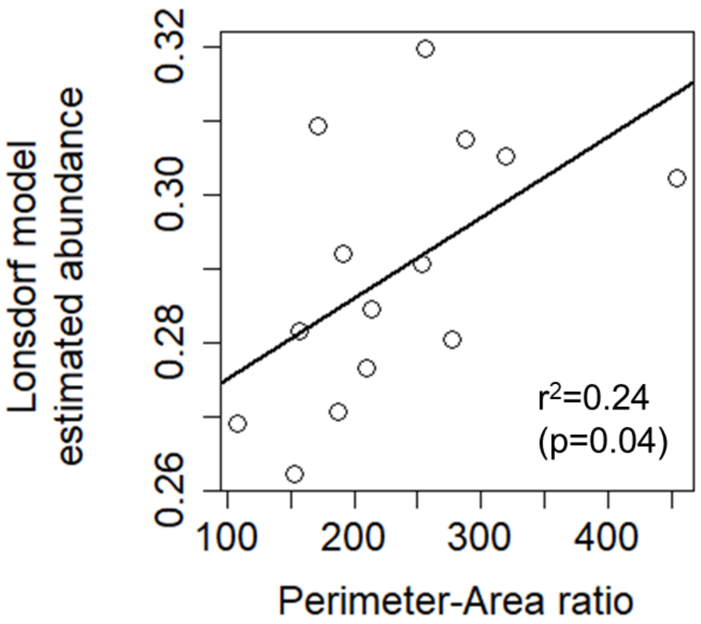


Figure 3.5. Simple linear regression for Lonsdorf model predictions in 14 Midcoast Maine, USA, lowbush blueberry fields and field perimeter-area ratio (PARA) as measured in Fragstats 4.2.

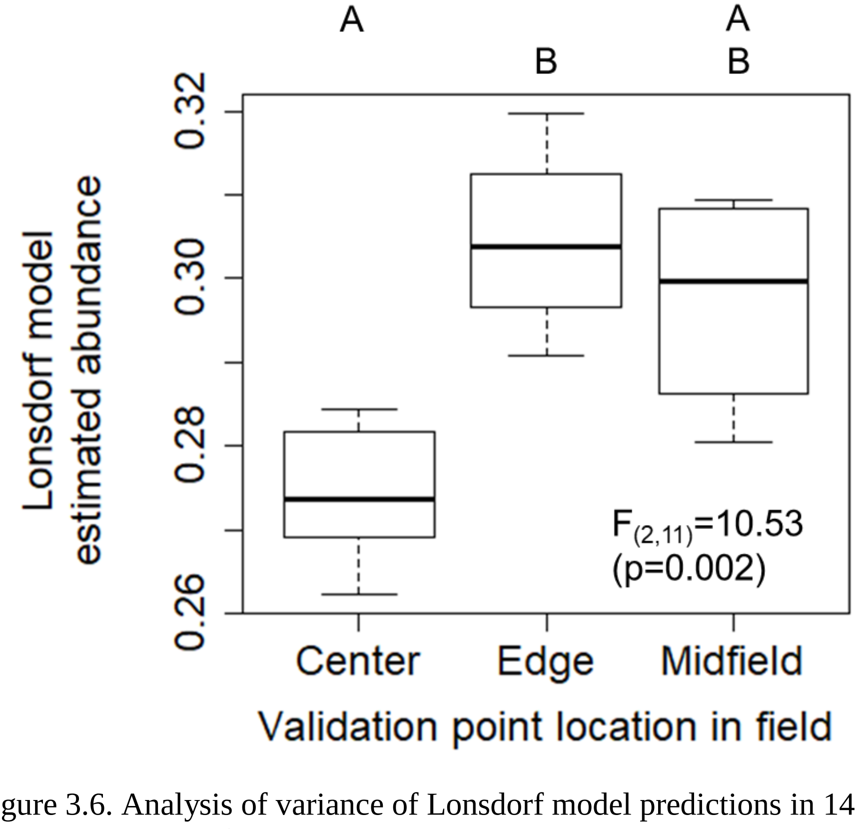


Figure 3.6. Analysis of variance of Lonsdorf model predictions in 14 Midcoast Maine, USA, lowbush blueberry fields by survey transect location within sampled fields.

Table 3.6. Average (± standard deviation) proportions of land cover classes surrounding lowbush blueberry crop fields (n=14) at four spatial scales in Midcoast Maine, USA.

Land cover	250m	500m	1000m	2000m
Deciduous/mixed forest edge	0.08 **(0.03)**[a]	0.08 **(0.02)**[a]	0.07 (0.01)	0.07 (0.01)
Urban/developed	0.04 **(0.02)**[d]	0.03 (0.01)	0.04 (0.01)	0.05 (0.02)
Coniferous forest	0.005 (0.005)	0.02 (0.02)	0.03 (0.02)	0.04 **(0.04)**[c]
Deciduous mixed forest	0.41 (0.18)	0.46 (0.19)	0.50 (0.17)	0.50 (0.10)
Emergent wetlands	0.07 (0.08)	0.07 (0.08)	0.08 **(0.07)**[c]	0.09 **(0.04)**[a]
Wetlands/water	0.03 (0.08)	0.05 (0.11)	0.05 (0.09)	0.05 (0.03)
Agriculture/pasture	0.09 **(0.10)**[a]	0.09 **(0.07)**[b]	0.09 (0.07)	0.08 (0.04)
Lowbush blueberry fields	0.24 (0.09)	0.16 (0.07)	0.09 (0.05)	0.06 (0.03)

a=significant relationship with Lonsdorf model predictions at $p \leq 0.05$ and >0.01
b=significant relationship with Lonsdorf model predictions at $p \leq 0.01$
c=significant relationship with bee abundance at $p \leq 0.05$
d=significant relationship with bee species richness at $p \leq 0.05$

3.4. Discussion

3.4.1. Comparison of parameterization methods

Field-based bee life history parameter values (specifically active flight season) improved prediction accuracy over expert-based values. Model sensitivity to active flight season has not been evaluated, although sensitivity to flight distance has been assessed (Lonsdorf et al. 2009). Groff et al. (2016) found greater prediction accuracy in the Downeast Maine growing region with smaller-bodied wild bees. Small bees encounter less land cover variation over shorter flight distances, decreasing the chance of prediction error. Our field-based, percentage-informed nesting suitability parameter values, particularly in lowbush blueberry, coniferous forest, and deciduous/mixed forest, led to a 26% increase in prediction accuracy over expert-based parameter values, specifically by reducing predictions in lowbush blueberry fields with few bees (Fig. 3.3). Groff et al. (2016) found the Lonsdorf model sensitive to the ground nesting parameter in deciduous/mixed forest, a dominant land cover type across the study landscape, and in lowbush blueberry fields, a dominant land cover surrounding the validation sites. Our work confirms these relationships.

Our improvements in prediction accuracy from field-based parameter values, however, did not outperform the best scenario from Groff et al. (2016), who achieved greatest prediction accuracy with nesting suitability and floral resource parameter values generated through an informed optimization process, whereby the parameter values were changed ±0.2 based on the results of a parameter sensitivity analysis (Table 7 in Groff et al. 2016). Those values reduced nesting and floral resource suitability of lowbush blueberry and coniferous forest compared to expert-based values; however, they increased suitability of deciduous/mixed forest and deciduous/mixed forest edge. Our field surveys suggest low suitability of deciduous/mixed forest, suggesting that the informed optimization parameter values of Groff et al (2016) may be inflated.

Field-based floral resource parameter values were much less than expert-based parameter values, leading to under-prediction in crop fields with high bee abundance. Expert-based parameter values likely generalized the patchiness of floral resource availability we recorded across our study landscape, leading to greater model prediction accuracy; however, this heterogeneity is a source of expert uncertainty (Koh et al. 2016). We acknowledge that this tradeoff in uncertainty and observed variability between estimating and quantifying resource heterogeneity in land cover types is difficult to balance.

Bee community proxy parameter values were consistently smaller in deciduous/mixed forest and larger in lowbush blueberry. Model scenarios informed by these values led to reduced prediction accuracy, though the results varied with landscape context. These scenarios over-predicted bee abundance in crop fields when there was a greater proportion of lowbush blueberry in the surrounding landscape. In contrast, they under-predicted bee abundance in crop fields surrounded by deciduous/mixed forest and little lowbush blueberry. The model is sensitive to changes in expert-based parameter values for these two dominant land cover types (Groff et al. 2016), and indirectly informing these parameter values with bee community proxies did not improve prediction accuracy over directly informing these parameter values with nesting suitability and floral resource availability field data.

When we attempted to more accurately describe heterogeneity in our study system by characterizing additional land cover types or time periods in the growing season, model performance did not improve, indicating that the expert-based models sufficiently described real-world conditions in lowbush blueberry agriculture. Introducing additional sources of variation may create more avenues for inaccurate model predictions and may be more successful in small, more homogeneous landscapes (Olsson et al. 2015; Kammerer et al. 2016).

3.4.2. Lonsdorf model performance across landscape contexts

Landscape configuration is not consistently correlated with bee abundance (Kennedy et al. 2013); however, here we link Lonsdorf model prediction accuracy to configuration metrics in a heterogeneous landscape. Prediction accuracy in the heterogeneous Midcoast region crop fields is reduced owing to complex field shapes (measured with the perimeter-area ratio) and local influence of non-crop land cover. Lonsdorf model predictions decrease dramatically with distance into crop fields from field edges (Kammerer et al. 2016); Midcoast crop fields may be too small and complex in shape for the model to include their resource suitability values in its predictions. Further, the Midcoast region contains more agriculture/pasture and deciduous/mixed forest edge than the Downeast region. These cover types have more diverse and abundant bee communities than the forested cover types that are dominant Downeast (Chapter 2, this dissertation) and were significantly positively correlated with Lonsdorf model predictions at small scales (Table 3.6). Including forest edge as a unique land cover class improves Lonsdorf model prediction accuracy (Kammerer et al. 2016), as the field/forest transition contains floral resources that benefit wild bee communities (Drummond et al. 2017a).

We found no correlation between coniferous forest and predicted bee abundance Midcoast, contrary to the negative correlation that Groff et al. (2016) found Downeast, nor did we find the positive correlation between bee abundance and deciduous/mixed forest that they report. Coniferous forest is relatively rare in the Midcoast, whereas deciduous/mixed forest is abundant and widely distributed among other more suitable cover types. We did find a significant positive correlation between proportion of urban/developed area and bee species richness at the 250 m scale Midcoast, which Groff et al. (2016) did not find Downeast. There is more urban land cover Midcoast than Downeast, and urban land cover has been linked to greater bee species richness at small scales (Simao et al. 2017). Global and national applications of the Lonsdorf model (Kennedy et al. 2013; Koh et al. 2016) have highlighted the need to assess model performance in varying habitat types and landscape contexts with parameter values informed by field data; our work indicates that these all influence prediction accuracy and are important to consider in future studies.

The variance to mean^2 ratio in Midcoast lowbush blueberry fields was 0.29 for field-collected bee abundance (r^2 of Lonsdorf model=-0.05) and 0.18 for bee species richness (r^2=0.007), whereas the ratios were 0.15 for abundance (r^2=0.164) and 0.07 for species richness (r^2=0.13) in Downeast crop fields. Ratios from the complex, heterogeneous landscape in Lonsdorf et al. (2009) were below 0.5 (r^2=0.04), suggesting that lowbush blueberry fields had a pollinator community with low variance, which could be a reason for low prediction accuracy.

Outside of lowbush blueberry fields in the Midcoast region, the ratios increase to 0.76 for abundance (r^2=0.31) and 0.36 for species richness (r^2=0.008), suggesting that there is greater variation in the bee community in non-crop land cover, though the Lonsdorf model explains little of the variance in bee species richness in the Maine lowbush blueberry production landscape. This supports the potential for broader applications of the model (Chapters 4 and 5, this dissertation), which can inform conservation planning at landscape scales beyond crop fields.

3.4.3. Caveats and improvements to Lonsdorf model prediction accuracy

One caveat of the Lonsdorf model is that it has been applied at too coarse of a spatial resolution (e.g., >30 m) to reflect fine scale nesting and floral resources in heterogeneous, mixed-use landscapes (Lonsdorf et al. 2009; Kennedy et al. 2013). Reducing the grain size of maps used in the Lonsdorf model may not lead to improved predictions in such landscapes (Groff et al. 2016; Nicholson et al. 2019). The Lonsdorf model has made accurate predictions of bee abundance in apple orchards in heterogeneous landscapes when the spatial resolution was very fine (1.5 m) and the landscape scale of application was limited to 500 m from the center of the orchard (Kammerer et al. 2016). However, applying the model at regional landscape scales with such fine spatial resolution is computationally intensive; therefore, this approach is not feasible for our application. Indeed, Kammerer et al. (2016) struggled to incorporate site to site variability in their model application, which was influenced by landscape context, as was the case in our study system.

By relying on distance from nesting locations to predict bee abundance, the Lonsdorf model overlooks local heterogeneity in resource availability. Incorporating patch forage quality and bee dispersal behavior improves model performance, particularly in complex landscapes (Olsson et al. 2015; Nicholson et al. 2019). However, this is a data-intensive approach and is more appropriate for application to smaller landscapes. While the model is sensitive to dominant land cover at field and regional scales, this is less of a problem in simple, homogeneous landscapes, but leads to inaccurate predictions in heterogeneous, mixed-use landscapes (Groff et al. 2016). One solution is to apply weights to dominant cover types that generally have low bee abundance though habitat suitability is relatively high, such as forest (Kammerer et al. 2016). Although forests can be rich in nesting resources, they are often poor in floral resources, leading to lower bee abundance (Chapter 2, this dissertation).

The Lonsdorf model makes deterministic predictions based on static estimates of resource availability, but bee abundance and species richness vary dramatically in the lowbush blueberry agroecosystem from one season to the next (Drummond et al. 2017b). The model, in its current form, does not account for annual fluctuation in resource availability or incorporation of other variables that may influence these changes in the bee community. These fluctuations in bee abundance year over year can influence model validation data, potentially causing mismatches between model predictions and field-collected bee abundance. Relying solely on resource availability to predict bee abundance ignores other influential variables (Lonsdorf et al. 2009; Koh et al. 2016). Lowbush blueberries are managed on a biennial cycle, in which a fruiting year, with abundant floral resources during a three week crop bloom, is followed by severe pruning and a vegetative regrowth year, with far fewer floral resources (Yarborough 2009). Wild bee communities are influenced by burning as a prune technique, which increases the abundance of Andrenid bees (Venturini et al. 2017b), and isolated lowbush blueberry fields on a single production cycle have fewer bees than fields that are split (fruiting and regrowth sections in the same field) (Venturini et al. 2017b). Further, density dependent (disease, predators) and density independent factors (such as weather) regulate bee populations in lowbush blueberry (Dibble et al. 2017). Pesticide exposure appears to be less important to the entire community (Bushmann and Drummond 2015), but there is a negative effect on mason bees (*Osmia* spp., Stubbs and Drummond 2001).

The Lonsdorf model is sensitive to nesting parameters, particularly in dominant cover types (Groff et al. 2016). Mechanics of the model support this; the nesting habitat present in a pixel is the assigned parameter value for the land cover type the pixel represents, whereas the floral resource value for that pixel is a weighted sum influenced by distance from the pixel. Predicted pollinator abundance per pixel is the nesting suitability value multiplied by the floral resource value (Lonsdorf et al. 2009), therefore the amount of floral resources available in each cover type has less importance than nesting suitability in determining pollinator abundance per pixel. This means that increasing the nesting suitability parameter values may artificially inflate baseline bee populations and reduce prediction accuracy (Nicholson et al. 2019). Additionally, nesting suitability is a key source of uncertainty in expert-based parameter values (Koh et al. 2016). Recent work on the role of nesting suitability in pollinator communities suggests it is highly dependent on crop system context (Sardiñas et al. 2015, 2016a,b). More field assessments of nesting habitat, particularly in non-crop land cover, would reduce uncertainty regarding habitat availability and improve model predictions.

3.4.4. Conservation value of the Lonsdorf model

When applied at national (Koh et al. 2016) and global (Kennedy et al. 2013) scales, the Lonsdorf model provides critical assessments of bee abundance that inform national and global pollinator management strategies (White House Pollinator Task Force 2015; IPBES 2016). These applications are crucial from a conservation perspective, and their methods are sound given the available data and the large spatial scales, but they overlook regional heterogeneity that is revealed in regional scale applications (Lonsdorf et al. 2009; Groff et al. 2016; Kammerer et al. 2016). Describing this regional heterogeneity with more targeted model applications reduces uncertainty associated with larger scale applications and creates more reliable conservation tools (Chapters 4 and 5, this dissertation).

Using field data collected on wild bee communities and habitat resources outside of crop fields throughout the growing season improved predictions of the Lonsdorf model across Maine’s lowbush blueberry production landscape. Crop pollination is no longer the sole argument for pollinator conservation (Kleijn et al. 2015), and this work demonstrates the larger benefit of exploring wild bee communities beyond crop fields. Assessing bee communities outside of crop fields is especially crucial in mixed-use landscapes, where bees are rarely isolated from natural habitat (Winfree et al. 2008). Further, bees in mixed-use landscapes can rely more on local resources instead of mass-flowering crops and supplemental plantings and may require resources outside the crop field to persist until the next crop bloom period. When combined with the Lonsdorf model, field data from a mixed-use landscape provides more accurate predictions of bee abundance at regional scales.

CHAPTER 4

PARTICIPATORY DEVELOPMENT OF A POLLINATION MANAGEMENT DECISION SUPPORT TOOL FOR LOWBUSH BLUEBERRY GROWERS

4.1. Introduction

Pollination security for specialty crops such as berries and nuts is at risk owing to threats to honeybee health (Kulhanek et al. 2017) and wild bee habitat (Kremen et al. 2002). Specialty crop growers are facing changes in pollination management as demand for commercially managed honeybee hives increases and the role of wild bees in crop pollination is clarified (Aizen and Harder 2009; Pettis and Delaplane 2010; Breeze et al. 2011; Garibaldi et al. 2011, 2013). Agricultural decision support systems (AgDSS), computer based tools that translate science to practitioners, may be used to aid crop growers in management decisions during times of rapid change and uncertainty (Matthews et al. 1999; McCown 2002a). Though many AgDSS face problems of implementation (McCown 2002b; Matthews et al. 2008), increasing emphasis on participatory development (Carberry et al. 2002; Jakku and Thorburn 2010) and simplifying available tools (Bergez et al. 2012; Clavel et al. 2012) may lead to greater end use by target audiences. Participatory development involves members of a target audience—in this case, crop growers—through the conceptualization, design, and implementation of a DSS (Carberry et al. 2002; Jakku and Thorburn 2010). Kates (2001) suggests internet-based tools to bridge the gap between scientists and practitioners, with participation from both parties during development. This process allows co-production of knowledge (Kates 2001), building consensus on important issues (Costanza and Ruth 1998), and ultimately wider dissemination of research results to practitioners (Mitter et al. 2014).

Crop pollination by wild animals, mostly bees (family Apoidea), is an ecosystem service that provides 35% of global crop production and is necessary for 66% of global crops (Klein et al. 2007). Ecosystem services (ES) are natural processes that benefit people (Daily 1997), and their provision can shift as a result of land use change (Polasky et al. 2011). Land use change that maximizes one output, such as intensifying crop production, will likely lead to a decline in ecosystem services (Millennium Ecosystem Assessment 2005). Efforts to incorporate ecosystem services into agriculturally-intense landscapes (e.g., pollinator plantings; Blaauw and Issacs 2014, Venturini et al. 2017a) seek to change perceptions and practices to preserve natural resources, but knowledge of social processes in these social-ecological systems is needed to achieve that goal (Tscharntke et al. 2005; Guerry et al. 2015). There are multiple decision support tools for assessing ecosystem services and creating management plans incorporating various services, each providing mapped output displaying ES provision across landscapes (Nelson et al. 2009; Villa et al. 2009; Peh et al. 2013). Communicating ES across landscapes through maps illustrates geographic variation in supply and demand for them, making maps useful decision support tools for ES management (Crossman et al. 2013).

Lowbush blueberry (*Vaccinium angustifolium* Aiton) is a North American native plant that has been cultivated by crop growers into open fields through vegetation management (Yarborough 2015). Maine is the world's largest producer of lowbush blueberries, harvesting 40-47 million kilograms annually since 2012 (Yarborough 2016). The plant is highly dependent on insect pollination to set fruit and is most effectively pollinated by wild bee species capable of buzz pollination (Javorek et al. 2012; Drummond 2016). Despite the effectiveness of wild bees, most lowbush blueberry growers invest heavily in commercially managed honeybee hives (Hanes et al. 2015; Asare et al. 2017). The number of honeybee hives entering the state each

May ranges from fewer than 30,000 to more than 70,000 depending on anticipated crop yield (J. Lund, Maine State Apiarist, pers. comm) in an effort to circumvent the inefficiency of honeybee pollination with a high number of flower visits. However, wild bees are abundant and diverse during crop bloom and can contribute up to 30% of fruit set (Bushmann and Drummond 2015; Drummond 2016; Asare et al. 2017).

Structure of the surrounding landscape affects wild bee communities in crop fields (Kennedy et al. 2013, Bushmann and Drummond 2015). There are two blueberry growing regions in Maine with contrasting landscape contexts. The Downeast region contains the largest and most intensively managed lowbush blueberry fields in a matrix dominated by coniferous forest managed for timber harvest. Non-blueberry agriculture and developed land cover are scattered and comprise little of this relatively homogeneous landscape. In contrast, the Midcoast region is heterogeneous, containing smaller, less intensively managed crop fields interspersed with other agriculture, including pasture, orchards, and small, diversified farms. Developed land in small towns is more prevalent in the Midcoast region than the Downeast region; however, in both growing regions, towns are classified as rural or exurban development along the common urban-rural development gradient (Kaminski et al., in review). The matrix in the Midcoast region is deciduous forest-dominant and less intensively harvested. Wild bee communities differ between these growing regions owing to these differences in landscape context (Chapters 1 and 2, this dissertation). Additionally, these growing regions differ in human and social capital (Collum 2016). Human dimensions research into pollination is relatively new; what research exists shows that social factors influence pollination practices (Hanes and Waring 2018).

Landscape-scale studies of pollinator behavior indicate that pollinator species richness and abundance, along with pollination efficiency, decline in agricultural fields with distance from natural habitat that contains nesting substrate and floral resources (Steffan-Dewenter et al. 2002, Kremen et al. 2004; Ricketts et al. 2008; Garibaldi et al. 2011). The Integrated Valuation of Environmental Services and Tradeoffs (InVEST) Crop Pollination Model is a spatially-explicit predictive model that estimates pollinator abundance across agricultural landscapes (Lonsdorf et al. 2009; hereafter referred to as the Lonsdorf model). The model combines parameter values describing nesting substrate suitability, floral resource availability, and bee life history traits with land cover data to predict relative pollinator abundance within each cell of an input land cover map. The output is a map predicting wild bee abundance across a landscape. We applied the Lonsdorf model across Maine's lowbush blueberry production landscape to estimate wild bee populations surrounding crop fields (Groff et al. 2016; Chapter 3, this dissertation). Crop growers are aware of the potential contribution natural habitat surrounding crop fields may provide to wild bee populations, but they may overestimate the effect (Hanes et al. 2015). Maps such as those created by the Lonsdorf model allow a landscape-level approach in translating the model predictions to growers, which can lead to a more holistic view of the role wild bees have in crop pollination (Tscharntke et al. 2005; Sandker 2010). Maps allow stakeholders to make decisions without needing to plug in farm-based information and are considered "bio-decisional" tools (Clavel et al. 2012). Such tools are intuitive and simple to use.

InVEST is a suite of ecosystem service models, many of which have been used in decision-making processes (Ruckelshaus et al. 2015; Sharp et al. 2016), but to our knowledge this is the first effort to translate output from the Lonsdorf model directly to crop growers. We created a collaboration between natural scientists, social scientists, technical developers, and crop growers to develop a multi-scale agricultural decision support system called BeeMapper to aid Maine lowbush blueberry growers in pollination management. We synthesized literature on sustainability science, agricultural decision support systems, and functional agrobiodiversity to provide theoretical context for our work.

4.2 Literature review

4.2.1 Using heuristics to overcome uncertainty

Lowbush blueberry growers face high uncertainty around crop pollination from wild bees in part owing to difficulty assessing wild bee populations in the field (Hanes et al. 2018). This motivates reliance on honeybee hive rentals and resistance to rapidly changing pollination management practices—in other words, lowbush blueberry growers follow a "muddling through" (Lindblom 1959, 1979) approach to pollination management decision making (Hanes et al. 2018). Understanding the abundance of wild bees in the landscape surrounding crop fields is one solution to reduce this uncertainty. When faced with high uncertainty, farmers will turn to "quick and simple" decision approaches—called heuristics—instead of more detailed, elaborate approaches (Ohlmer et al. 1998; Walker 2002). One heuristic lowbush blueberry growers use is an estimate of total wild bee pollination as one hive of honeybee pollination per acre (Hanes et al. 2018). There is a method to calculate wild bee populations in crop fields during bloom (https://www.youtube.com/watch?v=rgVav2byI8o), but it involves active monitoring of pollinating wild bees and knowledge of different groups of wild bees. BeeMapper provides a simple heuristic—a series of maps—that displays information on land cover type and predicted wild bee abundance in and around crop fields. It provides an incremental step in our understanding of wild bee contribution to lowbush blueberry crop yield. Small, incremental changes reduce uncertainty in complex systems and encourage adoption of new information (Lindblom 1979); interviews with crop growers indicate this incremental approach has largely informed their pollination management strategies over time (Hanes et al. 2018).

4.2.2. Iterative, participatory development: synthesizing sustainability science and DSS literature

Many case studies on decision support systems highlight a participatory development process, in which end users are involved in the conception, design, and prototype testing of a DSS (Walker 2002; Van Meensel et al. 2012; Valls-Donderis et al. 2014). Jakku and Thorburn (2010) explain how to incorporate participatory development into AgDSS. We aim to synthesize this literature with the broader principles of sustainability science (Clark and Dickson 2003). To translate science effectively to practitioners, it needs to be defined and framed so that all stakeholders involved can understand and use the science in practice. Stakeholders are more likely to view science effectively for policy and management if it is credible, salient, and legitimate (Cash et al. 2003). Credibility encompasses the quality of the science. Many examples of participatory DSS development begin with the introduction of a team of experts who will be working on the problem to establish basic credibility from the outset. Demonstrating accurate results from simple models early in the process also establishes credibility (Carberry et al. 2002). Saliency is the relevance of the science to the targeted decision makers. Farmers will not implement tools that have no practical value to them (McCown 2002a,b). Assessing stakeholder acceptance of a proposed DSS before development begins establishes saliency, and incorporating feedback collected during DSS development keeps the process salient to stakeholders (Andrews et al. 2003). The advancement of sustainability science is based on the co-production of knowledge and social learning around a salient central issue (Kates et al. 2001). This process is deemed legitimate if stakeholders perceive that their ideas, knowledge, and concerns have been addressed by scientists respectfully, genuinely, and without bias (Cash et al. 2003). Asking for input from stakeholders early in the DSS development process establishes legitimacy; continuing active communication throughout the process maintains legitimacy (Andrews et al. 2003; Sandker 2010). Assumptions about technical abilities of stakeholders cause legitimacy failures: by presenting stakeholders with an end product that they may not be able to use, the lack of consideration of the stakeholders needs indicates a lack of legitimacy of the development process (Bergez et al. 2012).

Boundary work, in which scientists and practitioners establish clear roles that utilize their respective expertise, promotes collaboration and co-learning among stakeholders in DSS development (Cash et al. 2003; Clark et al. 2011). This work can center on a boundary object (Jakku and Thorburn 2010), which integrates science and practice through a material representation to facilitate the exchange of knowledge and promote action (White et al. 2010). The boundary object in a participatory development process combines knowledge, ideas, and perspectives of stakeholders into a final product developed through shared learning (Jones et al. 2009; Voinov et al. 2016). Examples of boundary objects include collaboratively produced maps, working prototypes of tools, and written documents (Clark et al. 2011; Voinov et al. 2016). By focusing on the boundary object and being cognizant of stakeholder roles at the boundaries between their knowledge, successful participatory modeling processes can advance sustainability science (Cash et al. 2003; Clark et al. 2011).

An iterative, participatory development process with regular, active communication is critical for the success of an agricultural DSS (Walker 2002; Cash et al. 2003; Jakku and Thorburn 2010). Presenting early but accurate “throw-away” models kickstarts an iterative development process (Sandker 2010; Voinov and Bousquet 2010). Participatory development of a DSS is not enough to ensure uptake by users; active communication through multiple platforms may be needed to reach a wider audience and ultimately reduce uncertainty in decision making

(Carberry et al. 2002; Walker 2002; Bijlsma et al. 2011). Face to face communication is more effective in participatory development than emails or surveys (Mitter et al. 2014). Our collaboration and communication with crop growers throughout the iterative, participatory development of BeeMapper involved boundary work, with BeeMapper as the boundary object. Our affiliation with Cooperative Extension, which is viewed by growers as credible and legitimate owing to their work on problems salient to crop production (Cash 2001; Hanes and Waring 2018), provided us an open, favorable environment for tool development.

4.2.3. Lowbush blueberry industry background, grower perceptions, and learning outcomes

There are more than 350 lowbush blueberry growing enterprises in Maine (Rose et al. 2013). Lowbush blueberry growers are mostly male, over the age of 55, and have some college education (Rose et al. 2013; Hanes et al. 2015; Collum 2016). The crop is managed following four pest management strategies: conventional, Integrated Pest Management (IPM), no-spray, or certified organic. Most growers practice IPM, manage >40 ha of fields, and operate their blueberry farms on a part-time basis (Rose et al. 2013; Hanes et al. 2015; Collum 2016). Organic lowbush blueberry production rapidly expanded in the early 2000s (Drummond et al. 2012); in a 2015 survey, 23% of growers practiced certified organic or no-spray management (Collum 2016).

Lowbush blueberry growers perceive wild bee habitat around their crop fields to be plentiful (Hanes et al. 2015). Research conducted throughout the lowbush blueberry landscape indicates that growers may be overly optimistic (Bushmann and Drummond 2015; Groff et al. 2016; Chapters 1, 2, and 3; this dissertation). These are incongruent technological frames (Jakku and Thorburn 2010); growers and scientists hold disparate assumptions, beliefs, and expectations regarding wild bee communities and pollination of lowbush blueberry. However, though growers overestimate bee abundance surrounding their crop fields, they accurately perceive the contribution of wild bee pollination to lowbush blueberry fruit set (~25%; Hanes et al. 2015, Asare et al. 2017). Scientists have been collecting and sharing knowledge on wild bee pollination of lowbush blueberry for years (Drummond 2016); however, information on bee habitat outside of crop fields is newer knowledge (Groff et al. 2016; Dibble et al. 2018; Chapters 1, 2, and 3; this dissertation). BeeMapper and its development process promote co-learning between growers and scientists; they share ideas, provide feedback, and learn from each other (McCown 2002a,b). Participatory development leads to greater adoption by end users. The number of end users is typically the measure of success of DSS, but there are multiple outcomes for learning through this process (Jakku and Thorburn 2010). Growers obtain value regarding what DSS have to offer by simply hearing about them or being involved in prototype testing (Thorburn et al. 2011).

4.2.4. Functional agrobiodiversity at multiple scales

Emerging research focusing on functional agrobiodiversity calls for a landscape perspective to fully understand the effects of field-scale management and surrounding non-managed habitat types on landscape-scale diversity of plants, insects, and soils (Bianchi et al. 2013; Gonthier et al. 2014). Functional agrobiodiversity combines functional diversity, the number of functional roles species represent (Tilman et al. 1997) with agrobiodiversity, the biota in and around farms that provides ecosystem services (Jackson et al. 2012). This is based on the idea that agricultural land use does not always negatively affect natural habitat; for wild bees, agriculture provides a mass-flowering floral resource, benefitting bees in the surrounding landscape (Westphal et al. 2003; Chapter 1, this dissertation), and the surrounding landscape can provide nesting and foraging resources before and after crop bloom (Kremen et al. 2002, 2004;

Ricketts et al 2008; Chapters 2 and 3, this dissertation). The functional significance of field-scale biodiversity will only appear at larger spatial and temporal scales, therefore managing for diversity at the landscape scale requires cooperation and collaboration among crop growers in the target landscape (Tscharntke et al. 2005; Jackson et al. 2012; Bianchi et al. 2013; Gonthier et al. 2014). The conservation of diversity in agroecosystems is associated with local knowledge and its exchange (Jackson et al. 2012); lowbush blueberry growers seek out local knowledge and exchange it through industry gatherings (Hanes et al. 2018). However, integration of functional agrobiodiversity requires multiple components: the understanding of elements that support ecosystem services, translation of that knowledge into farm/landscape management practice, and involvement from various scientific disciplines and collaboration between stakeholder groups (Bianchi et al. 2013). Growers achieve much of this already at the farm level (Hanes et al. 2018), but formal landscape level knowledge is lacking. By providing information on wild bee abundance, important blueberry pollinating species, and habitat resources available in and around lowbush blueberry fields at multiple spatial scales, BeeMapper promotes the incorporation of functional agrobiodiversity into pollination management plans.

4.3. Methods

4.3.1 Spatial data

BeeMapper contains two maps: a land cover map and a predicted wild bee abundance map that cover the Downeast and Midcoast growing regions of Maine’s lowbush blueberry production landscape. The land cover map has 10 m pixel size and eight land cover classes representing different floral and nesting resources for wild bees: Agriculture/pasture, consisting of small diversified farms, orchard crops, or pasture; lowbush blueberry fields; coniferous forest; deciduous/mixed forest; deciduous/mixed forest edge; emergent wetland, an aggregation of forested wetland and scrub-shrub land cover; wetlands/water; and urban areas. We applied the Lonsdorf model to this map (Groff et al. 2016; Chapter 3, this dissertation) to create the predicted wild bee abundance map. We classified the predicted wild bee abundance map into five classes from Low to High and provided each class with an estimated number of wild bees present during pollination and their contribution to fruit set (Table 4.1).

Table 4.1. Predicted wild bee abundance classes in BeeMapper. Estimates of bee abundance and contribution to fruit set are provided by Frank Drummond from a long-term data set collected in blooming lowbush blueberry fields in Maine, USA.

Abundance class	**Number of bees (per 10 minutes)**	**Contribution to fruit set**
Low	1	12%
Low-Medium	2	18%
Medium	3	20%
Medium-High	4	25%
High	5-10	30%

We prepared these data for use in a web-based GIS tool; tool design and technical support were provided by the University of Maine Faculty Development Center and Advanced Computing Group. Full technical development details, including spatial data preparation and software framework, are described in Chapter 5 of this dissertation.

4.3.2. Grower participation

4.3.2.1. Large group participation

We proposed the idea for BeeMapper at a large growers meeting in July 2014. Growers were interested in developing the tool, therefore we made an open invitation for interested growers to work with us on tool development. We then presented an initial prototype of the tool to members of the Maine Lowbush blueberry Commission Advisory Board and Committee in November 2014. This audience included ~20 lowbush blueberry growers, advocates, and researchers. During this presentation, we asked for ideas regarding tool features, appearance, and utility. We incorporated feedback from the Advisory Board into the first working iteration of the tool. We held an open demonstration of the first iteration of the tool at a large growers meeting in March 2015, during which growers were able to sit down and try the tool on their crop fields. This generated excitement about the tool among growers and a productive dialogue between growers and scientists. Updates to tool development were presented to a large growers meeting in July 2015. Lastly, we presented the second iteration of the tool at two large growers meetings in March 2016. Through these presentations, we invited growers to visit the BeeMapper website, explore the tool on their own time, and submit feedback either through the BeeMapper feedback form or via email. Total attendance at both meetings was approximately 60 growers; we received feedback from three growers after the meetings via email.

4.3.2.2. Individual or small group participation

We tested the first iteration of BeeMapper through six interviews with growers practicing a range of management practices in March and April 2015 and tested the second iteration through a second round of five grower interviews in February 2016 (Table 4.2; Appendix E). We selected growers via purposive sampling to obtain variation in farm management strategies: high-, medium-, or low-input, or organic/no-spray (Yarborough and Cote 2014). Owing to concurrent spatial data development (Chapters 2 and 3, this dissertation), all interviews were conducted with growers in the Downeast growing region. We conducted four interviews at farm offices, six interviews in growers’ homes, and one interview over the phone. Five interviews included multiple growers working on the same farm; two interviews were with spousal pairs, and three interviews were with 2-4 farm employees. Interview locations needed to have internet access; we brought one laptop and an external mouse to standardize the hardware growers used for tool testing. However, the grower interviewed over the phone used their personal computer.

Interviews were roughly one hour long, and all but the phone interview were recorded with growers' permission. Growers were compensated $75 for their time (Appendices F and G).

Table 4.2. Farming strategies of lowbush blueberry growers interviewed to test BeeMapper.

2015	**Input level**	**Area managed (ha)**
1	High	>50
2	High	>50
3	Medium	10-20
4	Low	5-10
5	Organic	<5
6	Organic	5-10
2016		
7	High	20-50
8	Medium	10-20
9	Medium	10-20
10	Medium	5-10
11	Low	<5

We took a passive role during the interviews. Growers independently used the tool to assess pollinator habitat around (a) crop field(s) they manage and described their thought process as they worked through the tool. We asked growers a series of preliminary questions regarding their current pollination management strategies before opening the tool, then compared model predictions with grower perceptions as we examined the maps around a crop field. Growers also provided feedback on ease of use and data interpretation of the tool. We used feedback from the initial six interviews to extensively revise the tool into a second working iteration. In the second round of interviews, growers worked with the second iteration of the tool and were asked to independently navigate through the tool using a draft of the User's Guide (Appendix H). The purpose of these sessions was twofold: to test the updated iteration of BeeMapper and to evaluate the User's Guide. We asked growers for feedback on word choice and intuitiveness of the User's Guide and data interpretation of the updated tool.

4.3.3. Lonsdorf model refinement

While developing BeeMapper, we concurrently refined Lonsdorf model output in the Maine lowbush blueberry production landscape (Chapter 3, this dissertation). The model was initially informed by expert opinion; this opinion varied widely among experts and led to high variation in model output (Groff et al. 2016). We conducted field surveys across this landscape in 2014 and 2015 to assess wild bee communities, nesting resources, and floral resources throughout the growing season (Chapter 2, this dissertation). By informing the model with field-collected data, we sought more accurate predictions and ultimately better information for growers regarding wild bee abundance in the landscape surrounding their crop fields. We were transparent with growers about our model refinement work, which allowed us to discuss the uncertainty surrounding model output. Furthermore, refining the model output while working with growers allowed us to incorporate grower feedback on map inaccuracies during this process, leading to greater credibility and relevancy in the final product.

4.3.4. BeeMapper final version and tool launch

The final version of BeeMapper resides on a website (https://umaine.edu/beemapper) that provides a prominent link to the tool, multiple web pages of supporting documentation, a printable User’s Guide, and access to the open source web mapping architecture (Chapter 5, this dissertation). We were unable to test website layout with growers owing to time constraints; however, we incorporated grower feedback from all previous testing sessions and presentations into the site design. The site pages correspond to sections of the printable User’s Guide and function as an online guide to using and understanding the tool. Information displayed on the pages include large, clear pictures, and concise, simple text, which were repeatedly requested by growers throughout BeeMapper development.

We launched BeeMapper in July 2017 during the annual lowbush blueberry growers' field day at the University of Maine Cooperative Extension's Blueberry Hill Farm. This annual meeting is the largest Extension event held for lowbush blueberry growers, with 200-300 growers attending each year. We gave a short presentation to a large group of growers that included a walkthrough of how to use the tool, descriptions of tool and website features, and suggestions on using the data provided by the tool. After the presentation, we handed out printed User's Guide pamphlets for growers to take home and reference if they chose not to print out the long form User's Guide on the website. Finally, we held an open workshop over the lunch hour for growers to try BeeMapper and talk to the scientists who worked on the tool. This workshop had six laptops available and three scientists present, and approximately 40 growers, most of whom were not involved in the 1:1 testing sessions, attended. Concluding the BeeMapper development process with a participatory session between developers and end users allowed another opportunity for feedback from end users and for developers to maintain credibility with the end users.

4.4. Outcomes

4.4.1. Grower feedback

Growers were interested and engaged with BeeMapper throughout the development process. Positive interactions with entomologists over time (Hanes and Waring 2018; Hanes et al. 2018) may have encouraged growers to participate in BeeMapper development and increased their confidence in its output. During the testing sessions, growers found the maps easy to interpret, and they made the connection between land cover type and wild bee abundance. Some described how the tool could be used to make decisions about pollination management, including how many beehives to rent and where the hives should be placed. Some growers said they would use the tool to minimize risk to existing wild bee habitat—for example, they would not spray pesticides in the direction of abundant areas. The interviews suggested that growers would use the tool to assess their wild bee habitat, but would not change their current pollination practices unless they become unsustainable. The growers we interviewed were all frequent attendees of Cooperative Extension events; these growers are often early adopters of new scientific knowledge (Hanes et al. 2015) and may have biased the perceptions and feedback we received. Additionally, all interviewed growers operate farms in the Downeast Maine lowbush blueberry growing region, which contains more high-input farms (Rose et al. 2013) and fewer sources of high quality wild bee habitat (Chapter 2, this dissertation) than the Midcoast growing region.

Much of the feedback centered on the disparity between grower perception and model prediction of wild bee abundance. The values of estimated number of bees in fields during bloom and contribution to fruit set we provided in the legend of the predicted wild bee abundance map (Table 4.1) were generally accepted by growers. However, when the predicted wild bee abundance map was displayed, every grower interviewed said the model predictions were too low—growers see many wild bees in natural habitat patches or blooming crop fields, and the numbers provided by the model did not match their field-based experience. Growers know what kinds of habitat provide forage resources for bees, as many of them mentioned the presence of wildflowers in field edges and nearby wetlands. While these habitat types commonly occur around lowbush blueberry fields, growers are overly optimistic about their prevalence and the number of wild bees they contain. This could result from the time scale associated with grower perception. Growers are observing bees in crop fields during pollination, when the mass flowering crop is in bloom and likely the best available food source in the landscape. Wild bees are abundant and diverse in crop fields during bloom (Bushmann and Drummond 2015). The values in the map legend describe this time period, therefore they align with grower perception. The predicted wild bee abundance map provides a season-long prediction; while bee communities appear robust during crop pollination, over the entire growing season that number is much lower. This is new information for growers and may take time to be accepted.

Growers also corrected a number of inaccuracies in the land cover data provided in BeeMapper. BeeMapper is meant to be used at field scales; however, our land cover data was generated at a statewide scale and issued with caution regarding field-scale interpretation (Maine Office of GIS; https://www.maine.gov/megis/catalog/metadata/melcd.html). This was an unanticipated benefit of the participatory development process and led to a subsequent effort to improve land cover accuracy. Public participation GIS is an emerging field of study in which participants familiar with a target landscape identify features for developers; this can empower stakeholders to better understand conservation priorities and ecosystem service delivery in their region (Brown 2012; Fagerholm et al. 2012; Voinov et al. 2016).

Testing prototypes of web tools with growers can lead to a total overhaul of the tool (Clavel et al. 2012), and that was our experience. We were given many suggestions on how to make the tool more user-friendly and interpretable. The color scheme of the abundance map was adjusted multiple times based on grower feedback. We added navigational aids to help growers locate their fields using roads, rivers, and lakes. During the 1:1 interviews, the most consistent request was to provide a concise summary of the map data around a crop field through a simple chart. We implemented this by displaying a series of pie charts when the target field is clicked on (Fig. 4.1). Growers suggested we provide full documentation including background on the spatial data used and the Lonsdorf model both directly on the website and in print form; we complied with these requests.

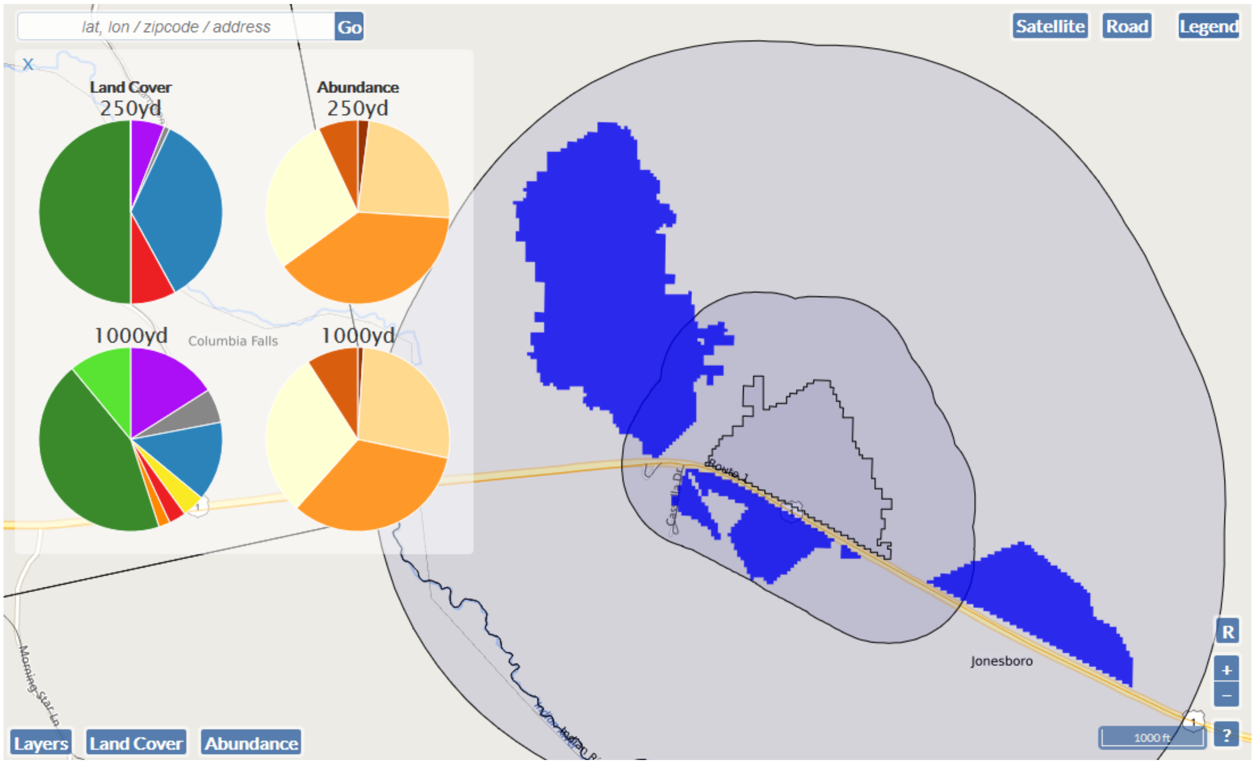


Figure 4.1. Summary of predicted wild bee abundance and land cover maps around a Maine, USA, lowbush blueberry field in BeeMapper for small bees (250 yd linear buffer distance from the focal field edge) and large bees (1000 yd linear buffer distance from the focal field edge). The pie chart display was suggested by crop growers through testing sessions to provide a simple interpretation of the information provided by BeeMapper.

4.4.2. Tool use despite uncertainty

We prioritized discussing the uncertainty of the predicted wild bee abundance map in BeeMapper with growers throughout the development process, emphasizing that the wild bee abundance map displayed predictions from a model and was not absolute. Further, although they contain field-realistic predictions, the results we obtained from the Lonsdorf model do not have high explanatory power (Groff et al. 2016; Chapter 3, this dissertation). However, growers revealed during testing sessions that they are accustomed to uncertainty in farming. Moreover, growers are aware of uncertainty in agricultural science. Lowbush blueberry growers have worked with Cooperative Extension scientists for nearly a century, and historically have vocalized a need for and incorporated findings from agricultural science conducted by Extension researchers, even with reported uncertainty (Hanes and Waring 2018; Hanes et al. 2018). The greatest source of uncertainty in BeeMapper is the generalization of habitat resources available in non-blueberry land cover types. Compared to similar pollination ecosystem service models, the Lonsdorf model uses more information about wild bee habitat, but is highly general in characterizing land cover quality (Vorstius and Spray 2015). This generality likely ignores patchiness in forested areas, for example, which are prevalent in Maine's lowbush blueberry landscape and could provide small refuge areas for wild bees. Porous and non-porous surfaces in urban landscapes also came up multiple times during interviews; though developed land is relatively scarce throughout the lowbush blueberry production landscape (Chapter 2, this dissertation), the habitat resources provided are generalized across urban green space and paved surfaces in the predicted wild bee abundance map.

4.4.3. Tool use and public engagement

We relied on WordPress statistics to count the number of website visits and list which pages and links users visited while on the BeeMapper website. We anticipated greater use of BeeMapper in early winter, when growers are making pollination management plans for the following growing season. Instead, we found the greatest number of page views immediately following launch in late July and early August 2017, which coincided with the start of the crop harvest. However, we attribute many of those views as a response to press coverage and interest outside of lowbush blueberry growers. Since then, we have observed cycles in BeeMapper site visits that align with our expectations, with few visits during the 2018 growing season and more visits in the off-season months (November-March) of 2018 and 2019 (Fig. 4.2). Given that there are ~350 growing enterprises in the state (Rose et al. 2013), we are encouraged by the consistency and number of site visits. Without a formal tool use evaluation process in place, however, we cannot explicitly determine how the tool is being used.

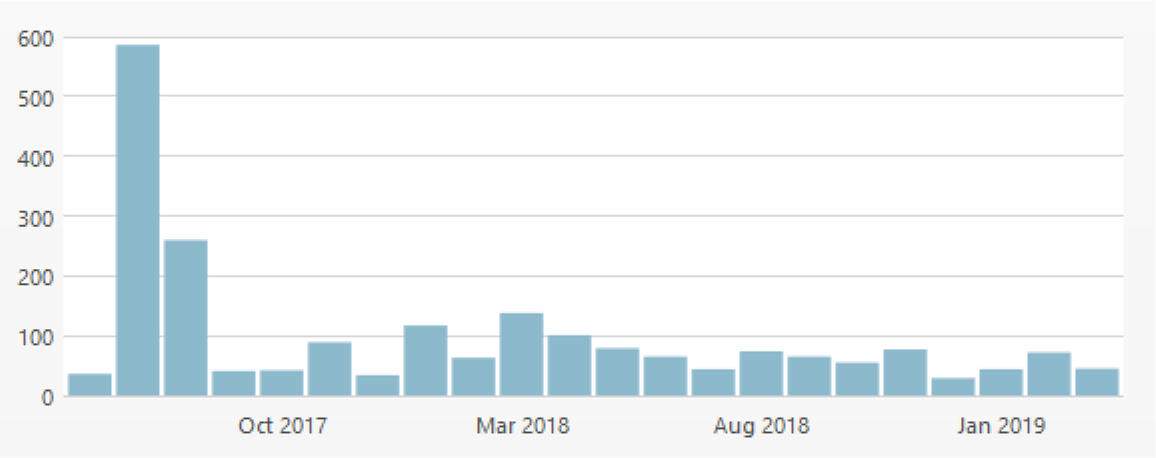


Figure 4.2. BeeMapper website visits from June 2017 to March 2019 via WordPress.com. With the exception of tool launch in July 2017, site visits generally follow a pattern of fewer visits in the growing season and more visits off-season.

The BeeMapper launch was accompanied by a University of Maine press release that was picked up by local television, public radio, and newspaper outlets and also ran in the Associated Press, leading to multiple national news briefs. Additionally, BeeMapper received local press coverage throughout the development process, primarily via University of Maine public relations. We presented two seminars at the University of Maine in 2016 that were open to the public and announced via email listservs; following these announcements, we were contacted by four local community groups to present our work with BeeMapper and more generally, bee habitat use. Three of these groups were beekeeping clubs and the fourth was a pollinator conservation group. These groups followed up after the release of BeeMapper, and one beekeeping group reported using BeeMapper to site new apiaries. Additionally, the Maine office of the U.S. Fish and Wildlife Service is considering using maps such as those in BeeMapper to locate potential habitat for the federally endangered rusty-patched bumble bee (*Bombus affinis*

Cresson), which was last recorded in the Maine lowbush blueberry production landscape in 2009.

4.4.4. Implementation problems

As with other DSS, BeeMapper faces hurdles to reaching widespread use among lowbush blueberry growers. The tool must be practical and address pollination management as completely as possible to have value to growers (McCown 2002a,b). Natural habitat for wild bees is one piece of pollination management, and growers indicated throughout the development process that if there were more management components involved in BeeMapper, they would be more likely to use the tool long-term. We received requests to incorporate ongoing work in lowbush blueberry pollination management, including pollinator plantings, on-farm monitoring of wild bee populations, and valuation of pollination services. For example, growers asked for the capability to create habitat enhancement scenarios and receive updated Lonsdorf model predictions on their farms. Owing to the dynamic nature of this information and the static architecture behind BeeMapper (Chapter 5; this dissertation), we were unable to accommodate these requests. However, the Lonsdorf model can be used to incorporate habitat enhancement scenarios (Nicholson et al. 2019), and a national scale tool exists that forecasts outcomes of these scenarios along with providing economic valuation of wild bee pollination services (Pollination Mapper BETA, www.pollinationmapper.org). Pollination services from wild bees may change with landscape context (Sardiñas and Kremen 2015); therefore, with our ongoing work in lowbush blueberry, we could incorporate these capabilities into BeeMapper in the future to provide context-relevant information. Pollination management is closely linked with integrated pest management (IPM), which is widely practiced in lowbush blueberry. A similar set of management strategies targeted at pollinator conservation on farms has recently emerged, called

Integrated Crop Pollination (ICP, Issacs et al. 2017). Following ICP and IPM principles, we can connect current knowledge of pollinator conservation strategies with existing chemical and non-chemical pest management strategies to provide more information for pollination management decisions and make BeeMapper more relevant to growers.

BeeMapper requires internet access and experience with using maps online. Downeast Maine is rural and can lack reliable internet, but this generally was not a problem. Growers were largely comfortable operating the web tool; presenting it to them as similar to widely used online mapping websites made BeeMapper more approachable. Back-end technical support will be provided by the development team for the immediate future, but long term support and maintenance needs to be determined. This is a common fate for AgDSS, but it can be overcome by remaining live on the internet and receiving incremental support (Voinov and Bousquet 2010). We also experienced time delays and gaps in communication between stakeholders throughout the development process. There are few opportunities to communicate with large groups of growers, so regular communication about tool progress was difficult; however, we made presentations at many meetings and venues to keep growers informed about BeeMapper development, and holding a large launch event was key to maintaining the awareness we aimed for throughout the process.

4.5. Conclusions

Though BeeMapper was not a grower-generated idea, growers were interested, involved, and engaged in its development, and we worked to ensure the tool was credible, legitimate, and salient to their needs. Active engagement techniques resulted in more feedback and more useful feedback than any passive technique we tried. Crop growers and Cooperative Extension researchers are interested in pursuing additional components to BeeMapper, including dynamic management simulations, chemical inputs, weed management, disease transmission and prevention, and economic effects. Linking BeeMapper to a new field-based lowbush blueberry pollination simulation model (Qu and Drummond 2018) could provide growers a detailed, multi-scale perspective on crop pollination mechanics and encourage incorporating functional agrobiodiversity into pollination management plans.

BeeMapper provides lowbush blueberry growers with a map-based, landscape-scale perspective on wild bee abundance surrounding their crop fields. The maps are supported by rigorous field sampling and extensive spatial analysis to display the most accurate information. Although uncertainty remains, our participatory development process gave growers more confidence in the data as well as the ability to independently operate BeeMapper and interpret the information it provides. Pollinator interactions with the surrounding landscape are context-dependent (Kennedy et al. 2013; Chapters 1, 2, and 3, this dissertation). The methodology we provide here, along with the adaptable open-source web architecture behind BeeMapper (Chapter 5, this dissertation), can be used to create similar AgDSS in other pollinator-dependent crop systems or other ecosystem service-based web mapping tools.

CHAPTER 5

BEEMAPPER: AN ONLINE AGRICULTURAL DECISION SUPPORT SYSTEM WITH AN ADAPTABLE OPEN SOURCE WEB MAPPING ARCHITECTURE

5.1. Introduction

Crop pollination is an essential ecosystem service required by nearly 75% of the world's crops (Klein et al. 2007). Globally, crop pollination by bees is valued at $391 billion (Lautenbach et al. 2012). Lowbush blueberry (*Vaccinium angustifolium* Aiton) is grown commercially in Maine (USA), Quebec (CA) and the Canadian Maritime Provinces. Fruit set is highly dependent on insect pollination, and wild bees are the most efficient and effective pollinators of the crop (Javorek et al. 2002; Asare et al. 2017). Pollination is primarily provided by rented honeybee (*Apis mellifera* L.) hives, making it one of the greatest input costs for lowbush blueberry growers (Asare et al. 2017). Growers are keen to reduce costs and maintain pollination services (Hanes et al. 2015; Hanes et al. 2018). Grower willingness to increase reliance on wild bee pollination services, however, is dependent on accurate information about wild bee populations and availability of nesting and foraging resources in the lowbush blueberry production landscape. Visualizing the resources available for wild bees in the landscape surrounding lowbush blueberry fields can aid growers in making pollination management decisions.

Multiple ecosystem service (ES) tools predict and map pollination resources at landscape scales (Bagstad et al. 2013; Crossman et al 2013), and we chose the InVEST Crop Pollination model (Lonsdorf et al. 2009) to apply to Maine's lowbush blueberry production landscape (Groff et al. 2016; Chapter 3, this dissertation). The model output is a map of predicted pollinator abundance presented as pixel values across the input map extent. This map output is intuitive to share with growers, and we distributed it broadly to Maine lowbush blueberry growers through a collaboratively-developed online framework.

We developed BeeMapper, an interactive online agricultural decision support system (agDSS) that allows lowbush blueberry growers to spatially explore and assess the wild bee habitat resources and predicted wild bee abundance in the landscape surrounding their crop fields (Chapter 4, this dissertation). Other online agDSS exist (Tayyebi et al. 2016); however, ours targets a specific set of decisions made by growers (i.e., pollination management) as an introduction to the application of these tools in our crop system. There are two other web map-based pollination agDSS (Pollination Mapper BETA, www.pollinationmapper.org; and Beescape, beescape.org); however, our tool is specific to the lowbush blueberry crop system, and here we provide the open source web mapping architecture behind our tool. BeeMapper allows growers to interact with various maps and map components; however, the maps cannot change or receive inputs from the growers. Thus, the tool meets the information needs of growers with a development approach that is practical for developers. The final version is a product of multiple grower-tested iterations that incorporates extensive grower feedback on tool features and design. Grower involvement in agDSS development promotes greater engagement with finished tools (Carberry et al. 2002; Chapter 4, this dissertation).

BeeMapper was developed with free and open-source software (FOSS) programs. Increased availability of FOSS-based GIS and web mapping programs has made developing web mapping tools more accessible (Steiniger and Hunter 2013; Smith 2016). By using FOSS, we created a flexible approach for an interactive web tool that can be adapted for use with maps created for other applications. This architecture is especially suited to projects in which access to proprietary software and advanced programming skills may be limiting, though a programmer is necessary to adapt the architecture to new tools. BeeMapper is a highly specific application of one model within the free and open-source InVEST model suite, comprising 18 ES models (Sharp et al. 2016). Most InVEST models and other ES models produce spatial data output appropriate for display and interaction through an online tool. Here we detail development of BeeMapper and the FOSS web mapping architecture that can be applied to other systems.

5.2. Methods

5.2.1 Spatial data preparation

BeeMapper displays three maps that depict bee habitat resources to lowbush blueberry growers: 1) the InVEST Crop Pollination model output (hereafter referred to as the predicted wild bee abundance map), 2) a land cover map with eight land cover classes (Groff et al. 2016; Chapter 2, this dissertation; this is the land cover map used to generate the predicted wild bee abundance map), and 3) a shapefile of lowbush blueberry fields created from the land cover map, on-screen digitizing, and GPS-tracks of the field perimeters. We reclassified the predicted wild bee abundance map from a continuous raster (values 0-1) to a thematic raster with five abundance classes with Natural Breaks (Jenks). We summarized predicted wild bee abundance in areas around each blueberry field that represent the wild bee source habitat for each field for small bees that fly up to 250 m (represented as yds in the tool) and large bees that fly up to 1000 m (or yds) (Greenleaf et al. 2007) (Fig. 5.1). We used a custom Python script (Kaszas 2012) to calculate the percent buffer area of each category of land cover (Fig. 5.1a) and predicted wild bee abundance (Fig. 5.1b).

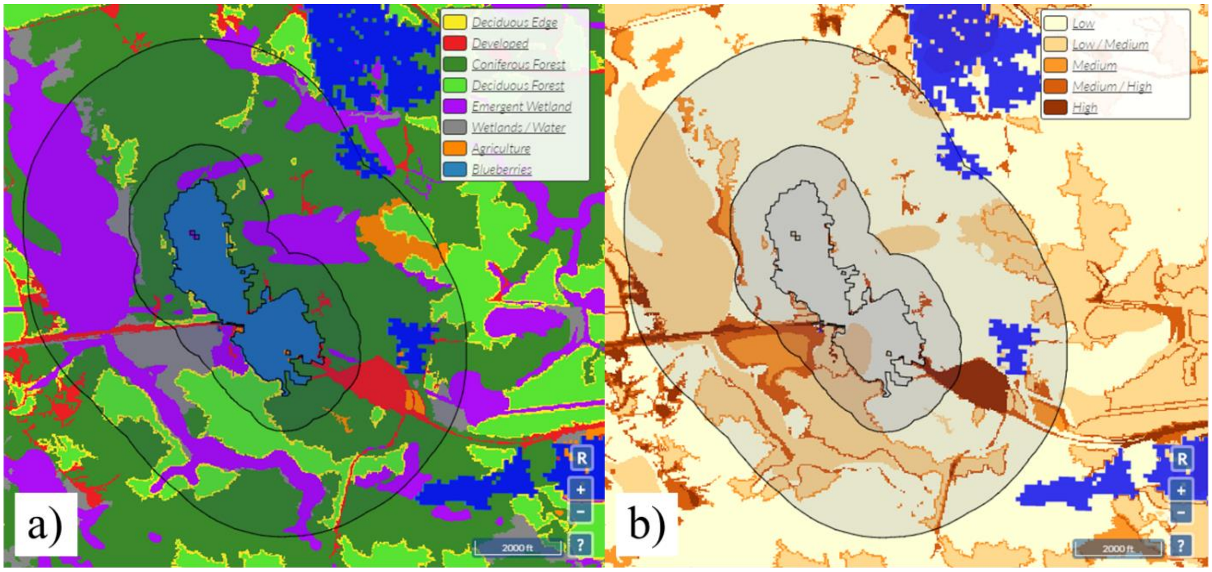


Figure 5.1. Maps presented in BeeMapper: a) land cover map; b) predicted wild bee abundance map. Additional information about the BeeMapper user interface is provided in Figure 5.3.

5.2.2 Web tool architecture

By using easily accessible FOSS, BeeMapper is both economically feasible and readily assembled, and its architecture can be adapted to build web mapping tools for other applications. BeeMapper is built on established software, including QGIS, MapProxy, and OpenLayers (Fig. 5.2), and the architecture follows common web development practices (reviewed in Smith 2016). QGIS (www.qgis.org) is a FOSS geographic information system (GIS) application that supports the viewing, editing, and analysis of geospatial data. An adapted version of QGIS, QGIS Server, served as our map server for BeeMapper. The map server is responsible for holding the raster data that will be displayed to end users. QGIS Server implements web map service (WMS) and web feature service (WFS) standard protocols to exchange GIS data via common web protocols such as HTTP (QGIS Development Team, 2009). QGIS offers a streamlined interface to access and modify GIS data that are displayed in the web application. Unlike other existing GIS applications such as GeoServer or MapServer, QGIS provides an interface to edit data in a “what

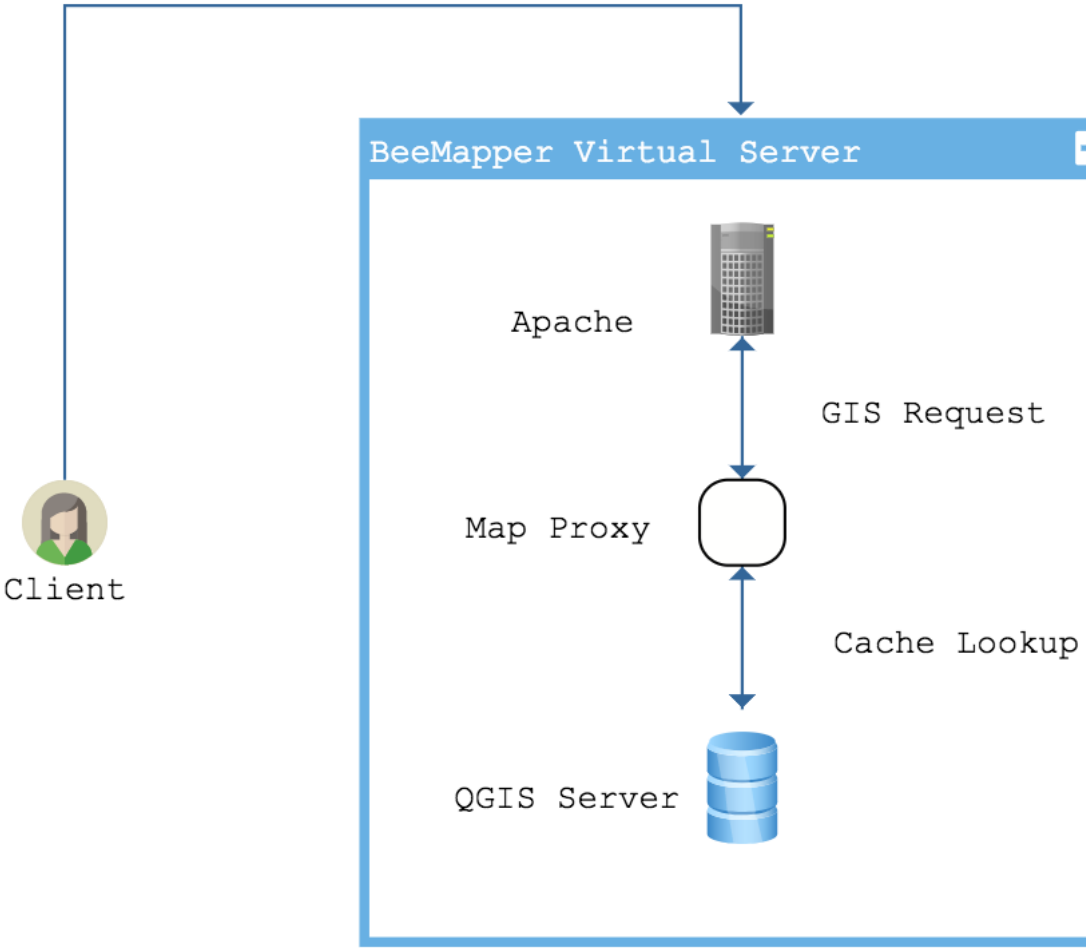


Figure 5.2. Architecture of the BeeMapper open source web mapping framework. The BeeMapper Virtual Server is hosted by the Advanced Computing Group at the University of Maine; the client (a person operating an internet-connected device) interacts with BeeMapper through a web browser to prompt the processes listed on the right using the programs listed on the left.

you see is what you get" (WYSIWYG) fashion. This approach increases the clarity of the data to developers, allowing them to preview and tweak styles on the fly (QGIS Development Team, 2009).

QGIS core development is not focused towards serving as a general networked mapping service, resulting in a rendering performance bottleneck when rapidly zooming or panning portions of the map in quick succession. However, because the raster data stored within QGIS are static, it is possible to cache generated map tiles for a significant improvement in performance. Use of a caching mechanism allows dynamically generated map sections to be saved for future use. If another end user looks at a cached portion of the map, the map server is skipped and the map tiles are directly loaded from memory and served. Caching is a well-established technique and is best used in situations where data are relatively static (MapProxy Development Team, 2017).

The FOSS MapProxy (https://mapproxy.org) software was selected as a map cache, as QGIS does not natively support caching for web map services. Within the BeeMapper architecture, the map cache receives web requests directly from end users and either a) performs a cache lookup and returns any cached data, or b) queries the QGIS server for new map data and caches the result (Fig. 5.2). If data are saved into the map cache, the map server is not queried again until either the data are updated or the cache is deleted. This leads to improved tool performance (i.e., faster load times) as more end users navigate the map, consequently caching a greater number of map sections. This benefit does have the drawback that it uses more space, as generated data need to be saved locally on the server. In our analysis, we found that caching the most frequently observed map views consumes roughly 1 GB of data for BeeMapper. It is also possible to pre-cache portions of the map to bootstrap the server to increase initial performance, though pre-caching tiles above level 8 can take days to compute, ultimately consuming more memory than available on the virtual server.

The Javascript framework OpenLayers (https://openlayers.org) powers the front-end of BeeMapper. OpenLayers is a well-established FOSS framework for developing modern GIS web applications. OpenLayers provides a developer abstraction to directly consume GIS data from the QGIS server and MapProxy cache. This lessens the developer burden of working with GIS data so that building a reactive interface to visualize the datasets is the focus (OpenLayers Development Team, 2017).

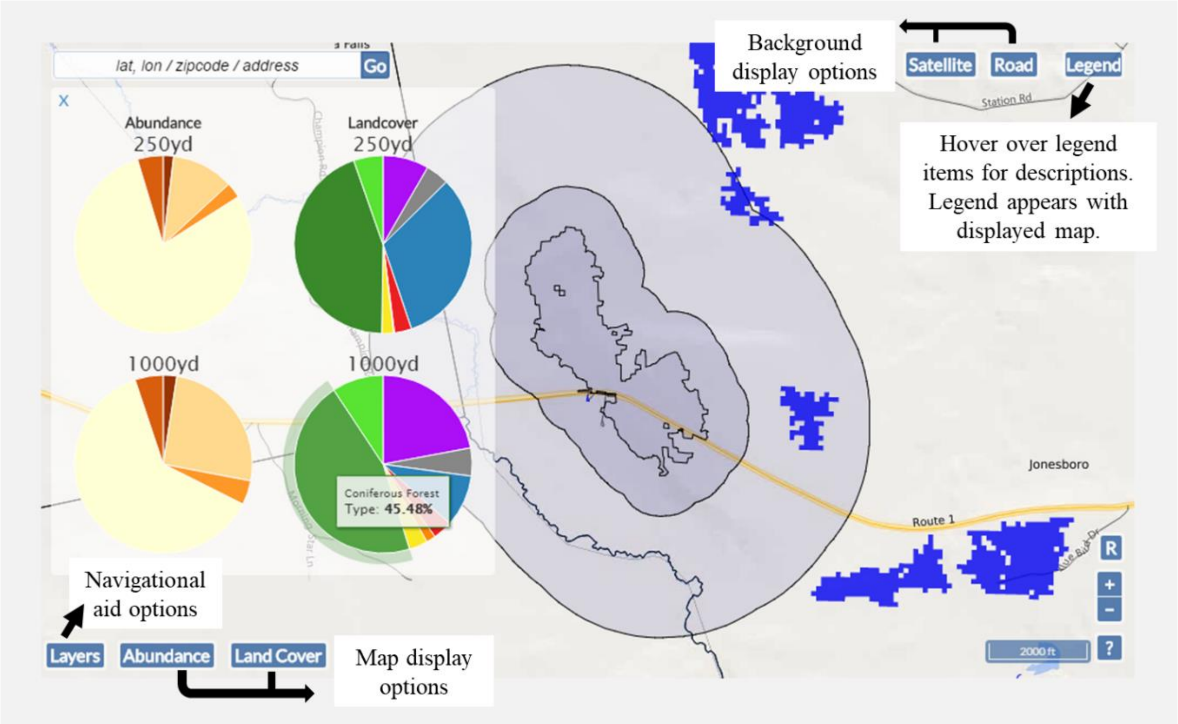
Several optimizations were required to address the performance and latency issues of providing end users a responsive interface rich with data. Using MapProxy to cache map tiles decreased the average tile rendering time for displaying the raster data sets. We used multiple techniques to optimize performance for the vector data sets. One technique involved reducing and pre-compressing the blueberry field and surrounding buffer shapefiles. First, each coordinate within the data was set to the minimum amount of significant digits needed to accurately represent its spatial location. Second, each vector dataset was pre-compressed with Apache's mod_gzip module to decrease the amount of data transferred to end users. Finally, necessary information from the attribute table of each vector data set was aggregated to a separate, shapeless, dataset. Partitioning the data into spatial and tabular components allows BeeMapper to load the minimum amount of data necessary to render the map, thus giving the appearance of a very responsive interface.

5.3. Results

The home screen of BeeMapper (Fig. 5.3) displays the full spatial extent of the tool and a series of navigational icons. Users navigate to a lowbush blueberry field and click on it.

Navigation occurs by either: 1) directly visually locating a crop field on the geographic base map, 2) entering the latitude and longitude coordinates of the field, or 3) by entering in a street address and/or postal code (U.S. = zipcode). When clicked, a window pops up displaying four pie charts that summarize the predicted wild bee abundance map and the land cover map in the source habitat for small and large bees surrounding the selected crop field (Fig. 5.3). Hovering over each slice of the pie reveals the name and percent of the corresponding class within each buffer area. This interactive screen is the fundamental output of the tool.

Users can view the source maps by clicking the “Abundance” and “Land Cover” buttons in the lower left corner. Once selected, map transparency is adjustable with a slider below the land cover or abundance map buttons. A legend appears in the upper right corner, and users can hover over each map class for a short description. The land cover map describes habitat quality for wild bees (Groff et al. 2016; Chapter 2, this dissertation), and the predicted wild bee abundance map describes estimated contribution to fruit set in any nearby lowbush blueberry field (Asare et al. 2017). These interactive legends and pie charts were requested by growers as part of the iterative development process.



Background display options

Hover over legend items for descriptions. Legend appears with displayed map.

Navigational aid options

Map display options

Figure 5.3. Summary of predicted wild bee abundance and land cover maps around a Maine, USA, lowbush blueberry field in BeeMapper for small bees (250 yd linear buffer distance from the focal field edge) and large bees (1000 yd linear buffer distance from the focal field edge). Annotations in white boxes have been added for clarity.

A printable User's Guide is available on the BeeMapper website (http://www.umaine.edu/beemapper/users-guide) for reference while navigating through the tool, or instructions may be accessed by toggling browser tabs. Additional resources available on the BeeMapper website include information on wild bee diversity and habitat resources, application of the InVEST Crop Pollination model to Maine's lowbush blueberry production landscape (Groff et al. 2016), and implementation of pollinator conservation practices.

5.4. Discussion

Here we describe the development of BeeMapper, an interactive online agricultural decision support system that aids Maine lowbush blueberry growers in decision making regarding pollination management, particularly with respect to more efficient wild bee pollinators. BeeMapper allows Maine lowbush blueberry growers to connect the habitat resources in the production landscape to the estimated wild bee abundance and contribution to fruit set in crop fields. Providing ES data to stakeholders via web tools such as BeeMapper connects science and practice and encourages sustainable management techniques (Kates et al. 2001; Chapter 4, this dissertation).

BeeMapper was developed with free and open-source software to create a flexible approach that can be implemented to place spatial output of ecosystem service analyses into practitioner-focused web tools. Many ES modeling programs, including InVEST, ARIES, and LUCI, produce spatial output (Bagstad et al. 2013). The InVEST model suite has a demonstrated record of knowledge production and application development in diverse stakeholder groups (Ruckelshaus et al. 2015), and contains multiple models relevant to agriculture including habitat quality, water retention, and nutrient retention (Terrado et al. 2014, 2016; Hamel et al. 2016). Additionally, although there are general trends, pollination services vary widely across crop systems (Ricketts et al. 2008), therefore the possibility exists for BeeMapper to be replicated in other agricultural landscapes.

Future directions for BeeMapper include incorporating economic valuation of wild bee pollination services. The InVEST Crop Pollination model ultimately produces a map of pollinator supply, a measure we can translate to lowbush blueberry crop yield from wild bee pollination based on field data (Asare et al. 2017). Adding dynamic capability to allow input of landscape change from users is a future avenue of development. BeeMapper provides simple pollinator habitat assessments that are easily obtainable and quick to interpret, which was the target outcome of the tool’s development.

5.5. Software availability

The open source web mapping architecture for BeeMapper was developed by Robert Powell (powellrw7@gmail.com) and can be accessed at (https://bitbucket.org/beduclos/beemapper). The architecture uses FOSS programs OpenLayers, MapProxy, and QGIS Server and is written in the programming languages Javascript and PHP. The architecture is free to use and available under the terms of the GNU Public License Version 3 (https://www.gnu.org/licenses/gpl-3.0.html).

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APPENDIX A: SUPPLEMENTARY MATERIAL, CHAPTER 1

Table A.1. Mann-Whitney U tests comparing percentage of land cover types surrounding ROW sites. All p-values are presented. If significant, median values of percentage of each land cover type are also presented for ROW sites in the Downeast (D), or Midcoast (M) growing region that are isolated from (I) or near to (N) lowbush blueberry fields. W=Mann-Whitney-Wilcoxon test value. N=12 for each type compared.

Coniferous	Region	Type
100m	**D=19.49, M=0, W=137, p>0.001**	0.412
250m	**D=9.55, M=0, W=131.5, p>0.001**	0.206
500m	**D=15.66, M=4.77, W=110.5, p=0.028**	**I=12.67, N=3.34 W=127,p=0.001**
1km	**D=22.36, M=9.21, W=116, p=0.012**	**I=16.58, N=9.12, W=110, p=0.03**

Blueberry	Region	Type
100m	0.3828	**I=0, N=0.1, W=36, p=0.007**
250m	0.7813	**I=0, N=9.82, W=0, p>0.001**
500m	0.6884	**I=0, N=16.14, W=0, p>0.001**
1km	0.3988	**I=0.15, N=14.17, W=0, p>0.001**

Deciduous	Region	Type
100m	**D=20.58, M=46.63, W=37, p=0.044**	0.3777
250m	**D=35.73, M=55.25, W=42, p=0.088**	0.3777
500m	**D=36.32, M=49.24, W=18, p=0.001**	0.5137
1km	**D=37.04, M=54.13, W=22, p=0.002**	0.6707

Edge	Region	Type
100m	**D=10, M=16.42, W=9, p>0.001**	0.5635
250m	**D=7.17, M=13.07, W=6, p>0.001**	0.5137
500m	**D=7.18, M=10.59, W=18, p=0.001**	0.16
1km	**D=5.62, M=8.95, W=10, p>0.001**	0.1432

Agriculture	Region	Type
100m	**D=0, M=1.45, W=39.5, p=0.027**	0.1038
250m	**D=0, M=4.26, W=17, p=0.001**	0.5335
500m	**D=0.04, M=6.23, W=22, p=0.003**	0.6625
1km	**D=0.43, M=9.74, W=12, p>0.001**	0.1748

Emergent	Region	Type
100m	0.1409	0.4024
250m	1	0.099
500m	0.3707	0.2854
1km	0.1432	0.2189

Table A.1 Continued.

Wetland	Region	Type
100m	**D=0, M=0, W=102, p=0.016**	0.1129
250m	**D=1.24, M=0,W=115, p=0.009**	0.008
500m	**D=3.49, M=0.15, W=131, p>0.001**	1
1km	**D=6.08, M=0.35, W=134, p>0.001**	0.6649

Urban	Region	Type
100m	0.1421	0.8339
250m	0.1885	0.074
500m	**D=1.57, M=5.55, W=30, p=0.014**	0.1782
1km	**D=1.18, M=6.29, W=19, p=0.002**	0.6649

Table A.2. Solitary bee species richness influenced by land cover types surrounding ROW sites in the Maine, USA, lowbush blueberry production landscape across growing regions.

	100 m	**250 m**	**500 m**	**1000 m**
Agriculture/pasture		df=1,22, dev=4.41, p=0.03		df=1.22, dev=1,22, p=0.002
Lowbush blueberry fields	df=1,22, dev=1.54, p=0.21	df=1,22, dev=1.32, p=0.25	df=1,22, dev=1.66, p=0.19	df=1,22, dev=1,22, p=0.27
Coniferous forest	df=1,22, dev=8.74, p=0.003	df=1,22, dev=10.14, p=0.001	df=1,22, dev=7.22, p=0.007	df=1,22, dev=7.08, p=0.007
Deciduous/mixed forest				
Deciduous/mixed forest edge	df=1,22, dev=4.78, p=0.02	df=1,22, dev=4.91, p=0.03		
Emergent wetland				
Wetland	df=1,22, dev=4.86, p=0.02	df=1,22, dev=4.99, p=0.03	df=1,22, dev=5.75, p=0.01	
Urban				

Table A.3. Social bee species richness influenced by land cover types surrounding ROW sites in the Maine, USA, lowbush blueberry production landscape across growing regions.

	100 m	**250 m**	**500 m**	**1000 m**
Agriculture/pasture		df=1,22, dev=5.70, p=0.01		
Lowbush blueberry fields				
Coniferous forest	df=1,22, dev=5.67, p=0.01	df=1,22, dev=5.45, p=0.01	df=1,22, dev=4.90, p=0.02	df=1,22, dev=5.75, p=0.01
Deciduous/mixed forest				
Deciduous/mixed forest edge				
Emergent wetland				
Wetland				
Urban				

Table A.4. Ground nesting bee species richness influenced by land cover types surrounding ROW sites in the Maine, USA, lowbush blueberry production landscape across growing regions.

	100 m	**250 m**	**500 m**	**1000 m**
Agriculture/pasture		df=1,22, dev=8.11, p=0.004	df=1,22, dev=3.98, p=0.04	df=1,22, dev=5.74, p=0.01
Lowbush blueberry fields				
Coniferous forest	df=1,22, dev=10.36, p=0.001	df=1,22, dev=10.93, p<0.001	df=1,22, dev=10.84, p<0.001	df=1,22, dev=12.61, p<0.001
Deciduous/mixed forest				
Deciduous/mixed forest edge	df=1,22, dev=4.30, p=0.03	df=1,22, dev=4.98, p=0.02		
Emergent wetland				
Wetland	df=1,22, dev=4.22, p=0.04	df=1,22, dev=4.25, p=0.04		
Urban	df=1,22, dev=3.61, p=0.05			

Table A.5. Cavity nesting bee species richness influenced by land cover types surrounding ROW sites in the Maine, USA, lowbush blueberry production landscape across growing regions.

	100 m	**250 m**	**500 m**	**1000 m**
Agriculture/pasture				
Lowbush blueberry fields				
Coniferous forest	df=1,22, dev=4.04, p=0.04	df=1,22, dev=4.62, p=0.03		
Deciduous/mixed forest				
Deciduous/mixed forest edge	df=1,22, dev=4.25, p=0.04			
Emergent wetland				
Wetland			df=1,22, dev=4.27, p=0.04	
Urban				

Table A.6. Solitary bee species richness influenced by land cover types surrounding ROW sites in the Downeast Maine, USA, lowbush blueberry growing region.

	100 m	**250 m**	**500 m**	**1000 m**
Agriculture/pasture				
Lowbush blueberry fields	df=1,10, dev=6.56, p=0.01	df=1,10, dev=8.94, p=0.002	df=1,10, dev=9.29, p=0.002	df=1,10, dev=10.27, p=0.001
Coniferous forest				
Deciduous/mixed forest				df=1,10, dev=3.57, p=0.05
Deciduous/mixed forest edge				
Emergent wetland				df=1,10, dev=6.10, p=0.01
Wetland				
Urban				

Table A.7. Ground nesting bee species richness influenced by land cover types surrounding ROW sites in the Downeast Maine, USA, lowbush blueberry growing region.

	100 m	**250 m**	**500 m**	**1000 m**
Agriculture/pasture				
Lowbush blueberry fields	df=1,10, dev=4.17, p=0.04	df=1,10, dev=5.12, p=0.02	df=1,10, dev=6.30, p=0.01	df=1,10, dev=7.07, p=0.007
Coniferous forest			df=1,10, dev=4.93, p=0.02	df=1,10, dev=6.82, p=0.008
Deciduous/mixed forest				
Deciduous/mixed forest edge				
Emergent wetland				df=1,10, dev=3.75, p=0.05
Wetland				
Urban				

APPENDIX B. FOUR LETTER BEE SPECIES CODES

Table B.1. Four letter species codes for all 168 bee species collected in the Maine lowbush blueberry production landscape, 2013-2015. Codes are presented alphabetically by scientific name.

Scientific name	Code	Scientific name	Code
Agapostemon texanus	AGTX	*Andrena virginiana*	ANVG
Agapostemon virescens	AGVS	*Andrena wheeleri*	ANWH
Andrena alleghaniensis	ANAG	*Andrena wilkella*	ANWI
Andrena braccata	ANBR	*Anthidium manicatum*	ADMA
Andrena bradleyi	ANBD	*Anthidium oblongatum*	ADOB
Andrena canadensis	ANCN	*Anthophora terminalis*	ATTE
Andrena carlini	ANCL	*Augochlora pura*	ACPU
Andrena carolina	ANCO	*Augochlorella aurata*	ALAU
Andrena crataegi	ANCT	*Augochloropsis metallica fulgida*	APMF
Andrena cressonii	ANCR	*Bombus bimaculatus*	BOBI
Andrena distans	ANDI	*Bombus borealis*	BOBO
Andrena forbesii	ANFO	*Bombus fernaldae*	BOFE
Andrena frigida	ANFR	*Bombus griseocollis*	BOGR
Andrena hippotes	ANHP	*Bombus impatiens*	BOIM
Andrena hirticincta	ANHI	*Bombus perplexus*	BOPE
Andrena imitatrix	ANIM	*Bombus sandersoni*	BOSA
Andrena integra	ANIN	*Bombus ternarius*	BOTN
Andrena milwaukeensis	ANML	*Bombus terricola*	BOTR
Andrena miranda	ANMI	*Bombus vagans*	BOVA
Andrena miserabilis	ANMS	*Calliopsis andreniformis*	CLAN
Andrena nasonii	ANNA	*Ceratina calcarata*	CECA
Andrena nigrihirta	ANNG	*Ceratina dupla*	CEDU
Andrena nivalis	ANNV	*Ceratina mikmaqi*	CEMQ
Andrena nubecula	ANNB	*Coelioxys rubitorsis*	CXRU
Andrena nuda	ANND	*Colletes americanus*	COAM
Andrena personata	ANPE	*Colletes consors*	COCO
Andrena placata	ANPL	*Colletes simulans*	COSI
Andrena regularis	ANRG	*Dialictus* species	DISP
Andrena rufosignata	ANRF	*Epeolus scutellaris*	EPSC
Andrena rugosa	ANRU	*Eucera hamata*	EUHA
Andrena sigmundi	ANSI	*Halictus confusus*	HACO
Andrena spiraeana	ANSP	*Halictus ligatus*	HALI
Andrena thaspii	ANTH	*Halictus rubicundus*	HARU
Andrena vicina	ANVC		

Table B.1 Continued.

Heriades carinata	HECA
Heriades variolosus/leavitti	HEVA
Hoplitis producta	HPPR
Hoplitis spoliata/pilosum	HPSP
Hylaeus affinis	HYAF
Hylaeus annulatus	HYAN
Hylaeus basalis	HYBA
Hylaeus mesillae	HYME
Hylaeus modestus	HYMO
Hylaeus verticalis	HYVE
Lasioglossum abanci	LAAB
Lasioglossum acuminatum	LAAC
Lasioglossum admirandum	LAAD
Lasioglossum albipenne	LAAL
Lasioglossum anomalum	LAAN
Lasioglossum atwoodi	LAAT
Lasioglossum cinctipes	LACI
Lasioglossum coriaceum	LACO
Lasioglossum cressonii	LACR
Lasioglossum ellisiae	LAEL
Lasioglossum ephialtum	LAEP
Lasioglossum foxii	LAFO
Lasioglossum heterognathum	LAHE
Lasioglossum hitchensi	LAHI
Lasioglossum imitatum	LAIM
Lasioglossum inconditum	LAIN
Lasioglossum katherineae	LAKA
Lasioglossum laevissimum	LALA
Lasioglossum leucocomum	LALC
Lasioglossum leucozonium	LALZ
Lasioglossum lineatulum	LALI
Lasioglossum macoupinense	LAMA
Lasioglossum nelumbonis	LANE
Lasioglossum nigroviride	LANI
Lasioglossum nymphaearum	LANY
Lasioglossum oblongum	LAOB
Lasioglossum paradmirandum	LAPA
Lasioglossum pectorale	LAPC
Lasioglossum perpunctatum	LAPP
Lasioglossum pilosum	LAPI
Lasioglossum planatum	LAPL
Lasioglossum platyparium	LAPY
Lasioglossum quebecense	LAQU
Lasioglossum smilacinae	LASM
Lasioglossum subversans	LASV
Lasioglossum subviridatum	LASD
Lasioglossum taylorae	LATA
Lasioglossum tegulare	LATE
Lasioglossum timothyi	LATY
Lasioglossum trigeminium	LATG
Lasioglossum truncatum	LATM
Lasioglossum versans	LAVS
Lasioglossum versatum	LAVT
Lasioglossum viridatum	LAVI
Lasioglossum weemsi	LAWE
Lasioglossum zonulum	LAZO
Macropis nuda	MANU
Megachile gemula	MEGE
Megachile inermis	MEIN
Megachile lapponica	MELP
Megachile latimanus	MELT
Megachile melanophaea	MEME
Megachile relativa	MERE
Megachile rotundata	MERO
Melissodes desponsa	MLDE
Melissodes druriella	MLDR
Melissodes illata	MLIL
Melissodes subillata	MLSU
Melissodes apicata	MLAP
Melitta americana	MTAM
Nomada articulata	NOAR
Nomada bidentate group	NOBI
Nomada cressonii	NOCR
Nomada denticulata	NODT
Nomada depressa	NODP
Nomada illinoensis/sayi	NOIL
Nomada nr. *imbricata*	NOIM
Nomada inepta	NOIN
Nomada luteoloides	NOLU

Table B.1. Continued.

Nomada maculata	NOMA
Nomada ovata	NOOV
Nomada perplexa	NOPE
Nomada pygmaea	NOPY
Nomada sayi	NOSY
Osmia atriventris	OSAT
Osmia bucephala	OSBU
Osmia inermis	OSIN
Osmia inspergens	OSIP
Osmia lignaria	OSLI
Osmia proxima	OSPR
Osmia pumila	OSPU
Osmia virga	OSVI
Peponapis pruinosa	PEPR
Pseudopanurgus aestivalis	PSAE
Pseudopanurgus andrenoides	PSAN
Pseudopanurgus species	PSSP
Sphecodes cressonii	SPCR
Sphecodes davisii	SPDA
Sphecodes species	SPSP
Trachandrena species	TRSP

APPENDIX C. SUPPLEMENTARY MATERIAL, CHAPTER 2

Table C.1. Model estimates of abundance and species richness of bees associated with the proportion of eight land cover types in the Maine, USA, lowbush blueberry landscape. a) Small bees have a maximum foraging distance of up to 500 m and b) large bees with a maximum foraging distance of 500-2000 m. P-values are reported in parentheses; bold values are statistically significant ($p \leq 0.05$), and N/As represent models that did not converge.

a) SMALL BEES		Ag	Blue	Con	Dec	Edge	Emg	Urb	Wet
All	Abundance								
	250m	-0.13 (0.593)	0.367 (0.159)	-0.164 (0.591)	-0.204 (0.447)	-0.119 (0.507)	0.132 (0.6)	0.089 (0.707)	-0.047 (0.832)
	500m	-0.233 (0.317)	0.396 (0.081)	0.055 (0.808)	0.002 (0.99)	0.032 (0.87)	-0.237 (0.367)	0.037 (0.87)	-0.101 (0.662)
	Richness								
	250m	-0.099 (0.633)	0.172 (0.41)	-0.116 (0.658)	-0.018 (0.935)	0.064 (0.686)	-0.094 (0.658)	0.058 (0.777)	-0.039 (0.833)
	500m	-0.174 (0.374)	0.234 (0.216)	-0.01 (0.95)	0.112 (0.564)	0.124 (0.446)	-0.234 (0.281)	0.032 (0.87)	-0.081 (0.674)
Early	Abundance								
	250m	0.158 (0.45)	-0.005 (0.98)	**-0.436** **(0.031)**	0.0001 (0.999)	-0.233 (0.179)	-0.001 (0.99)	0.191 (0.405)	0.054 (0.744)
	500m	0.10 (0.609)	-0.204 (0.318)	-0.108 (0.519)	-0.005 (0.975)	-0.107 (0.487)	-0.045 (0.808)	0.114 (0.581)	0.112 (0.512)
	Richness								
	250m	-0.049 (0.774)	0.06 (0.704)	**-0.423** **(0.01)**	0.065 (0.694)	-0.122 (0.366)	-0.067 (0.672)	0.218 (0.132)	-0.017 (0.9)
	500m	-0.075 (0.639)	-0.102 (0.546)	-0.074 (0.61)	0.038 (0.788)	-0.057 (0.659)	-0.188 (0.228)	0.195 (0.186)	0.045 (0.747)
Mid	Abundance								
	250m	**0.40** **(0.037)**	0.213 (0.269)	-0.176 (0.402)	**-0.413** **(0.03)**	**-0.374** **(0.016)**	-0.058 (0.775)	0.185 (0.434)	-0.142 (0.461)
	500m	0.297 (0.105)	0.084 (0.679)	0.094 (0.548)	N/A	-0.283 (0.07)	0.063 (0.765)	-0.001 (0.99)	0.016 (0.921)
	Richness								
	250m	0.202 (0.123)	0.188 (0.144)	-0.235 (0.117)	-0.14 (0.322)	-0.135 (0.256)	-0.144 (0.308)	0.057 (0.688)	-0.043 (0.746)
	500m	0.098 (0.467)	N/A	0.026 (0.833)	-0.147 (0.264)	-0.12 (0.309)	-0.078 (0.583)	-0.004 (0.97)	0.063 (0.601)
Late	Abundance								
	250m	-0.13 (0.593)	0.367 (0.159)	-0.164 (0.591)	-0.204 (0.447)	-0.119 (0.507)	0.132 (0.6)	0.089 (0.707)	-0.047 (0.832)
	500m	-0.233 (0.317)	0.396 (0.081)	0.055 (0.808)	0.002 (0.99)	0.032 (0.87)	-0.237 (0.367)	0.037 (0.87)	-0.101 (0.662)
	Richness								
	250m	-0.099 (0.633)	0.172 (0.41)	-0.116 (0.658)	-0.018 (0.935)	0.064 (0.686)	-0.094 (0.658)	0.058 (0.777)	-0.039 (0.833)
	500m	-0.174 (0.374)	0.234 (0.216)	-0.01 (0.95)	0.112 (0.564)	0.124 (0.446)	-0.234 (0.281)	0.032 (0.87)	-0.081 (0.674)

Table C.1 Continued.

b) LARGE BEES		Ag	Blue	Con	Dec	Edge	Emg	Urb	Wet
All	Abundance								
	1000m	0.173 (0.317)	-0.059 (0.707)	0.2508 (0.095)	-0.085 (0.568)	-0.185 (0.185)	**-0.554** **(0.001)**	0.252 (0.162)	-0.223 (0.173)
	2000m	0.0611 (0.738)	0.012 (0.644)	0.217 (0.133)	-0.093 (0.495)	-0.079 (0.581)	**-0.482** **(0.005)**	0.124 (0.463)	-0.085 (0.416)
	Richness								
	1000m	0.103 (0.307)	-0.052 (0.595)	0.058 (0.524)	-0.052 (0.594)	-0.011 (0.899)	**-0.298** **(0.007)**	**0.217** **(0.02)**	-0.087 (0.384)
	2000m	0.111 (0.251)	-0.005 (0.716)	0.048 (0.583)	-0.014 (0.873)	0.061 (0.498)	**-0.275** **(0.013)**	0.147 (0.111)	-0.145 (0.427)
Early	Abundance								
	1000m	0.014 (0.939)	-0.13 (0.598)	0.098 (0.552)	0.053 (0.728)	-0.276 (0.158)	-0.216 (0.33)	-0.06 (0.724)	0.06 (0.709)
	2000m	0.06 (0.724)	0.023 (0.527)	0.029 (0.861)	0.123 (0.457)	-0.08 (0.625)	-0.383 (0.096)	-0.094 (0.607)	-0.039 (0.85)
	Richness								
	1000m	0.029 (0.852)	-0.163 (0.387)	0.155 (0.269)	-0.154 (0.307)	-0.262 (0.106)	-0.114 (0.527)	0.09 (0.487)	0.07 (0.631)
	2000m	0.07 (0.624)	0.007 (0.797)	0.137 (0.334)	-0.118 (0.456)	-0.157 (0.306)	-0.238 (0.214)	0.037 (0.805)	0.009 (0.954)
Mid	Abundance								
	1000m	0.247 (0.346)	-0.018 (0.936)	0.401 (0.076)	-0.201 (0.354)	-0.276 (0.163)	**-0.658** **(0.017)**	0.369 (0.201)	-0.407 (0.128)
	2000m	0.024 (0.932)	0.021 (0.608)	0.385 (0.067)	-0.197 (0.274)	-0.18 (0.374)	**-0.624** **(0.026)**	0.162 (0.534)	-0.173 (0.512)
	Richness								
	1000m	0.092 (0.569)	0.027 (0.849)	0.134 (0.352)	-0.170 (0.262)	-0.112 (0.407)	-0.275 (0.125)	0.233 (0.115)	-0.139 (0.397)
	2000m	0.082 (0.617)	0.01 (0.659)	0.135 (0.323)	-0.134 (0.314)	-0.046 (0.733)	-0.262 (0.145)	0.159 (0.275)	-0.083 (0.605)
Late	Abundance								
	1000m	0.285 (0.162)	-0.006 (0.971)	0.114 (0.507)	-0.189 (0.321)	0.046 (0.777)	**-0.467** **(0.033)**	0.38 (0.054)	-0.303 (0.107)
	2000m	0.209 (0.322)	-0.013 (0.633)	0.106 (0.527)	-0.14 (0.423)	0.106 (0.523)	-0.243 (0.267)	0.31 (0.091)	-0.31 (0.125)
	Richness								
	1000m	0.213 (0.098)	-<0.001 (0.99)	-0.042 (0.74)	0.015 (0.907)	0.095 (0.41)	N/A	0.172 (0.204)	-0.117 (0.38)
	2000m	0.204 (0.101)	-0.016 (0.419)	-0.039 (0.742)	0.062 (0.618)	N/A	-0.136 (0.335)	0.155 (0.203)	-0.224 (0.102)

APPENDIX D: SUPPLEMENTARY MATERIAL, CHAPTER 3

Table D.1. Field-based Lonsdorf model parameter values including an additional period of the growing season for application to the Maine, USA lowbush blueberry production landscape.

	Nesting resources		Floral resources			
	Ground	Cavity	Spring	Early summer	Mid-summer	Late summer
Deciduous/mixed forest edge	0.4	0.8	0.9	0.9	1.0	1.0
Urban/developed	0.7	0.5	1.0	0.9	0.9	1.0
Coniferous forest	0.3	0.6	0.1	0.1	0.1	0.1
Deciduous mixed forest	0.3	0.6	0.7	0.5	0.4	0.4
Emergent wetlands	0.4	0.8	0.7	0.6	0.6	0.6
Wetlands/water	0.2	0.8	0.3	0.2	0.4	0.5
Agriculture/pasture	0.6	0.2	0.9	0.7	0.7	0.9
Lowbush blueberry fields	0.5	0.2	0.4	1.0	0.7	0.5

Table D.2. Lonsdorf model bee life history parameter values including an additional period of the growing season for the Maine, USA lowbush blueberry production landscape.

	Preferred nesting substrate		Active flight season				
Species	Ground	Cavity	Spring	Early summer	Mid-summer	Late summer	Maximum foraging distance (m)
Andrena carlini	1	0	0.25	0.25	0.25	0.25	598
Andrena carolina	1	0	0.5	0.5	0	0	246
Andrena vicina	1	0	0.25	0.25	0.25	0.25	569
Augochlorella aurata	1	0	0.25	0.25	0.25	0.25	60
Colletes inaequalis	1	0	0.33	0.33	0.33	0	1091
Halictus ligatus	1	0	0.25	0.25	0.25	0.25	148
Lasioglossum acuminatum	1	0	0.25	0.25	0.25	0.25	186
Lasioglossum cressonii	0	1	0.25	0.25	0.25	0.25	63
Lasioglossum heterognathum	1	0	0.25	0.25	0.25	0.25	16
Lasioglossum leucocomum	1	0	0.25	0.25	0.25	0.25	31
Lasioglossum pectorale	1	0	0.25	0.25	0.25	0.25	81
Lasioglossum versatum	1	0	0.25	0.25	0.25	0.25	79
Osmia atriventris	0	1	0.5	0.5	0	0	186
Osmia inspergens	0	1	1.0	0	0	0	495

Table D.3. Field-based Lonsdorf model parameter values including two additional land cover types for the Maine, USA lowbush blueberry production landscape.

	Nesting resources		Floral resources		
	Ground	Cavity	Early summer	Mid-summer	Late summer
Deciduous/mixed forest edge	0.4	0.8	0.9	0.9	1.0
Urban/developed	0.7	0.5	1.0	0.9	1.0
Coniferous forest	0.3	0.6	0.1	0.1	0.1
Deciduous mixed forest	0.3	0.6	0.7	0.5	0.4
Emergent wetlands	0.4	0.8	0.7	0.6	0.6
Wetlands	0.2	0.8	0.3	0.2	0.5
Agriculture/pasture	0.6	0.2	0.9	0.7	0.9
Lowbush blueberry fields	0.5	0.2	0.4	1.0	0.5
Mixed Forest	0.3	0.6	0.4	0.3	0.2
Open Water	0	0	0	0	0

Table D.4. Wilcoxon rank sum pairwise comparisons test values of ground and cavity nesting resource amount and condition for eight land cover types in the Maine, USA lowbush blueberry production landscape. P-values are in parentheses. Bold entries are significant at p≤0.05.

a) Ground: Exposed bare soil

		Lowbush blueberry fields	Agriculture/ pasture	Coniferous forest	Deciduous/ mixed forest	Deciduous/ mixed forest edge	Emergent wetlands	Wetlands /water
Agriculture/ pasture	Amount	**2 (0.02)**						
	Condition	**1 (0.03)**						
Coniferous forest	Amount	**2 (0.03)**	9 (0.49)					
	Condition	**0 (0.01)**	6 (0.12)					
Deciduous/mixed forest	Amount	**3.5 (0.05)**	7 (0.24)	13 (1.0)				
	Condition	3 (0.09)	16 (0.48)	**21 (0.05)**				
Deciduous/mixed forest edge	Amount	**3 (0.05)**	10.5 (0.74)	12 (1.0)	10 (0.65)			
	Condition	3.5 (0.11)	17 (0.36)	20.5 (0.10)	13.5 (0.91)			
Emergent wetlands	Amount	**1 (0.02)**	**0 (0.01)**	5 (0.24)	4 (0.10)	7 (0.51)		
	Condition	**0 (0.02)**	3 (0.07)	7 (0.45)	2 (0.05)	3 (0.09)		
Wetlands/water	Amount	**0 (0.009)**	**1 (0.01)**	5.5 (0.14)	**4 (0.05)**	8 (0.36)	9 (0.88)	
	Condition	**0 (0.01)**	**3 (0.04)**	7.5 (0.27)	**2 (0.02)**	3 (0.06)	9 (0.88)	
Urban/developed	Amount	4 (0.08)	16.5 (0.40)	18 (0.27)	18 (0.26)	16.5 (0.44)	**19 (0.03)**	**24 (0.01)**
	Condition	8.5 (0.79)	**23(0.02)**	**25 (0.009)**	20 (0.12)	19 (0.17)	**20 (0.01)**	**25 (0.01)**

b) Cavity: Woody shrubs

		Lowbush blueberry fields	Agriculture/ pasture	Coniferous forest	Deciduous/ mixed forest	Deciduous/ mixed forest edge	Emergent wetlands	Wetlands /water
Agriculture/ pasture	Amount	10.5 (0.73)						
	Condition	5.5 (0.50)						
Coniferous forest	Amount	12.5 (1.0)	14.5 (0.73)					
	Condition	9 (0.89)	12 (0.66)					

Table D.4 Continued.

Deciduous/mixed forest	Amount	11 (0.81)	13.5 (0.90)	11 (0.81)				
	Condition	8 (0.68)	11.5 (0.76)	13.5 (0.90)				
Deciduous/mixed forest edge	Amount	18 (0.27)	19 (0.18)	18 (0.27)	19.5 (0.15)			
	Condition	9.5 (0.76)	12.5 (0.20)	13 (0.51)	14.5 (0.28)			
Emergent wetlands	Amount	**19 (0.03)**	**19 (0.03)**	**19 (0.03)**	**20 (0.01)**	15 (0.24)		
	Condition	13 (0.17)	**15 (0.04)**	17 (0.09)	**18 (0.04)**	12 (0.27)		
Wetlands/water	Amount	**24 (0.01)**	**24 (0.01)**	**24 (0.01)**	**25 (0.01)**	19 (0.19)	10 (1.0)	
	Condition	15.5 (0.19)	**18.5 (0.03)**	20.5 (0.10)	**22 (0.04)**	14 (0.34)	9 (0.88)	
Urban/developed	Amount	9 (0.48)	11.5 (0.90)	9 (0.48)	10 (0.63)	4.5 (0.10)	**0 (0.01)**	**0 (0.01)**
	Condition	5 (0.13)	7.5 (0.37)	7.5 (0.17)	7.5 (0.17)	2.5 (0.04)	**0 (0.01)**	**0 (0.006)**

c) Cavity: Fallen dead wood

		Lowbush blueberry fields	Agriculture/ pasture	Coniferous forest	Deciduous/ mixed forest	Deciduous/ mixed forest edge	Emergent wetlands	Wetlands /water
Agriculture/ pasture	Amount	**1.5 (0.03)**						
	Condition	**0 (0.01)**						
Coniferous forest	Amount	**19.5 (0.02)**	**25 (0.008)**					
	Condition	13.5 (0.90)	**20 (0.01)**					
Deciduous/mixed forest	Amount	**20 (0.009)**	**25 (0.005)**	**22.5 (0.02)**				
	Condition	18 (0.27)	**18 (0.04)**	16 (0.51)				
Deciduous/mixed forest edge	Amount	**18.5 (0.0**3)	**25 (0.008)**	8.5 (0.43)	**2.5 (0.02)**			
	Condition	10 (0.60)	**20 (0.01)**	9.5 (0.51)	6 (0.18)			
Emergent wetlands	Amount	4.5 (0.25)	15.5 (0.15)	**0 (0.01)**	**0 (0.009)**	**0 (0.01)**		
	Condition	11.5 (0.79)	14 (0.06)	10.5 (1.0)	9.5 (1.0)	12 (0.68)		
Wetlands/water	Amount	10.5 (1.0)	21 (0.07)	**3 (0.05)**	**0 (0.007)**	5 (0.12)	13.5 (0.41)	
	Condition	19.5 (0.14)	20 (0.01)	18 (0.27)	14 (0.82)	21 (0.07)	12.5 (0.61)	
Urban/developed	Amount	**0 (0.009)**	10 (0.42)	**0 (0.006)**	**0 (0.003)**	**0 (0.006)**	**2.5 (0.03)**	**2.5 (0.02)**
	Condition	**0 (0.006)**	10 (N/A)	**0 (0.006)**	**2.5 (0.02)**	**0 (0.005)**	**2.5 (0.04)**	**0 (0.007)**

Table D.4 Continued.

d) Cavity: Standing dead wood

		Lowbush blueberry fields	Agriculture/ pasture	Coniferous forest	Deciduous/ mixed forest	Deciduous/ mixed forest edge	Emergent wetlands	Wetlands /water
Agriculture/ pasture	Amount	10 (0.60)						
	Condition	4 (0.10)						
Coniferous forest	Amount	**23 (0.02)**	**24 (0.01)**					
	Condition	16 (0.50)	**18 (0.04)**					
Deciduous/mixed forest	Amount	**23 (0.02)**	**24 (0.01)**	14.5 (0.74)				
	Condition	16 (0.50)	**18 (0.04)**	12.5 (1.0)				
Deciduous/mixed forest edge	Amount	**4 (0.01)**	**24.5 (0.01)**	12.5 (1.0)	11.5 (0.91)			
	Condition	19.5 (0.14)	**20 (0.01)**	16 (0.48)	16 (0.48)			
Emergent wetlands	Amount	13 (0.49)	14 (0.30)	5 (0.25)	5 (0.25)	5 (0.22)		
	Condition	10 (1.0)	14 (0.06)	6.5 (0.41)	6.5 (0.41)	3 (0.07)		
Wetlands/water	Amount	18 (0.26)	19 (0.15)	9 (0.51)	8 (0.39)	9.5 (0.57)	12 (0.68)	
	Condition	16.5 (0.44)	16 (0.10)	15 (0.66)	15 (0.66)	13.5 (0.91)	13 (0.52)	
Urban/developed	Amount	7.5 (0.17)	10 (0.42)	**0 (0.007)**	**0 (0.007)**	**0 (0.006)**	5 (0.12)	5 (0.07)
	Condition	5 (0.07)	10 (N/A)	2.5 (0.02)	2.5 (0.02)	0 (0.006)	2.5 (0.03)	5 (0.07)

Table D.5. Expert-based Lonsdorf model bee life history parameter values assigned by Groff et al. (2016).

	Preferred nesting substrate		Active flight season			
Species	Ground	Cavity	Early summer	Mid-summer	Late summer	Maximum foraging distance (m)
Andrena carlini	1	0	0.33	0.33	0.33	598
Andrena carolina	1	0	0.25	0.5	0.25	246
Andrena vicina	1	0	0.33	0.33	0.33	569
Augochlorella aurata	1	0	0.17	0.33	0.5	60
Colletes inaequalis	1	0	0.33	0.33	0.33	1091
Halictus ligatus	1	0	0.43	0.29	0.38	148
Lasioglossum acuminatum	1	0	0.17	0.33	0.5	186
Lasioglossum cressonii	0	1	0.29	0.29	0.43	63
Lasioglossum heterognathum	1	0	0.17	0.33	0.5	16
Lasioglossum leucocomum	1	0	0.29	0.29	0.43	31
Lasioglossum pectorale	1	0	0.29	0.29	0.43	81
Lasioglossum versatum	1	0	0.29	0.29	0.43	79
Osmia atriventris	0	1	0.25	0.5	0.25	186
Osmia inspergens	0	1	0	1.0	0	495

APPENDIX E: IRB APPROVAL FOR BEEMAPPER DEVELOPMENT

APPLICATION FOR APPROVAL OF RESEARCH WITH HUMAN SUBJECTS
Protection of Human Subjects Review Board
114 Alumni Hall, 581-1498

PRINCIPAL INVESTIGATOR: Brianne Du Clos
EMAIL: brianne.duclos@maine.edu **TELEPHONE:** 581-2939
CO-INVESTIGATOR(S):
FACULTY SPONSOR (Required if PI is a student): Dr. Samuel Hanes
TITLE OF PROJECT: Participatory Development of a Pollinator Habitat Assessment Tool for Maine Blueberry Growers

START DATE: 3/18/15 ~~3/9/2015~~ **PI DEPARTMENT:** Wildlife, Fisheries, and Conservation Biology
MAILING ADDRESS: 5775 Nutting Hall, Rm 210
FUNDING AGENCY (if any): US Department of Agriculture, Mitchell Center for Sustainability Solutions

STATUS OF PI:
FACULTY/STAFF/GRADUATE/UNDERGRADUATE Graduate

1. If PI is a student, is this research to be performed:

☐ for an honors thesis/senior thesis/capstone?
☒ for a doctoral dissertation?
☐ other (specify)
☐ for a master's thesis?
☐ for a course project?

2. Does this application modify a previously approved project? No (Y/N). If yes, please give assigned number (if known) of previously approved project:

3. Is an expedited review requested? Yes (Y/N).

SIGNATURES: All procedures performed under the project will be conducted by individuals qualified and legally entitled to do so. No deviation from the approved protocol will be undertaken without prior approval of the IRB.

Faculty Sponsors are responsible for oversight of research conducted by their students. By signing this application page, the Faculty Sponsor ensures that the conduct of such research will be in accordance with the University of Maine's *Policies and Procedures for the Protection of Human Subjects of Research.*

2/7/2015
Date

Principal Investigator

Faculty Sponsor

Co-Investigator

Co-Investigator

****

FOR IRB USE ONLY Application # 2015-02-19 Date received 2/18/15 Review (F/E): E
Expedited Category: ______

ACTION TAKEN:

✓ Judged Exempt; category 2. Modifications required? Y (Y/N) Accepted (date) 3/18/15
____ Approved as submitted. Date of next review: by ________. Degree of Risk: ________
____ Approved pending modifications. Date of next review: by ________. Degree of Risk: ________
Modifications accepted (date): ________.
____ Not approved. (See attached statement.)
____ Judged not research with human subjects

Date: 2/20/15 Chair's Signature: Cynthia A. Erdley

10/09

APPENDIX F: INFORMED CONSENT FOR BEEMAPPER TESTING SESSIONS

Project Title: Participatory Development of a Bee Habitat Assessment Tool for Maine Blueberry Grower

Project Description: You are invited to participate in a research project being carried out by Brianne Du Clos, a graduate student at the University of Maine working with Dr. Cyndy Loftin, Dr. Frank Drummond, and Dr. Samuel Hanes. The project is funded by the US Department of Agriculture and Mitchell Center for Sustainability Solutions. The purpose of this research is to enlist growers' help in designing an online tool showing the quality of wild bee habitat around blueberry fields.

What Will You Be Asked To Do: If you agree to participate, Ms. Du Clos will show you a demonstration version of the tool and ask you questions about how to make it more useful. Here are a few sample questions: *What would you change about the way you find your fields? Do the terms in the habitat key make sense or should we reword them? How might we do this? How could we make this tool more useful for small growers?* We estimate your participation will take between twenty minutes and one hour. Interviews will be recorded.

Confidentiality: Du Clos will keep your participation confidential. Du Clos will not tell anyone that she has talked to you, with the exception of her graduate advisors. No one else will know that you participated and no identifying information will be published. Du Clos will keep the audio recording of this interview on her password protected computer for five years before deleting it.

Benefits and Risks: With the exception of your time and inconvenience, there are no risks to you from participating in this study. The project expects to improve a tool the can help growers better assess their wild bee habitat. This is likely to benefit Maine blueberry growers.

Compensation: You will be compensated $75 for your time.

Voluntary: Your participation is completely voluntary and you are free to withdraw at any point. You are always free skip any question or to end participation altogether. You will receive full compensation if you withdraw immediately prior to or during the interview.

Contact Information: If you have any questions, concerns, or additional comments, please contact the Principal Investigator:

Brianne Du Clos
5755 Nutting Hall, room 244
Orono, Maine 04469
207-581-2939
brianne.duclos@maine.edu

If you have any question about your rights as a research participant, you may contact Gayle Jones, Assistant to the University of Maine's Protection of Human Subjects Review Board, 207-581-1498, <gayle.jones@umit.maine.edu>.

APPENDIX G: INTERVIEW PROTOCOL FOR BEEMAPPER TESTING SESSIONS

Du Clos Interview Protocol

Project Title: Participatory Development of a Bee Habitat Assessment Tool for Maine Blueberry Grower

1.) What do you think is **good bee habitat**?

2.) This tool is meant to show you what the bee habitat is like around your blueberry field. Does this information **interest** you? How do you think you could use this information?

3.) This is a web-based tool. Can you tell us about your **experience** or comfort level with the internet?

4.) How do you think we can make this tool more **accessible** to growers?

5.) Can you find your field(s) in the web tool? Are you able to **navigate** through the available data once you find your field(s)?

6.) Does the way the data is **displayed** (colors, labels, arrangement) make sense to you? If not, how do you think we can improve it?

7.) What does each data layer mean to you? What do you think this means for bees? Specifically, let's look at these buffers around the field(s). How do you interpret this distance? **Can you connect what the maps show within the buffers to bees**? If not, what kind of information can we provide to make that connection clearer?

8.) Are you interested in the **data sources** we used and/or the model used to make the abundance map?

9.) Since this is a predictive model using satellite-collected land cover data and expert opinion, there are multiple sources of **uncertainty** in these maps. How likely is incorrect information going to affect your use and interpretation of this tool? Why/why not?

10.) Looking at these maps, how does the data affect your **perspective** of bee habitat around your field(s)?

11.) Any other comments, questions, or ideas regarding the web tool?

APPENDIX H: BEEMAPPER USER'S GUIDE

BeeMapper Users Guide

http://www.umaine.edu/beemapper

Development of BeeMapper was generously supported by:

1865 THE UNIVERSITY OF MAINE

NSF

MAINE EPSCoR

USDA

NIFA

NORTHEAST SARE
Sustainable Agriculture
Research & Education

Wild Blueberry
Commission of Maine

MAINE
COOPERATIVE
Fish and Wildlife
Research Unit

BeeMapper User's Guide Table of Contents:

1. Introduction to BeeMapper

2. Using BeeMapper

3. Interpreting BeeMapper information

Appendices

List of Figures

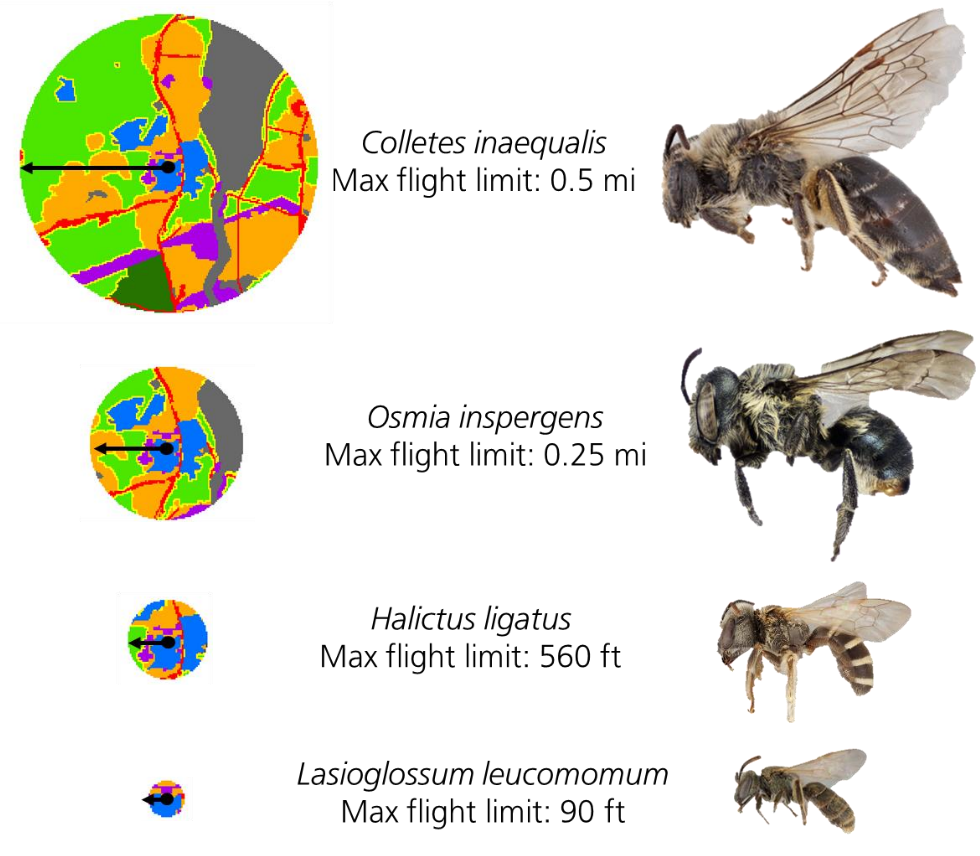
List of Tables

Section 1. Introduction to BeeMapper

BeeMapper was developed to aid Maine lowbush blueberry growers in making pollination management decisions on their farms. The tool provides maps of wild bee habitat resources and predicted wild bee abundance and allows crop growers to interact with these maps in the landscape surrounding their crop fields. BeeMapper summarizes the information in the maps surrounding each crop field in terms of habitat suitability and wild bee contribution to fruit set from the perspective of small wild bees that fly less than 250 yards as well as large wild bees that can fly up to 1000 yards. This information can be used to aid decisions about the number and placement of rented honey bee hives or installation and location of pollinator plantings to promote wild bee populations.

1.1 Landscape ecology of wild bees

Landscape ecology explores how the composition and arrangement of different types of land across a landscape affects the organisms within that landscape. These landscapes vary in size depending on the organism(s) studied. For example, a wild bee landscape is much smaller than a human landscape (Figure 1).



Photos © Laurence Packer 2014 via Discover Life

Figure 1. Landscape size and maximum flight limits of four Maine wild bees.

Bee landscape size is determined using two principles. First, bees are **central place foragers**, meaning they find food, or forage, in the area surrounding their nest and then return to their nest. Second, the **maximum flight limit** of a bee can be estimated by a measure of body size called the intertegular wingspan. This is the distance between the two tegula, the shield-like coverings at the base of a bees wings (Figure 2). Honey bees are the exception to this relationship, however, and have repeatedly demonstrated their ability to fly up to 5 miles to find food. Maximum flight limits for common Maine wild bees can be found in Appendix B.

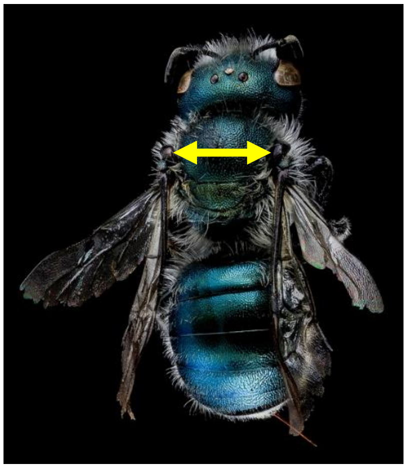


Figure 2. Intertegular wingspan of the wild bee *Osmia atriventris*.

The small size of wild bee landscapes limits where wild bees can survive. Wild bees need the habitat resources necessary to survive within these landscapes, which include nesting substrate and flowering plants for food. Bee habitat resource availability varies across Maine's lowbush blueberry production landscape, and therefore some types of land are better suited for wild bee habitat than others. BeeMapper presents eight land cover types in Maine's lowbush blueberry production landscape that each provide a unique set of habitat resources to wild bees (Figure 3). More information on these land cover types can be found in Appendix C.

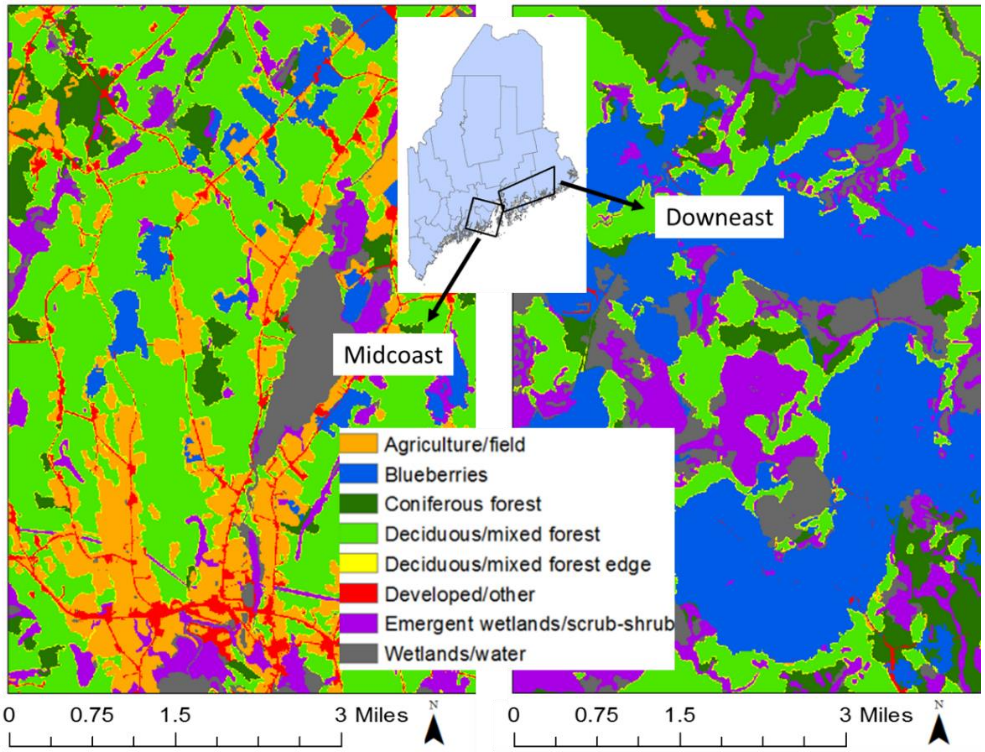


Figure 3. Composition and arrangement of eight land cover types in two growing regions of Maine's lowbush blueberry production landscape.

1.2 Wild bees and Maine’s lowbush blueberry production landscape

Maine’s lowbush blueberry production landscape differs from most well-studied agricultural landscapes in that it is forest-dominant and contains a large amount of natural habitat for wild bees within forest and crop field edges and forage associated with wetlands, grasslands, and developed areas. Furthermore, there are two blueberry growing regions within Maine that vary in the composition and arrangement of the eight land cover types providing habitat resources to wild bees (Figure 3).

The **Downeast** region covers coastal Hancock and Washington counties and is characterized by large, intensively-managed crop fields surrounded by coniferous forest and emergent wetland. The **Midcoast** region covers Knox County and parts of Lincoln and Waldo counties and is characterized by smaller, more often organically managed crop fields surrounded by deciduous forest and interspersed with other agriculture and urban areas. This dichotomy provides an opportunity to compare the effects of landscape composition and arrangement on wild bee communities. Research suggests that more complex landscapes, such as that of the Midcoast region, harbor bee communities that are more diverse and abundant than simpler landscapes such as the Downeast region. Ongoing bee community surveys in these regions will determine if that is the case.

1.3 Predicting wild bee abundance across agricultural landscapes

Ecosystem services are the economic contributions made by natural phenomena. Crop pollination by wild bees is an ecosystem service, and more than 120 species of wild bee (excluding bumble bees) have been collected in blooming lowbush blueberry fields in Maine (Bushmann and Drummond 2015). In order to harness wild bee resources more effectively for crop pollination, we need to understand their habitat use outside of crop fields. The **InVEST Crop Pollination model** (Lonsdorf et al. 2009) uses a land cover map along with habitat suitability scores to predict wild bee abundance across agricultural landscapes. We have applied this model to Maine’s lowbush blueberry production landscape (Groff et al. 2016) to produce a map of predicted wild bee abundance. This map highlights areas of high wild bee abundance and indicates areas to improve bee abundance through habitat enhancement. We validated the map predictions using data collected through Maine’s lowbush blueberry production landscape to produce accurate and reliable predictions of wild bee abundance. Appendix D details application of the InVEST Crop Pollination model to Maine lowbush blueberry.

We developed BeeMapper to share these maps with lowbush blueberry growers and collaborated with growers throughout the development process. We collected feedback from growers who use a variety of management practices on multiple prototypes of the tool, ultimately leading to a simple, straightforward, interactive interface. This User’s Guide describes the features of BeeMapper, demonstrates how to use the tool and interpret the map data, and provides suggestions on pollination management practices to enact given those data.

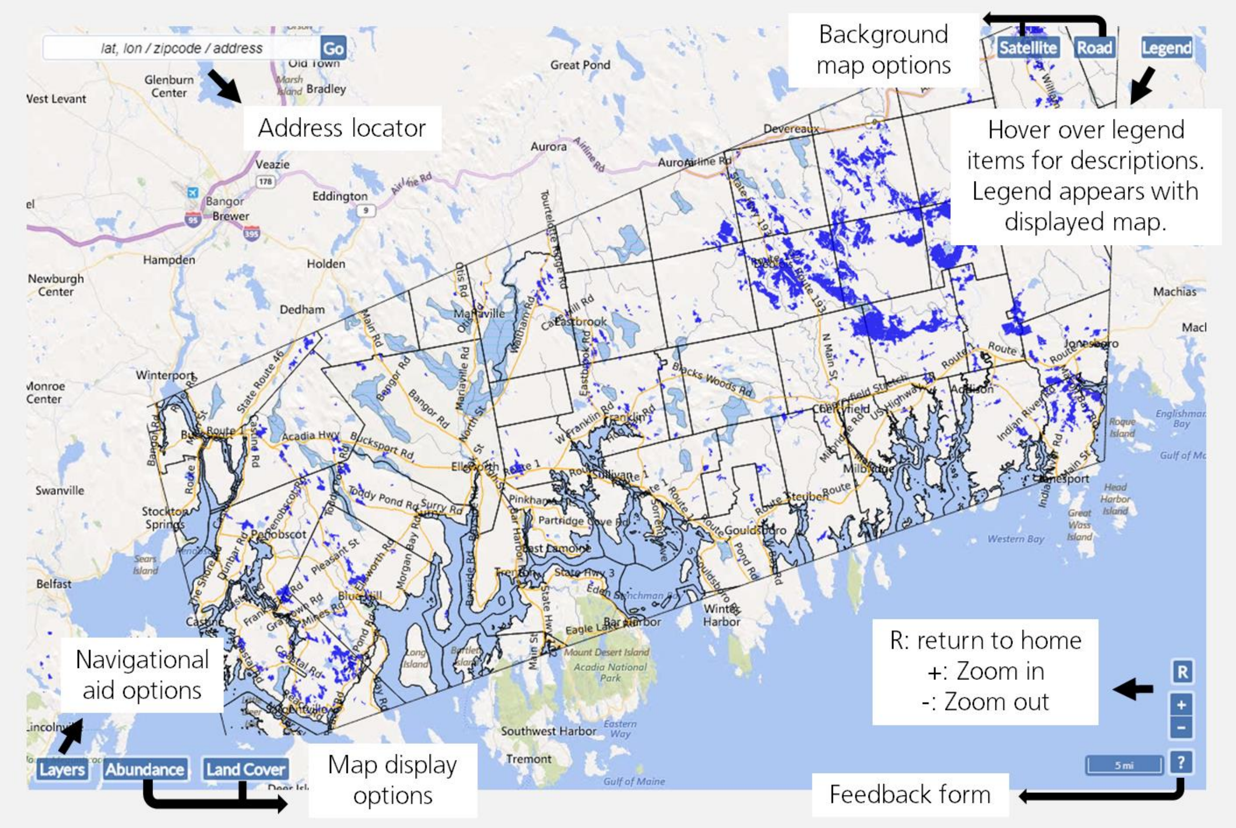
Section 2: Using BeeMapper

This section is a guide to the use of BeeMapper, the information it provides, and how you can use this information to make pollination management decisions.

2.1: Opening BeeMapper and Exploring Tool Features

To access the web tool, please visit the homepage at http://www.umaine.edu/beemapper. Recommended web browsers for BeeMapper are Google Chrome, Mozilla Firefox, Safari, and Opera. BeeMapper is only compatible with Internet Explorer versions 9.0 or newer. Once at the homepage, launch BeeMapper by clicking on the image of the tool.

Now that that tool is open, let's explore the features of the BeeMapper home screen (Figure 4).



Background map options

Address locator

Hover over legend items for descriptions. Legend appears with displayed map.

Navigational aid options

Map display options

R: return to home
+: Zoom in
-: Zoom out

Feedback form

Figure 4. BeeMapper home screen, which appears upon launch of the tool.

Home screen icons:

- The **address locator** is in the top left corner. You can use this to find your field on the map.
- You can choose between two **background map options**: 1) a road map or 2) a satellite image map. Choose a background map using the "Road" and "Satellite" buttons in the top right corner.
- The **legend** button will display the legend for the current map layer. If no map layers are displayed (this is the default setting), no legend will be displayed.
- There are three **map layer buttons** in the bottom left corner (Figure 5):

Figure 5. Navigational aid options found by clicking the Layers button. These maps can be turned off and on using the check boxes next to their names.

  - Layers: this button displays a menu of navigational aids to help locate your field(s). These navigational aids can be turned off and on using the check boxes next to their names. They include: lakes, rivers and streams, town boundaries, roads, and lowbush blueberry fields.
  - Land Cover: This map displays land cover, or the type of land found across the lowbush blueberry production landscape. See Section 2.4 for details on this map.
  - Abundance: this map displays the predicted wild bee abundance across the lowbush blueberry production landscape. See Section 2.4 for details on this map.

- The **tool navigation buttons** in the bottom right corner allow you to zoom in [+], zoom out [-], or return to the entire coverage of the map [R]. There is also a button for a **feedback form** [?] to send questions, comments, or corrections back to the BeeMapper development team. See Appendix A for more information about the feedback form.

2.2: Locating a blueberry field

The first step of using BeeMapper is locating your blueberry field. There are two ways to locate a lowbush blueberry field:

Method 1: Use the address locator box in the top left corner. Type in the town, street address or latitude-longitude coordinates of a field, and the tool will zoom in on this location.

Method 2: Manually navigate to a field using the roads, rivers, lakes, and town boundaries provided in the tool. Place the cursor over the location of the field and scroll up to zoom in. You can also zoom in using the button in the lower right corner, then click and drag the map to the location of your field.

a. To click and drag the map: Click on any area in the map and hold down the mouse. Drag the mouse across the screen, and the map will move along with it.
b. If the navigational aids are creating too much clutter on the screen, they can be turned off by clicking the "Layers" button and unchecking the boxes next to the layer names (Figure 5).

2.3: Pollinator habitat assessment

Once at the blueberry field, click on it. Two shaded regions appear around the field, which represent the distance different sized wild bees can fly to access that blueberry field (Figure 6).

- The small circle encloses 250 yards from the edge of the blueberry field. Small wild bees can fly from within this area into your blueberry field for pollination. For more information about small wild bees, see Appendix B.
- The large circle encloses 1000 yards from the edge of the blueberry field. Large wild bees, such as bumblebees, can fly from within this area into your blueberry field for pollination.

These circles are your wild bee source habitat. Wild bees that can contribute to crop pollination in your field have their nests and find forage before and after crop bloom here.

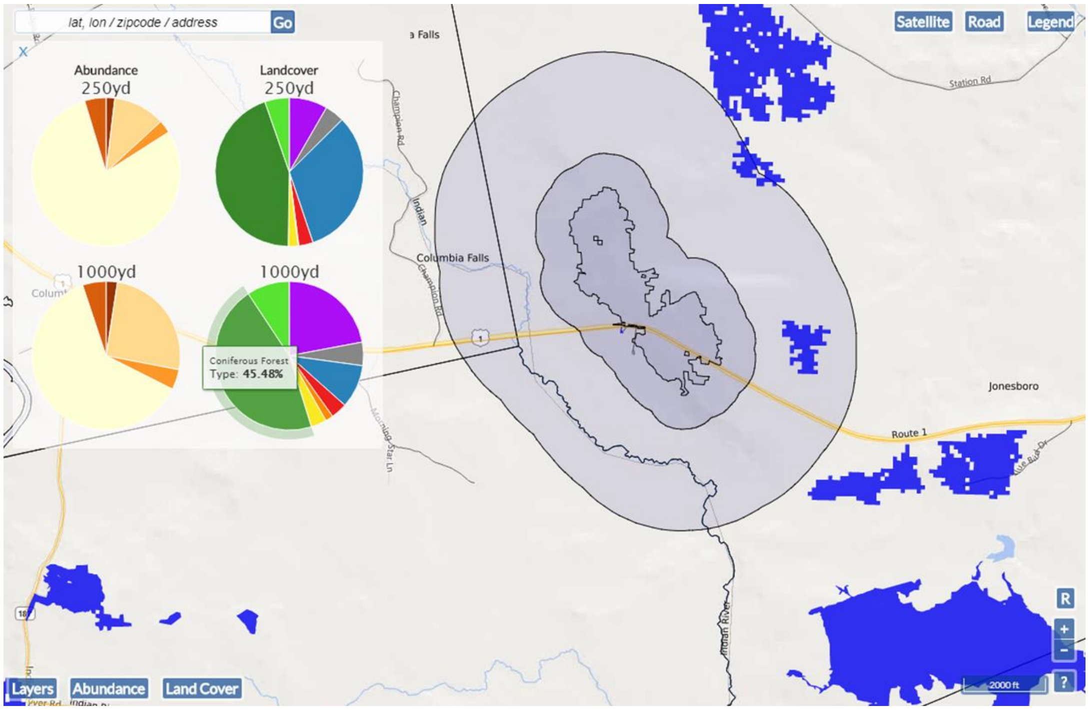


Figure 6. Wild bee source habitat (250 yd for small bees; 1000 yd for large wild bees) and pollinator habitat assessment summary box for a lowbush blueberry field.

When you click on a field, a summary box with four pie charts appears in the top left corner (Figs. 6 and 7). These pie charts summarize the land cover and predicted wild bee abundance maps for the small wild bee source habitat (250 yd) and large wild bee source habitat (1000 yd) surrounding a field. Hover over each wedge for a category label and percent total value. To close the summary box, click the X in the top left corner.

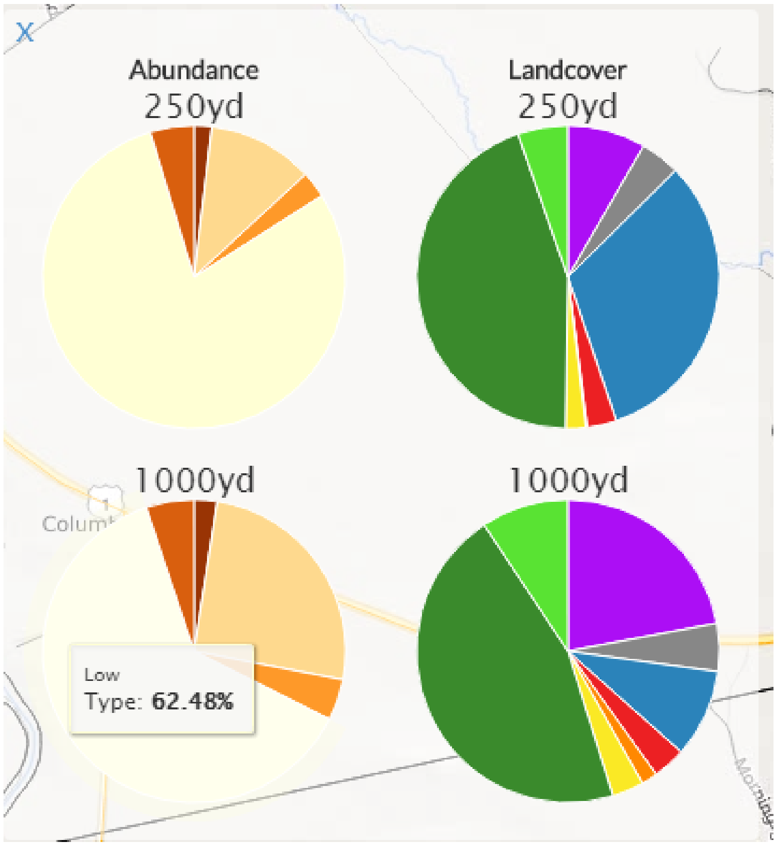


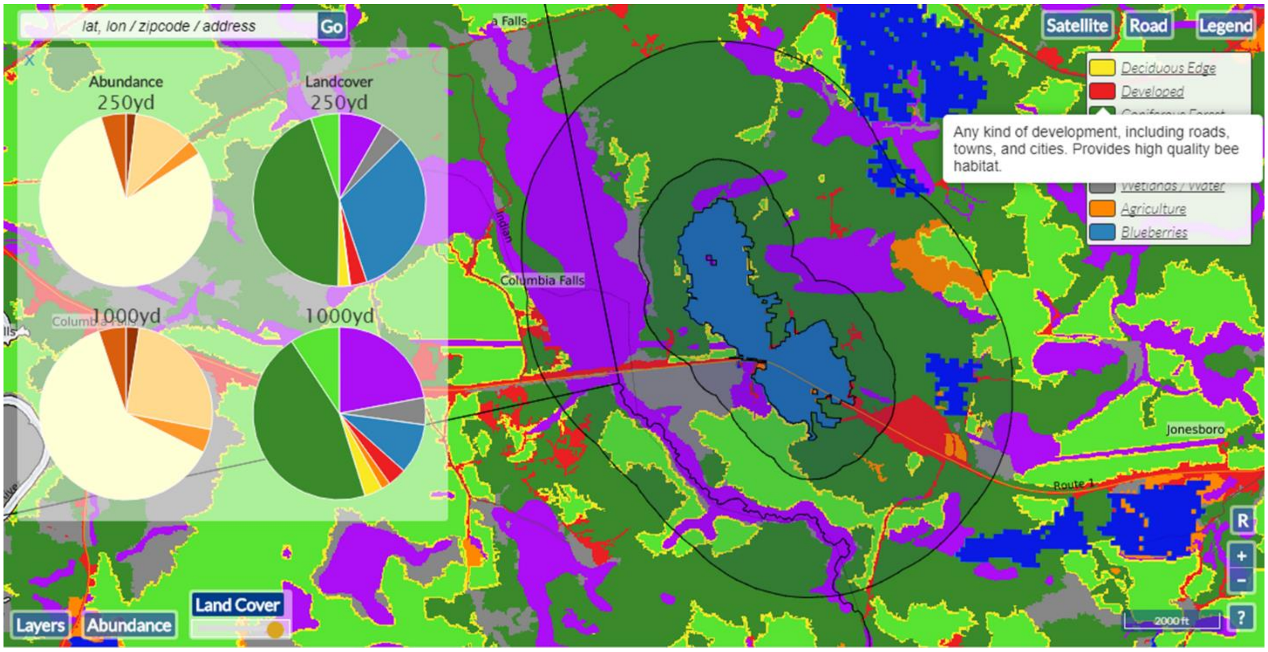
Figure 7. Pollinator habitat assessment summary charts.

2.4. Understanding the maps

BeeMapper is based on two maps:

- The **land cover map** displays eight land cover types that each offer a unique set of habitat resources to wild bees (Figure 8). For more information on these land cover types, see Appendix C.
- The **predicted wild bee abundance map** displays our prediction of wild bee abundance across the Maine lowbush blueberry production landscape (Figure 9). For more information on how this map was generated, see Appendix D.

To display the **land cover map**, click the "Land Cover" button in the bottom left corner. When the map appears, a corresponding legend appears under the "Legend" button in the top right corner (Figure 8). Hover over each land cover type in the legend for a short description. The legend can be turned off and on by clicking the "Legend" button.

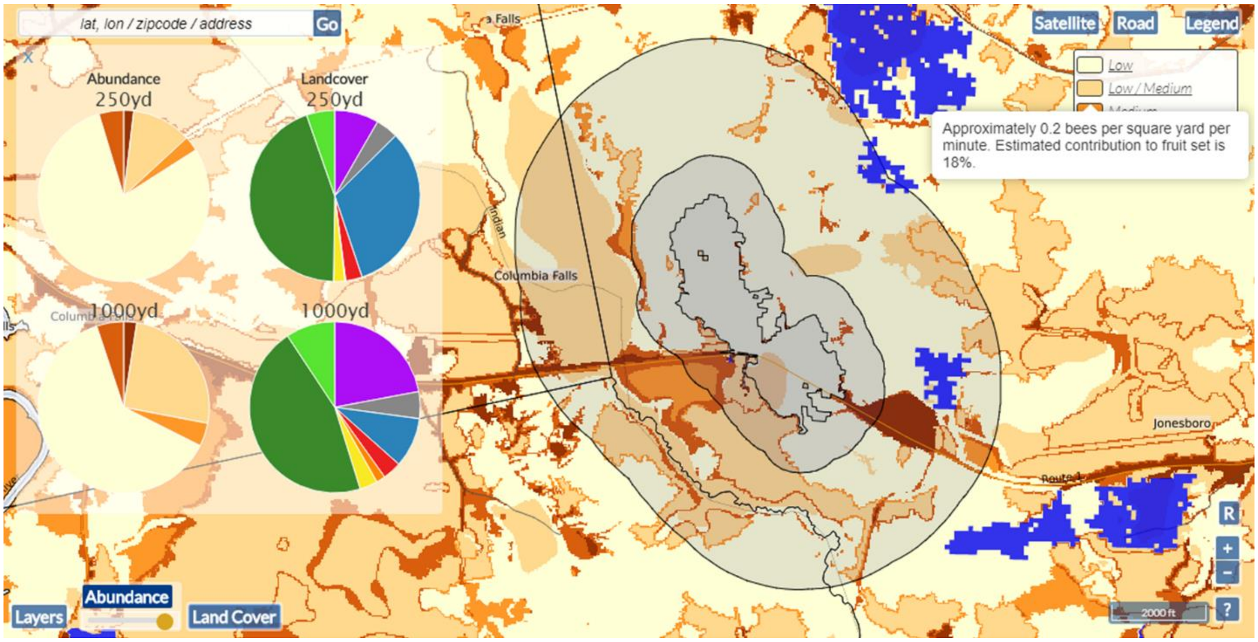


Any kind of development, including roads, towns, and cities. Provides high quality bee habitat.

Figure 8. Land cover map and legend.

See Section 3.1 for more information on land cover type and pollinator habitat suitability.

To display the **predicted wild bee abundance map**, click the “Abundance” button in the bottom left corner. A light to dark brown shaded map appears with a corresponding legend, displaying predicted wild bee abundance across the landscape (Figure 9).



Approximately 0.2 bees per square yard per minute. Estimated contribution to fruit set is 18%.

Figure 9. Predicted wild bee abundance map and legend.

The abundance map is categorized into 5 classes. Hover over each category in the legend for a brief description. Predicted wild bee abundance is typically low across the Maine lowbush blueberry production landscape (Groff et al. 2016). The predictions used to make this map are a combination of the land cover type and habitat suitability for wild bees (see Appendix D for more information). The estimates for number of bees and contribution to fruit set are based off of a large data set on wild bee density collected by Dr. Frank Drummond at the University of Maine:

- Low: Approximately 0.1 bees per square yard per minute (1 bee per clone every 10 minutes). Estimated contribution to fruit set is 12%.
- Low-Medium: Approximately 0.2 bees per square yard per minute (2 bees per clone every 10 minutes). Estimated contribution to fruit set is 18%.
- Medium: Approximately 0.3 bees per square yard per minute (3 bees per clone every 10 minutes). Estimated contribution to fruit set is 20%.
- Medium-High: Approximately 0.4 bees per square yard per minute (4 bees per clone every 10 minutes). Estimated contribution to fruit set is 25%.
- High: Approximately 0.5-1.0 bees per square yard per minute (5-10 bees per clone every 10 minutes). Estimated contribution to fruit set is 30%.

Section 3. Interpreting BeeMapper information

BeeMapper illustrates the connection between land cover type and wild bee habitat resources. The types of land surrounding lowbush blueberry fields play a very strong role in determining the wild bee community present. Working with the landscape surrounding your crop fields can affect your wild bee pollination resource.

3.1 Land cover type and pollinator habitat suitability

Wild bees prefer habitat that has a variety of wildflowers for collecting pollen and nectar, ample sun exposure for warmth and easy flying, and dead wood or open, sandy soils for building nests. Using this information, experts predict that deciduous/mixed forest edge and urban/developed land cover types will provide good bee habitat. Other land cover types can provide more wildflowers (emergent wetlands, agriculture) or better nesting areas (blueberries, deciduous/mixed forest). Coniferous forest and wetlands/water provide less wild bee habitat resources than the other land cover types.

Look at the land cover map within the shaded regions surrounding your fields.

- What is the most common land cover within these buffers?
- What do you think this could mean for bees?
    - Does this land cover provide high quality or poor quality bee habitat?

With this information in mind, look at the predicted wild bee abundance around your blueberry fields. Compare the abundance map to the land cover map.

- Can you see how the land cover affects the predicted wild bee abundance?
    - What types of land correspond with high bee abundance? With low bee abundance?
- What is the predicted bee abundance around your blueberry fields? Why?

3.2. Making pollination management decisions

Areas with high wild bee abundance can provide up to 30% of fruit set to a nearby lowbush blueberry field. If these patches are found around your field, you might strategically place rented honey bee hives or purchased bumblebee quads away from these areas. You can concentrate managed pollinators in areas of your crop field that are not surrounded by high quality wild bee habitat. Additionally, conserving areas with high wild bee abundance ensures that wild bees will continue to pollinate your crop. If your crop field is surrounded by poor quality wild bee habitat with low predicted wild bee abundance, you may consider habitat enhancement to promote wild bee populations around your crop field. See Appendix E for additional resources on pollination management.

3.3 Wild bee conservation

Wild bees are an important part of crop pollination because they are more efficient lowbush blueberry pollinators than honey bees. The lowbush blueberry landscape often can be harsh for wild bees, but there are actions you can take to manage, promote, and conserve wild bee populations around your blueberry fields. See Appendix E for additional resources on wild bee conservation.

- Installing bee pasture will provide ample forage resources for wild bees. Instructions on bee pasture installation are provided by the University of Maine Cooperative Extension. To create similar resources with less effort, you may consider leaving fallow areas near your fields to flower or allowing wildflowers along field edges to bloom.
- Provide nesting resources for wild bees by installing nesting boxes for cavity nesting bees or leave open patches of sandy soil available for ground nesting bees. Allowing woody shrubs near crop fields also provides nesting resources for cavity nesting bees.
- Reduce pesticide applications, and aim to use pesticides with low toxicity to wild bees.

3.4 Limitations

The land cover map displayed in BeeMapper is based on the 2004 Maine Land Cover Dataset (MeLCD, http://www.maine.gov/megis/catalog/metadata/melcd.html). Any change in land use since 2004 will not be accounted for in this map. In Maine, this generally means missing forest harvest, which may or may not lead to land cover change. Research in Maine is developing and ongoing as to the pollinator habitat suitability of recently harvested forest, information that may be of critical importance for lowbush blueberry growers. The map is static and does not support user-generated modifications, such as the effects of installing a pollinator planting on wild bee abundance. BeeMapper provides a baseline pollinator habitat assessment for Maine lowbush blueberry growers to inform pollination management decisions. We have discovered that wild bee abundance is difficult to predict accurately in blueberry fields that are small or irregularly-shaped. Model predicted bee abundance is lower, but more accurate in large, square-shaped fields with simple edges and is often overpredicted in small, elongated fields with complex edges. This does not affect predictions in other land cover types, which we have found to be accurate owing to the large amount of these other cover types in comparison to lowbush blueberry.

Appendix A: Using the BeeMapper feedback form

We welcome comments, suggestions, and corrections to BeeMapper through the feedback form, which is accessed by clicking the button with the question mark [?] in the bottom right corner of the tool window (Figure 10). The feedback form will appear in the top left corner of the window.

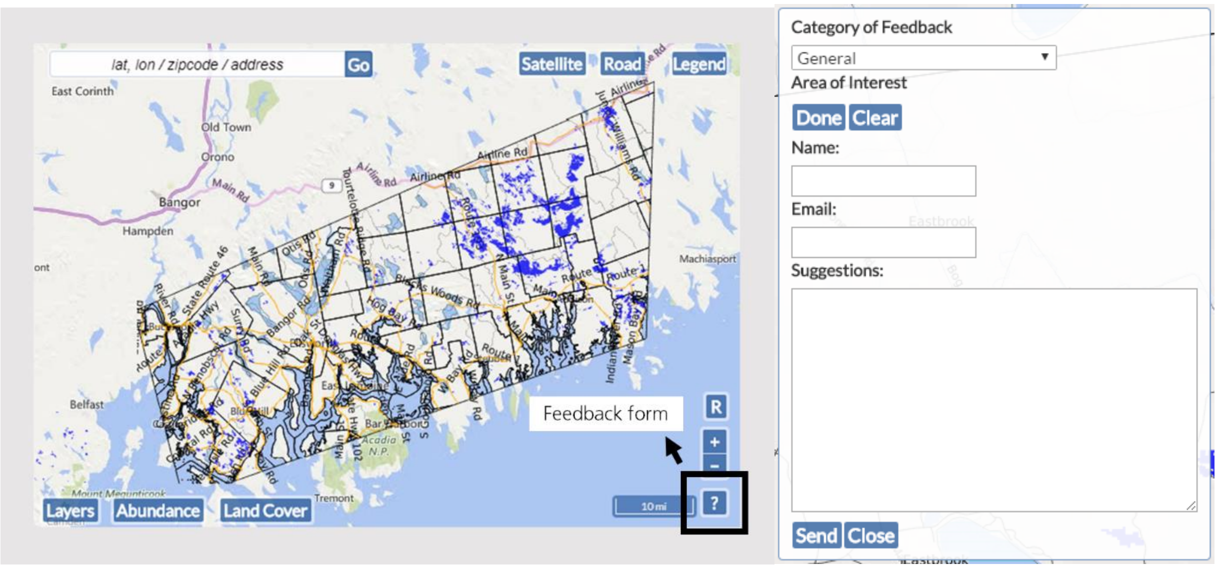


Figure 10. Location of the feedback form button in the BeeMapper home screen and the feedback form, which appears in the top left corner of the tool window.

All feedback goes to the BeeMapper technical development team, who will work to address any problems and answer any questions.

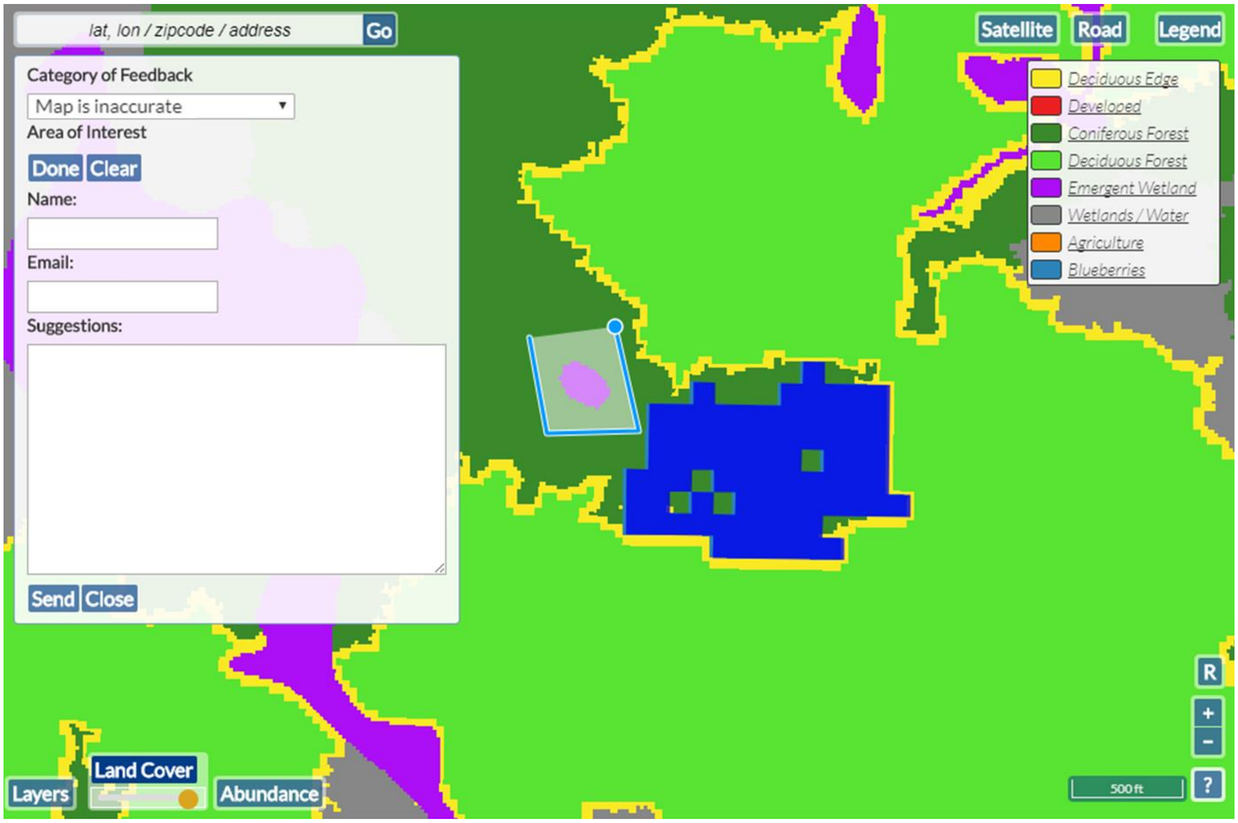
There are three categories of feedback:

1. General: Any questions or comments beyond data inaccuracies or website problems can be submitted under this category.
2. Map is inaccurate: If your blueberry field is not classified as blueberry in BeeMapper, please let us know through this category on the feedback form. You also can alert us to other data inaccuracies, such as an agricultural area classified as a forest, etc. Please provide a street address or lat/long coordinates so we can locate the area and make the corrections.
    a. You can also send us a picture of the inaccurate area using the “Area of Interest” menu on the feedback form. To do this, click “Select,” then draw the area that is incorrect. When finished, click “Done.” If you need to re-draw the area, click the “Clear” button and try again. See Appendix A.2 for more details on this process.
3. Technical troubles with website: If buttons aren’t working, the maps take too long to load, or if the summary box is not displaying correctly, please let us know using this category of feedback.

Please provide your name and email address or other contact information to allow the development team to contact you with any questions. Provide feedback within the “Suggestions” box, then click “Send” to send your comments. The “Close” button will close the feedback form.

A.2: Submitting feedback for inaccurate data

When submitting feedback regarding inaccurate map data, you may delineate the inaccurate area using the **Area of interest** function of the feedback form. To provide an area of interest, first click the "Select" button on the feedback form. This turns the cursor into a drawing tool. Begin drawing a shape around the inaccurate area on the map (Figure 11).



Category of Feedback: Map is inaccurate

Figure 11. Drawing an area of interest around an inaccurate data area of the Land Cover map.

To complete the shape, double click and the shape border will turn orange (Figure 12). You may select multiple areas of interest to submit. To clear the area(s) of interest, click the "Clear" button on the feedback form. To finish delineating areas of interest, click the "Done" button on the feedback form.

Category of Feedback

Map is inaccurate

Area of Interest

Name:

BeeMapper Example

Email:

beemapper-group@mair

Suggestions:

This "emergent wetland" area is actually a blueberry field.

Figure 12. Completed area of interest and additional comments in the BeeMapper feedback form.

Appendix B: Common wild bees in Maine lowbush blueberry fields

We collected information on nesting preference, flight season, and foraging distance for these 14 wild bee species commonly found in blooming lowbush blueberry fields (Bushmann and Drummond 2015) from published scientific literature and expert opinion. This information was input into the InVEST Crop Pollination Model (Appendix D) applied to Maine's lowbush blueberry production landscape.

Andrena carlini:

Family	**Andrenidae**
Nesting preference	Ground nesting
Flight season	March-August
Foraging distance	653 yd

Andrena carolina:

Family	**Andrenidae**
Nesting preference	Ground nesting
Flight season	April-July
Foraging distance	270 yd

Andrena vicina:

Family	**Andrenidae**
Nesting preference	Ground nesting
Flight season	March-August
Foraging distance	622 yd

Augochlorella aurata:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	April-October
Foraging distance	65 yd

Colletes inaequalis:

Family	**Colletidae**
Nesting preference	Ground nesting
Flight season	March-September
Foraging distance	1193 yd

Halictus ligatus:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	March-November
Foraging distance	161 yd

Lasioglossum acuminatum:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	April-October
Foraging distance	203 yd

Lasioglossum cressonii:

Family	**Halictidae**
Nesting preference	Cavity nesting
Flight season	March-October
Foraging distance	68 yd

Lasioglossum heterognathum:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	April-September
Foraging distance	17 yd

Lasioglossum leucomomum:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	March-October
Foraging distance	34 yd

Lasioglossum pectorale:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	March-November
Foraging distance	88 yd

Lasioglossum versatum:

Family	**Halictidae**
Nesting preference	Ground nesting
Flight season	March-October
Foraging distance	86 yd

Osmia atriventris:

Family	**Megachilidae**
Nesting preference	Cavity nesting
Flight season	April-July
Foraging distance	203 yd

Osmia inspergens:

Family	**Megachilidae**
Nesting preference	Cavity nesting
Flight season	May-June
Foraging distance	541 yd

While not incorporated into the InVEST Crop Pollination model, bumble bees are very important lowbush blueberry pollinators. Bumble bee queens, which are the only caste of bumble bee present during lowbush blueberry bloom, are much larger than the solitary wild bees featured here. Therefore, bumble bee queens can fly much longer distances than solitary wild bees.

Bombus species:

Family	**Apidae**
Nesting preference	Ground and cavity nesting
Flight season	Queens: May Workers: June-September
Foraging distance	Queens: 4.7 miles Workers: 1.3 miles

Pictured: orange banded bumble bee (*Bombus ternarius*)

All photos are © Laurence Packer via Discover Life.

Appendix C: Land cover types and wild bee habitat resources

We summarized land cover in Maine’s lowbush blueberry production landscape into eight land cover types relevant to wild bees. Each of these cover types offers a unique set of habitat resources to wild bees. Wild bee habitat resources include nesting substrate and flowering plants for food. Nesting substrate can be bare patches of sandy soil for ground nesting bees or hollow twigs and downed woody debris for cavity nesting bees. Flowering plants should be abundant and diverse throughout the growing season to provide ample and nutritious food for wild bee populations.

Coniferous forest: Consists of softwood trees. Coniferous forest is poor bee habitat. Although it provides some ground and ample cavity nesting resources, the lack of light in the understory does not allow many flowering plants to grow. Furthermore, the density of trees in coniferous forest is difficult for wild bees to fly through, making coniferous forest a potential barrier to accessing nearby patches of abundant floral resources. However, recently harvested patches of coniferous forest may provide high quality bee habitat for a few years until trees become dominant again.

Deciduous/mixed forest: Consists of hardwood or a mixture of hardwood and softwood trees. Deciduous/mixed forest is moderate quality bee habitat, providing some ground nesting resources and ample cavity nesting resources. Sunlight through the tree canopy allows some wildflowers and flowering shrubs to provide pollen and nectar for wild bees throughout the growing season. Flowering trees, particularly maple, are a crucial pollen and nectar source in the early spring and provision many lowbush blueberry pollinating wild bees.

Deciduous/mixed forest edge:

The transition between forests with hardwood or a mixture of hardwood and softwood trees and another land cover type. This is very high quality bee habitat, with excellent ground and cavity nesting resources. Woody shrubs provide hollow twigs, and bare patches of sandy soil are common. There are also plenty of wildflowers and flowering shrubs and trees to provide pollen and nectar throughout the growing season. Wild bee communities in edge habitat are very diverse and abundant owing to these ample resources. Forest edge along lowbush blueberry fields makes great habitat for wild bees.

Emergent wetland:

Emergent wetland is wetland habitat that is not consistently submerged throughout the growing season. It provides moderate quality bee habitat. Ground nesting resources are limited owing to wet soils, but cavity nesting resources are plentiful among the abundant woody shrubs and hollow flower stems. Emergent wetland provides a unique set of blooming plants to wild bees, including woody shrubs, bog plants and close relatives of lowbush blueberry. They are a good source of pollen and nectar throughout the growing season. Their proximity to blueberry fields in the Downeast region is important for wild bee population survival.

Wetlands/water: This cover type consists of either submerged wetlands or open water. These areas typically are poor bee habitat—owing to the dominance of open water, they provide almost no ground nesting and few cavity nesting resources. Furthermore, they offer little pollen and nectar throughout the growing season as few flowering plants can establish in the wet soils. Submerged wetlands can offer cavity nesting resources in standing dead wood or hollow twigs and stems and may have flowering plants available at the water's edge.

Agriculture/Grassland: Either non-blueberry agriculture or open, grass-dominated fields. These areas provide moderate quality bee habitat. Agricultural and grassland areas provide ground nesting resources via exposed patches of soil if the soil is not compacted from heavy farm machinery, but a lack of woody shrubs and woody debris means they provide few cavity nesting resources. Abundant flowering plants can provide ample pollen and nectar to wild bees throughout the growing season, especially on small, diversified farms and grassy fields with constant wildflower bloom.

Urban/Developed: Any kind of development, including roads, towns, and cities. Urban/developed areas provide high quality bee habitat. They have excellent ground nesting resources in exposed sandy soils found along roadsides and in gardens, parks, and yards. Cavity nesting resources are also abundant in woody shrubs used for landscaping. Flowering plants are also abundant throughout the growing season from gardens, landscaping in public and residential areas, and fallow strips along roadsides. Reduced lawn mowing and pesticide applications are encouraged in urban/developed areas to promote wild bee populations.

Blueberries: Blueberry fields that may be managed or unmanaged. Blueberry fields provide moderate quality bee habitat. There are excellent ground nesting resources owing to patches of exposed, sandy soils, but few cavity nesting resources within blueberry fields. The crop bloom in late spring provides an incredible source of food for wild bees, but there is little pollen and nectar throughout the rest of the growing season. Wild bees rely on nearby habitat to sustain their populations after crop bloom, therefore it is crucial to have ample floral resources nearby. Unsprayed field edges and installed pollinator plantings can promote wild bee habitat in blueberry fields.

Appendix D. BeeMapper map development

Here, we describe the development of the two maps presented in BeeMapper: a land cover map and a predicted wild bee abundance map.

D.1: Land cover map

The land cover map is based on the 2004 Maine Landcover Dataset (MeLCD), which is freely available from the Maine Office of GIS (Landcover – MELCD 2004, http://www.maine.gov/megis/catalog/). This dataset has 5m spatial resolution, which captures landscape variation that is important to wild bees. We classified the original map into 8 land cover classes that each provide a unique set of resources for wild bees (Appendix C). We further modified this map to include roads and railroads, enhance wetland diversity, and provide the most extensive lowbush blueberry coverage. Additional data sources used for the land cover map are:

- Roads: MEDOTPUBRDS, http://www.maine.gov/megis/catalog/
- Railroads: RAILROUTESYS, http://www.maine.gov/megis/catalog/
- Wetlands: National Wetlands Inventory, http://www.fws.gov/wetlands/NWI/Index.html
- USDA Croplands Dataset: CDL; http://nassgeodata.gmu.edu/CropScape/

D.2: Predicted wild bee abundance map

The abundance map is output from the **InVEST Crop Pollination Model** (Lonsdorf et al. 2009) applied to Maine's lowbush blueberry production landscape. The InVEST Crop Pollination Model requires three components to predict bee abundance across a landscape:

1) A **land cover map**. The land cover map presented in BeeMapper and described in section D.1 is the same land cover map we used to predict wild bee abundance with the InVEST Crop Pollination Model. We resampled this map to 10m spatial resolution for computational efficiency, with no measurable loss in model performance.

2) **Habitat suitability values** for wild bees within each land cover type within the land cover map. These values were provided by expert opinion. We asked 12 experts to rank eight land cover types for their ability to provide:
   - Ground nesting resources (open soil, gravel)
   - Cavity nesting resources (rotting logs, dead shrubs with hollow branches)
   - Forage resources (pollen and nectar from blooming flowers) in the early, middle, and late summer (3 separate scores). Assessing forage resources throughout the growing season accounts for seasonal variability in the abundance and diversity of blooming flowers and leads to more accurate model predictions.

   Expert opinion-derived habitat suitability parameters are listed in Table 1. Each land cover type is ranked on a scale of 0 to 1, with 1 being most suitable habitat for wild bees.

3) **Bee life history traits** for wild bees associated with the focal crop. We collected information for nesting preference, foraging distance, and flight season of 14 wild bee species found in blooming lowbush blueberry fields (Appendix B). Due to model constraints, we did not incorporate bumble bees (*Bombus* species), an important blueberry pollinator, into the model.

Table 1. Expert-opinion derived parameters for the InVEST Crop Pollination Model applied to Maine lowbush blueberry.

Land cover type	Ground nesting	Cavity nesting	Late spring forage	Early summer forage	Late summer forage
Agriculture/grass	0.7	0.2	0.9	0.7	0.9
Blueberries	1.0	0.4	0.4	1.0	0.5
Coniferous forest	0.5	0.6	0.1	0.1	0.1
Deciduous/mixed forest	0.6	0.9	0.7	0.5	0.4
Deciduous/mixed forest edge	0.9	1.0	0.9	0.9	1.0
Emergent Wetland	0.2	0.4	0.7	0.6	0.6
Urban/developed	0.9	0.6	1.0	0.9	1.0
Wetlands/water	0.1	0.1	0.3	0.2	0.5

The InVEST Crop Pollination Model predicts bee abundance at each point across the input land cover map for each bee species using bee foraging distance and flight season in tandem with the resources offered by each land cover type throughout the growing season. These maps are then summed to create the model output, an overall predicted wild bee abundance map. Each point in this map is given an index value between 0 and 1, with 1 representing the highest wild bee abundance. We classified this index into five abundance classes for clearer interpretation.

For more details on the InVEST Crop Pollination model, please visit http://data.naturalcapitalproject.org/invest-releases/3.3.3/userguide/croppollination.html

Full details of the development of the land cover map and application of the InVEST Crop Pollination Model to the Downeast lowbush blueberry growing region can be found in Groff et al. (2016) and Chapin (2014). Additional details regarding application of the InVEST Crop Pollination model to the Midcoast lowbush blueberry region and model accuracy in non-blueberry cover types are forthcoming.

Appendix E: Additional Resources

The lowbush blueberry web page of the University of Maine Cooperative Extension has many resources on pollinator management and conservation. Recommending reading includes:

- Fact Sheet 301: Field Conservation Management of Native Leafcutting and Mason Osmia Bees
- Fact Sheet 630: Wild Bee Conservation for Lowbush blueberry Fields
- Farming for Bees: Guidelines for Providing Native Bee Habitat on Farms
- Enhancing Wild Bees for Crop Pollination: Sowing Bee Pasture for New England's Wild Lowbush Blueberry

You can find these resources and additional information on wild bees by visiting the Cooperative Extension lowbush blueberry web page: https://extension.umaine.edu/blueberries/factsheets/bees/

A series of YouTube videos details multiple aspects of wild bee management and conservation in Maine lowbush blueberry:

- Dr. Frank Drummond demonstrates how to count wild bees in lowbush blueberry fields: https://www.youtube.com/watch?v=rgVav2byI8o
- Hear why the landscape is important for pollination management: https://www.youtube.com/watch?time_continue=120&v=aY9GKAH231I
- Learn more about pollinator plantings: https://www.youtube.com/watch?v=J1kFxmiYncA

Academic references:

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BIOGRAPHY OF THE AUTHOR

Brianne (née Looze) Du Clos was born in Menomonie, Wisconsin on June 25, 1987. She was raised in La Crosse, Wisconsin with her six younger siblings and graduated from La Crosse Central High School in 2005. She attended the University of Wisconsin-Superior and graduated in 2009 with a Bachelor of Science degree in Biology with a minor in Geographic Information Systems. She entered graduate school at the University of Maine in the fall of 2009. She conducted research in forest landscape ecology and received her Master of Science degree in Forest Resources in 2012. She worked as a stewardship intern at the Beech Hill Preserve lowbush blueberry farm in Rockport, Maine, in the summer of 2012 before re-entering graduate school at the University of Maine, this time to conduct research in pollination landscape ecology. Brianne is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences from the University of Maine in May 2019.