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Parameterization of the InVEST Crop Pollination Model to spatially predict abundance of wild blueberry (*Vaccinium angustifolium* Aiton) native bee pollinators in Maine, USA

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Non-native honeybees historically have been managed for crop pollination, however, recent population declines draw attention to pollination services provided by native bees. We applied the InVEST Crop Pollination model, developed to predict native bee abundance from habitat resources, in Maine's wild blueberry crop landscape. We evaluated model performance with parameters informed by four approaches: 1) expert opinion; 2) sensitivity analysis; 3) sensitivity analysis informed model optimization; and, 4) simulated annealing (uninformed) model optimization. Uninformed optimization improved model performance by 29% compared to expert opinion-informed model, while sensitivity-analysis informed optimization improved model performance by 54%. This suggests that expert opinion may not result in the best parameter values for the InVEST model. The proportion of deciduous/mixed forest within 2000 m of a blueberry field also reliably predicted native bee abundance in blueberry fields, however, the InVEST model provides an efficient tool to estimate bee abundance beyond the field perimeter.

1. Introduction

Maine is the world's largest producer of wild blueberries (*Vaccinium angustifolium* Aiton), with over 91.1 million pounds harvested in 2012 primarily from Hancock, Washington, Knox, and Waldo counties (Yarborough, 2009). Wild blueberries require insect pollination (Drummond, 2002; Jones et al., 2014), and Maine is the country's second largest importer of non-native honeybees (Apis mellifera) for wild blueberry pollination, with >75,000 hives rented annually (A. Jadczak, Maine Department of Agriculture, pers. comm.). Declining populations of managed honeybee colonies (~59% during 1947–2005; Potts et al., 2010), which pollinate crops worth $5–14 billion annually in the United States (Kremen et al., 2002), has led to increased cost of hive rentals for wild blueberry pollination (Pettis and Delaplane, 2010), enhancing interest in the freely available ecosystem service of native pollinators, which are adapted to forage in reduced light and cooler temperatures common where wild blueberries grow (Cane and Payne, 1988; Hanes et al., 2013).

Native bees are mobile and dependent on discrete resources that may vary spatially and temporally across a landscape (Kremen et al., 2007), and access to those resources depends on the bee's foraging and dispersal ability (Patricio-Roberto and Campos, 2014). Understanding factors affecting pollination services on a farm requires understanding the relationships between bee diversity or abundance in the crop and the spatial and temporal distribution of pollinator-supporting habitat surrounding a farm (Kremen et al., 2007). The proportion of pollinator habitat surrounding and within a crop field is a determinant of the bee community diversity and abundance and hence pollination by native pollinators. In this case, habitat is any landscape feature that offers shelter, nesting grounds, or food resources (Ricketts et al., 2008). Native bee

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visitation to crop bloom decreases with isolation from bee habitat areas, and may lead to a decrease in crop pollination despite added honeybee visits (Garibaldi et al., 2011). Native bee abundance within a field can be predicted by composition of habitat adjacent to the field (Steffan-Dewenter et al., 2002; Taki et al., 2007; Watson et al., 2011). Pollinator abundance may be affected not only by land cover type, but also by the pattern and arrangement of land cover in the landscape surrounding the focal crop (Brosi et al., 2008; Ricketts et al., 2008; Lonsdorf et al., 2009, 2011), as well as the scale and extent at which the landscape is evaluated (Lonsdorf et al., 2009, 2011).

The Natural Capital Project's InVEST Crop Pollination Model (Lonsdorf et al., 2009, 2011) is a spatially explicit, geographic landscape computer algorithm that produces geo-referenced predictions of bee abundance in grid cells across a landscape, based on nesting resources within the focal cell and floral resources surrounding the cell, within the confines of the modeled bee's foraging range. InVEST is adaptable to any crop for which it can be validated, potentially providing a tool to help growers enhance use of pollination services. The model requires a spatial land cover dataset and parameters relating land cover suitability for providing habitat resources given the modeled bee's life history strategy (Lonsdorf et al., 2009, 2011). In the absence of empirical data, parameters can be assigned based on published values or expert opinion. Expert opinion often is used to inform spatial models (Compton et al., 2007; Lonsdorf et al., 2009; Spear et al., 2010; Kennedy et al., 2013), although predictive accuracy of the model is not necessarily improved with this knowledge (Charney, 2012).

We evaluated the InVEST Crop Pollination Model (Sharp et al., 2015) in Maine's wild blueberry crop system. Our analyses addressed the following questions: 1) Is the InVEST model predictive ability affected by the focal landscape? 2) Does expert opinion ranking of bee habitats (the most common parameterization technique used for InVEST) provide predictive capability for estimating bee abundance? 3) Do informed or uniformed parameterization techniques improve predictive capability of the InVEST model over expert opinion parameterization? and, 4) Does a proportional land cover model provide comparable predictive capability to that provided by the InVEST model?

Our analysis investigated relationships between landscape composition and native bee abundance predicted with the InVEST model in two phases. First, we examined the InVEST model performance across three spatial extents in the wild blueberry production landscape, reflecting differences in land cover data source, type, patch size, and validation datasets. Second, we evaluated change in the model's predictive ability with four parameterization approaches: expert opinion, sensitivity analysis, model optimization with sensitivity analysis based (informed) calibration, and model optimization with simulated annealing (uniformed) calibration. Finally, we compared the results of the InVEST model prediction of bee abundance to the results of bee abundance predicted from near-field habitat composition.

2. Study area and methods

2.1. Study area

We evaluated the predictive ability of the InVEST model based on land cover type-associated nesting and forage suitability across three areas in Downeast Maine (Fig. 1). The *Eastern* extent covers 3000 km^2 and includes eight focal blueberry fields (<1–11 ha). The *Blue Hill* area covers 705 km^2 of southwestern Hancock County including 26 focal blueberry fields (<1–17 ha). The *Downeast* extent spans 4802 km^2, overlapping the *Blue Hill* extent and approximately half of the *Eastern* extent, and includes 40 focal blueberry fields (<1–17 ha). These extents were bounded based on the spatial distribution of the field sites and collected field data, as well as the availability of the spatial data (e.g., the Eastern extent was bounded by the footprint of the SPOT imagery we obtained). Habitat that provides nesting and foraging resources to bees in Maine is represented on land cover maps as deciduous/mixed forest, deciduous/mixed forest edge, and old fields and grasslands in these extents.

2.2. Methods

2.2.1. Spatial land cover

We developed and evaluated land cover datasets from a variety of source data to identify the extent and cell resolution with the greatest model prediction accuracy. The *Downeast* and *Blue Hill* extents (Fig. 1) were represented by a land cover map that merged several source datasets.

The Maine Landcover Dataset 2004 (MELCD 2004; http://www.maine.gov/megis/catalog/) combines the National Landcover Dataset 2001 (NLCD 2001; http://www.mrlc.gov/nlcd01_data.php), based on 1999–2001 Landsat Thematic Mapper 5 and 7 imagery (30 m pixel resolution), with classification of 2004 SPOT 5 imagery (5 m pixel resolution), to create a 5-m resolution raster dataset with 23 land cover classes. The blueberry field category represents commercial wild blueberry operations with an accuracy of 89.7% in Maine. We updated the 2004 MELCD with ancillary datasets (ArcGIS® version 10.0; Esri, Redlands, CA, United States), including railroads (RAILROUTESYS) and roads (MEDOTPUBRDS, NG911; http://www.maine.gov/megis/catalog/) and the MELCD wetlands classes (wetland forest, wetlands, scrub-shrub) with the National Wetland Inventory (NWI; http://www.fws.gov/wetlands/NWI/Index.html) to capture wetland diversity potentially important to foraging bees. We created a *deciduous/mixed forest edge* class by applying a 10 m buffer around *deciduous forest* and *mixed forest* pixels. We resampled the 30 m USDA Croplands Dataset (CDL 2012; http://nassgeodata.gmu.edu/CropScape/) to 5 m pixels using the nearest neighbor technique, and we updated the MELCD "blueberry field" class with wild blueberry fields >4 ha in the CDL, capturing fields omitted from the original MELCD dataset while excluding wild blueberries growing outside managed fields. All spatial data were obtained between January 2012 and May 2012. We digitized the perimeter of wild blueberry fields where bee samples were collected but that were missing from the compiled land cover dataset. The final land cover 5 m pixel dataset (non-enhanced) used to evaluate model predictions in the *Downeast* and *Blue Hill* extents was reclassified from 42 classes into eight land cover types: *deciduous/mixed forest edge*, *developed/other*, *coniferous forest*, *deciduous/mixed forest*, *emergent/shrub–shrub wetlands*, *other wetlands/water*, *agriculture/field* and *blueberries*.

The *Eastern* extent (Fig. 1) was represented by a land cover map that combined additional datasets. We updated the blueberry class in the MELCD land cover layer with a single 10 m hyper-spectral SPOT image of a 3600 km^2 area of Washington County collected May 2011 (Airbus Defense and Space 2014; http://www.geo-airbusds.com/). We improved the classification among land cover types by using the MELCD as a guide to extract all pixels from the image that were not classified as water and wetlands and then conducted an isocluster unsupervised classification on the extracted pixels in ArcGIS 10.0. We developed training sets for land cover classes grouped with *blueberries* in the unsupervised classification, using the MELCD dataset and aerial imagery as guides for developing training sets distinguishing among roads and gravel pits, conifers, and wild blueberry fields (Bing Maps 2010; https://www.bing.com/maps/). This maximum likelihood supervised classification created additional *blueberries* pixels to add to the MELCD *blueberries* class. The final land cover dataset included 42 classes

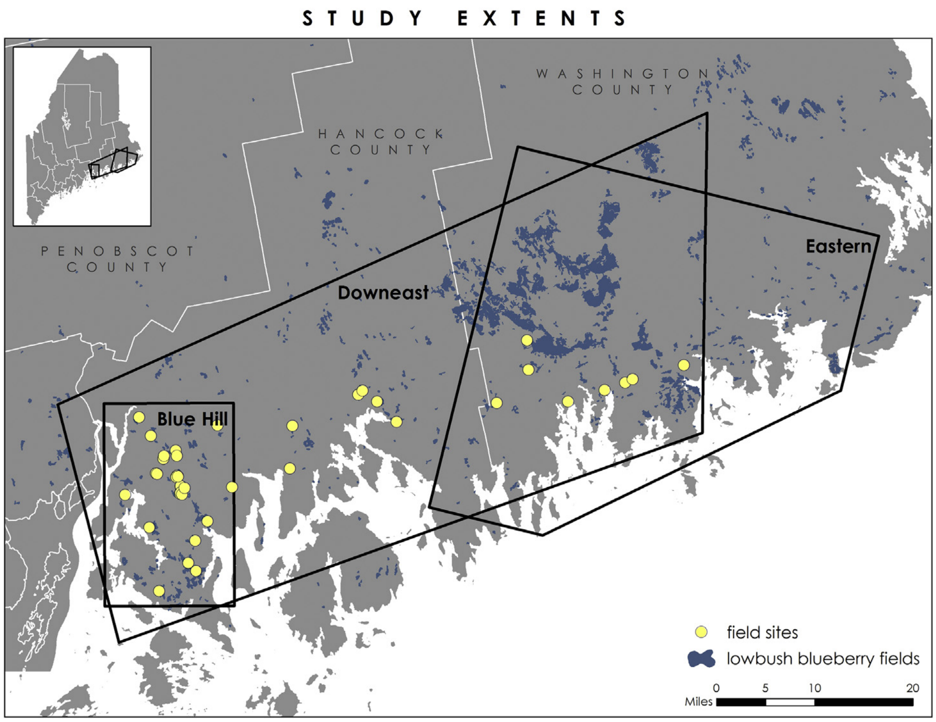

Fig. 1. Modeled extents and wild lowbush blueberry field sites used for validation of the InVEST model, Maine, USA.

reclassified into 8 land cover types: *deciduous/mixed forest edge*, *developed/other*, *coniferous forest*, *deciduous/mixed forest*, *emergent/shrub–shrub wetlands*, *other wetlands/water*, *agriculture/field* and *blueberries*.We resampled the 5 m resolution dataset to 10 m to decrease InVEST model run time. This land cover dataset (SPOT-enhanced) was used to evaluate the model predicted bee abundance in the *Eastern* extent (Fig. 1).

We characterized landscape pattern in the three modeled extents (Fig. 1) with metrics calculated with Fragstats 4.2 (McGarigal et al., 2012). For each land cover class we calculated the proportion of the extent in that class, patch density (number per 100 ha (ha)), mean patch area (ha), and a measure of spatial configuration (i.e., interspersion/juxtaposition index, IJI). We also calculated a landscape scale mean patch area (ha) and IJI for each modeled extent.

2.2.2. Model parameterization

2.2.2.1. Bee species life history and foraging distance. We modeled 14 of the most common native bee species (Table 1) in four families in the wild blueberry solitary bee community (Bushmann and Drummond, 2015). We assigned life history parameters (i.e., nesting preferences, flight seasonality) based on expert opinion and literature references (Michener, 1966; Osgood, 1972; Cane, 1992; Michener, 2000; Asher and Pickering, 2013, Table 1).

We estimated foraging distances of locally captured bees (Bushmann and Drummond, 2015) from inter-tegular (IT) width (i.e., distance between the wing bases in mm) measured with a Dino-Lite® mobile digital microscope and analyzed images in Dino-Capture 2.0 (AnMo Electronics Corporation, Hsinchu, Taiwan). We recorded five measurements per specimen and measured 10 specimens per species, except for *Osmia atriventris*, with only eight specimens available. We averaged the measured IT widths by species ($n = 50$; $n = 40$ for *O. atriventris*) and estimated maximum and typical foraging ranges (m) from the measured IT width with regression (Greenleaf et al., 2007) (Table 1, Supplemental Material).

Table 1
Life history traits of modeled common native bee species found in wild blueberry. Typical foraging distances calculated with the statistical relationship defined by Greenleaf et al. (2007) and data from Bushmann and Drummond (2015).

Species	Family	Nest substrate	Typical foraging distance (m)	Flight season
Andrena carlini	*Andrenidae*	ground	598	Mar–Aug
Andrena carolina	*Andrenidae*	ground	246	Apr–Jul
Andrena vicina	*Andrenidae*	ground	569	Mar–Aug
Augochlorella aurata	*Halictidae*	ground	60	Apr–Oct
Colletes inaequalis	*Colletidae*	ground	1091	Mar–Sept
Halictus ligatus	*Halictidae*	ground	148	Mar–Nov
Lasioglossum acuminatum	*Halictidae*	ground	186	Apr–Oct
Lasioglossum cressonii	*Halictidae*	cavity	63	Mar–Oct
Lasioglossum heterognathum	*Halictidae*	ground	16	Apr–Sept
Lasioglossum leucocomum	*Halictidae*	ground	31	Mar–Oct
Lasioglossum pectorale	*Halictidae*	ground	81	Mar–Nov
Lasioglossum versatum	*Halictidae*	ground	79	Mar–Oct
Osmia atriventris	*Megachilidae*	cavity	186	Apr–Jul
Osmia inspergens	*Megachilidae*	cavity	495	May–June

We parameterized the InVEST model with mean typical foraging range per species (Table 1).

2.2.2.2. Land cover parameterization by expert opinion and model calibration. We evaluated the predictive ability of the model in the *Downeast*, *Eastern*, and *Blue Hill* extents, representing land cover with the two datasets developed from modified MELCD data and informing the model parameters with expert opinion. We then calibrated the InVEST model in a subset of the focal area by assigning suitability values with four model parameterization methods: 1) assigned through expert opinion, 2) developed through sensitivity analyses, 3) developed through informed optimization; and, 4) developed through uninformed, simulated annealing optimization. We applied the InVEST model to the 14 native solitary bee species in all assessments, and we validated all models with bee data collected from 40 blueberry fields during 2010–2012 (Bushmann and Drummond, 2015).

We surveyed 16 entomologists, ecologists, and botanists familiar with Maine's landscapes for their evaluation of land cover type suitability for bee floral (foraging) and nesting habitat. Twelve experts provided responses that ranked (0 = unsuitable to 10 = most suitable) land cover class suitability for ground and cavity nesting bees, and spring, early summer and late summer forage (Supplemental Material). Although we included *Bombus* spp. in the survey, we omitted *Bombus* spp. from our model evaluation. We summarized and rescaled (1–10) survey responses by land cover type range, mode and average, omitting the *coniferous forest-clearcut* land cover type given its omission from the MELCD land cover dataset. We used the average scaled response (rescaled to 0.1–1.0 to match InVEST model parameter requirements) as the suitability ranking for the land cover or nesting substrate (Table 2). We evaluated the relationship between output from the expert-informed InVEST model and the field-collected bee abundance data with simple linear regression and percent change in the Pearson product moment correlation coefficients (r) compared to the model parameterized by expert opinion.

We evaluated the effect of uncertainty in parameter choice on model prediction calibration with a sensitivity analysis. We varied each of the 40 nesting and floral resource suitability parameters (0–1) individually by ± 0.1 in 74 model iterations. Parameters assigned a value of 1 through the expert opinion survey were not evaluated by +0.1 owing to model restrictions (Table 2).

We also conducted a validation analysis by evaluating the relationship between the InVEST model output and the field-collected bee abundance data with simple linear regression and percent change in the Pearson product moment correlation coefficients (r) compared to the model parameterized by expert opinion.

We calibrated the InVEST model informed by the sensitivity analysis by varying the number of parameters altered and the amount of change in suitability values in nine model iterations. For example, one iteration decreased suitability of *blueberries* for nesting and forage by 0.2, whereas, another run altered all parameters by ±0.2, with direction determined by the sensitivity analysis. We evaluated the relationship between the informed InVEST model output and the field-collected bee abundance data with linear regression and the Pearson product moment correlation coefficient (r).

We used simulated annealing calibration to parameterize the model with uninformed suitability values optimized to the validation dataset (Kirkpatrick et al., 1983). Simulated annealing is an optimization process that enables a function to escape local minimums and local maximums, with the goal to instead find a global optimum. The function is able to move both uphill and downhill, first with large jumps, and then with subsequent smaller jumps as the function approaches the optimum (Goffe et al., 1994). We performed this technique by embedding the InVEST model into a function and running it through the Python programming language *scip.optimize.anneal* function (Oliphant, 2007). We set initial parameter values to those assigned through the expert opinion survey, and all parameters varied simultaneously for each run. *Scip.optimize.anneal* is a minimizing function (i.e., seeks the minimum optimal value), therefore, we set the function to attempt to maximize the correlation coefficient by multiplying it by −1 to convert the value to positive. We evaluated the relationship between the InVEST model outputs for each optimized run against the field-collected bee abundance data with simple linear regression and calculated the Pearson product moment correlation coefficients (r) (R, http://www.R-project.org/).

We calculated the average proportion of land cover types in 500, 1000, 1500 and 2000 m buffers surrounding the 40 fields where bees were collected (Table 3) using Geospatial Modeling Environment (Beyer, 2012), to compare with sampled bee abundance in these fields. We compared the land cover proportion in each buffer for each of the 14 species' abundances included in the InVEST model evaluation, as well as for total bee abundance based on all species collected at each field site (6–45 species), with simple linear regression and the Pearson product–moment correlation coefficient (r).

3. Results

3.1. Landscape pattern assessment and comparison of model predictions among extents

Regardless of focal extent, *coniferous forest*, *deciduous/mixed forest*, and *wetlands/water* comprised more than half the land area. While mean patch area generally was similar among *Eastern*, *Blue Hill*, and *Downeast* extents, mean patch sizes of both the *deciduous/mixed forest* and *blueberries* classes were larger than the mean patch area in each extent (Table 4). The landscape IJI values were similar among extents and indicate land cover patches are broadly distributed across the focal landscapes.

InVEST model predictions of native bee abundance differed among modeled extents and bee species. The SPOT-enhanced land cover map on the *Eastern* extent did not improve accuracy of predicted total abundance for the 14 native bee species, however, bee

Table 2
Average (±standard deviation) scaled land cover suitability values assigned by expert opinion in Maine, USA.

Land cover	Ground nesting	Cavity nesting	Spring forage	Early summer forage	Late summer forage
Deciduous/mixed forest, edge	0.9 (0.17)	1.0 (0.19)	0.9 (0.24)	0.9 (0.24)	1.0 (0.22)
Developed/other	0.9 (0.25)	0.6 (0.30)	1.0 (0.27)	0.9 (0.26)	1.0 (0.22)
Coniferous forest	0.5 (0.23)	0.6 (0.28)	0.1 (0.24)	0.1 (0.21)	0.1 (0.29)
Deciduous forest/mixed forest	0.6 (0.21)	0.9 (0.22)	0.7 (0.21)	0.5 (0.29)	0.4 (0.18)
Emergent wetlands/scrub-shrub	0.2 (0.14)	0.4 (0.24)	0.7 (0.22)	0.6 (0.25)	0.6 (0.20)
Wetlands/water	0.1 (0)	0.1 (0.05)	0.3 (0.20)	0.2 (0.16)	0.5 (0.18)
Agriculture/field	0.7 (0.29)	0.2 (0.18)	0.9 (0.31)	0.7 (0.27)	0.9 (0.33)
Blueberries	1.0 (0.25)	0.4 (0.26)	0.4 (0.29)	1.0 (0.28)	0.5 (0.26)

Table 3
Average (±standard deviation) proportions of land cover classes within a 500, 1000, 1500 and 2000 m buffer surrounding field sites (n = 40) in Maine, USA.

Land Cover	500 m	1000 m	1500 m	2000 m
Deciduous/mixed forest, edge	0.06 (0.02)	0.06 (0.01)	0.05 (0.02)	0.05 (0.01)
Developed/other	0.04 (0.03)	0.04 (0.02)	0.04 (0.02)	0.04 (0.02)
Coniferous forest	0.29 (0.18)	0.34 (0.15)	0.35 (0.14)	0.36 (0.14)
Deciduous forest/mixed forest	0.30 (0.18)	0.28 (0.16)	0.27 (0.14)	0.26 (0.12)
Emergent wetlands/scrub-shrub	0.08 (0.07)	0.09 (0.07)	0.09 (0.05)	0.10 (0.04)
Wetlands/water	0.04 (0.08)	0.06 (0.09)	0.08 (0.10)	0.10 (0.10)
Agriculture/field	0.05 (0.04)	0.04 (0.03)	0.04 (0.03)	0.04 (0.02)
Blueberries	0.14 (0.13)	0.10 (0.09)	0.08 (0.07	0.06 (0.06)

Table 4
Pattern metrics for each land cover type and region in Maine, USA.

Land cover/metric	Eastern		Blue hill		Downeast	
	% Land	Mean patch area (ha)	% Land	Mean patch area (ha)	% Land	Mean patch area (ha)
Deciduous/Mixed Forest edge	4.0	1.5	4.3	1.2	4.3	1.3
Developed/Other	1.5	1.1	4.4	2.2	2.7	1.8
Coniferous Forest	24.5	6.6	34.4	10.0	28.7	8.8
Deciduous/Mixed Forest	24.1	11.6	21.3	6.0	26.3	10.3
Emergent/Scrub-Shrub Wetland	11.9	4.4	8.6	3.1	10.6	3.7
Wetlands/Water	27.5	5.9	20.0	5.9	21.0	5.3
Agriculture/Fields	1.3	1.0	3.3	1.6	1.9	1.3
Blueberries	5.3	11.0	3.7	5.6	4.4	10.1
mean patch area (ha)	5.3		4.6		5.2	
IJI	73.7		74.1		73.6	

abundance prediction accuracy improved when bee species were partitioned into those with estimated foraging distances <200 m (9 bee species, Pearson's $r = +0.77$; $P = 0.02$) and <100 m (6 bee species, Pearson's $r = +0.86$; $P < 0.01$) (Table 5).

In the *Downeast* extent accuracy of predicted total abundance of the combined 14 bee species (Pearson's $r = +0.32$; $P = 0.04$) and species that forage < 200 m (9 bee species, Pearson's $r = +0.36$; $P = 0.02$) was similar, however, there was a non-significant correlation of sampled bee abundances and predicted abundance of bee species that forage < 100 m (6 bee species, Pearson's $r = +0.26$; $P = 0.08$). InVEST predicted and sampled bee abundances were not significantly correlated in the *Blue Hill* extent, regardless of the number of bee species or foraging distance.

3.2. Model parameterization

Twelve of 16 experts completed the survey, with greatest agreement in the value of *wetlands/water*, and least agreement in the value of *agriculture/field*. Bee abundance predictions in the *Downeast* extent based on expert-informed parameters were significantly correlated with field-collected total bee abundances of the 14 modeled species (Pearson's $r = +0.315$; $P = 0.047$), as well as with the total bee abundance of each species (6–45 species) captured at each site (Pearson's $r = +0.343$; $P = 0.030$), however, predicted abundances were not correlated with the total bee species richness at each site (Pearson's $r = +0.277$; $P = 0.083$). The average (±SD) abundance prediction across all 14 sites was 0.45 (±0.059).

Assessment of model sensitivity to change in parameter values by ±0.1 resulted in a change in correlation coefficient values of −7.09 to +9.09% (Table 6). Decreasing the value of all suitability parameters (i.e., forage and nesting by seasons) for the *blueberry* class increased correlations of predicted and sampled bee abundance, whereas, increasing the value of the ground nesting parameter and early summer and summer floral suitability for *deciduous/mixed forest* increased correlations with bee abundance (Table 6).

Model parameterization with informed optimization altered the expert-informed parameter values by ±0.2, with direction indicated in the sensitivity analysis (Table 7). Model predictive ability ($r = +0.486$; $P = 0.002$) for the 14 native bee species was 54% better than the expert opinion parameterization model, and model predictions were significantly correlated with both total bee abundance (Pearson's $r = +0.561$; P = 0.0001) and total bee richness (Pearson's r = +0.530; P = 0.0004). The average (±SD) abundance prediction across all 14 sites was 0.301 (±0.059).

The model calibrated with uniformed or simulated annealing optimization of parameter values resulted in correlation coefficients ranging $r = -0.460$ to $+0.404$. The optimization truncated after 87 iterations owing to computer resource limitations, at which point the best performing model ($r = +0.404$; $P = 0.010$) performed 29% better than the expert-informed model. The average (±SD) abundance prediction across all 14 sites was 0.207 (±0.032).

Proportions of land cover classes in 500, 1000, 1500, and 2000 m buffers around focal fields generally were positively correlated with bee abundance of the 14 species in the focal field, with the exception of *deciduous/mixed forest* in the 1000 m buffers and *developed/other* land cover class in the 500 and 1000 m buffers (Table 8). The proportion of *deciduous/mixed forest* was positively correlated with total abundance of all bees, whereas, the

Table 5
Pearson's r correlation and P values between InVEST model-predicted and observed bee abundance for the three focal spatial extents in Maine.

Extent	Land cover	Species Modeled	*r*	*P*
Eastern	SPOT-enhanced	14 species	0.52	0.19
		14 species	0.52	0.19
	SPOT-enhanced	9 species (foraging < 200 m)	0.77	0.02
		9 species (foraging < 200 m)	0.77	0.02
		6 species (foraging < 100 m)	0.86	0.01
Blue Hill		14 species	0.32	0.12
		9 species (foraging < 200 m)	0.33	0.11
Downeast		14 species	0.32	0.04
		9 species (foraging < 200 m)	0.36	0.02
		6 species (foraging < 100 m)	0.26	0.08

Table 6
Sensitivity analysis parameterization, with cell values indicating percent change in Pearson correlation coefficient (r) for ± 0.1 change in parameter value compared to the baseline (expert opinion parameterized) model.

	Deciduous/mixed forest, edge	*Developed/other*	*Coniferous forest*	*Deciduous/ mixed forest*	*Emergent wetlands/scrub shrub*	*Wetlands/water*	*Agriculture/field*	*Blueberries*
cavity (−)	−0.46[a]	−0.92[a]	0.50[a]	−1.98[a]	0.02[a]	−0.38[a]	0.11[a]	3.34[a]
cavity (+)	–	0.90[a]	−0.51[a]	1.91[a]	−0.04[a]	−0.12[a]	−0.12[a]	−3.21
ground (−)	−1.87[a]	−3.42	1.47*	−7.09	−0.12[a]	−1.40[a]	0.60[a]	9.09[a]
ground (+)	1.80[a]	3.32[a]	−1.64[a]	6.30[a]	−0.04[a]	1.36[a]	−0.74[a]	–
spring (−)	−0.67[a]	−1.15[a]	1.24[a]	−2.98[a]	0.03[a]	−1.01[a]	0.38[a]	4.83[a]
spring (+)	0.66[a]	–	−1.34[a]	2.83[a]	−0.04[a]	1.00[a]	−0.40[a]	−4.69
early sum. (−)	−0.93[a]	−1.52[a]	1.52[a]	−5.03	−0.06[a]	−0.59[a]	0.62[a]	6.72[a]
early sum. (+)	0.90[a]	1.50[a]	−1.72[a]	4.62[a]	0.02[a]	0.58[a]	−0.66[a]	–
summer (−)	−1.08[a]	−1.81[a]	1.74[a]	−4.09	0.05[a]	−0.70[a]	0.42[a]	6.71[a]
summer (+)	–	–	−1.91[a]	3.83[a]	−0.09[a]	0.69[a]	−0.47[a]	−6.52

[a] Model run significant at <0.05.

Table 7
Parameters used in the best performing model through informed optimization. Expert assigned parameters are in parentheses.

Land cover	Ground nesting	Cavity nesting	Spring forage	Early summer forage	Late summer forage
Deciduous/mixed forest, edge	1.0 (0.9)	1.0 (1.0)	1.0 (0.9)	1.0 (0.9)	1.0 (1.0)
Developed/other	1.0 (0.9)	0.8 (0.6)	1.0 (1.0)	1.0 (0.9)	1.0 (1.0)
Coniferous forest	0.3 (0.5)	0.4 (0.6)	0.0 (0.1)	0.0 (0.1)	0.0 (0.1)
Deciduous forest/mixed forest	0.8 (0.6)	1.0 (0.9)	0.9 (0.7)	0.7 (0.5)	0.6 (0.4)
Emergent wetlands/scrub-shrub	0.2 (0.2)	0.2 (0.4)	0.5 (0.7)	0.8 (0.6)	0.4 (0.6)
Wetlands/water	0.3 (0.1)	0.3 (0.1)	0.5 (0.3)	0.4 (0.2)	0.7 (0.5)
Agriculture/field	0.5 (0.7)	0.0 (0.2)	0.7 (0.9)	0.5 (0.7)	0.7 (0.9)
Blueberries	0.8 (1.0)	0.2 (0.4)	0.2 (0.4)	0.8 (1.0)	0.3 (0.5)

Table 8
Land cover and observed bee abundance Pearson product–moment correlation coefficients (r) for 14 selected species (first cell value) and total observed bee abundance (sum of all taxa abundance; second cell value) at 500, 1000, 1500 and 2000 m (m) from the focal field.

Land cover	500 m	1000 m	1500 m	2000 m
Deciduous/mixed forest, edge	0.20; 0.25	0.27; 0.26	0.32; 0.33[a]	0.34[b]; 0.41[b]
Developed/other	0.09; 0.09	0.15; 0.09	0.40[b]; 0.35[a]	0.46[b]; 0.40[b]
Coniferous forest	−0.23; - 0.32[a]	−0.24; −0.36[a]	−0.30[a]; −0.42[b]	−0.34[a]; −0.47[b]
Deciduous/mixed forest	0.31[a]; 0.40[b]	0.27; 0.36[a]	0.32[a]; 0.42[b]	0.34[a]; 0.45[b]
Emergent wetlands/scrub-shrub	−0.01; 0.00	0.06; 0.07	−0.12; −0.12	−0.18; −0.19
Wetlands/water	0.19; 0.28	0.15; 0.27	0.18; −0.28	0.19; 0.29
Agriculture/field	−0.29; −0.32[a]	−0.30[a]; −0.36[a]	−0.31[a]; −0.37[b]	−0.27; −0.31
Blueberries	−0.18; −0.26	−0.22; −0.28	−0.27; −0.32[a]	−0.22; −0.26

[a] Significant at <0.05 and > 0.01.
[b] Significant at ≤0.01.

proportion of *coniferous forest* was negatively correlated with total bee abundance (Table 8). Both relationships were strongest at the 2000 m scale.

4. Discussion

4.1. Model prediction sensitivity to landscape composition and pattern and bee diversity

The InVEST model has been applied in many landscapes to estimate native bee abundances (Lonsdorf et al., 2009, 2011; Kennedy et al., 2013; Polce et al., 2013; Zulian et al., 2013) by combining information about landscape composition in a land cover map interpreted from remotely sensed data, a list of native bee species likely found in the landscape, bee movement distance estimated from bee size, and expert-derived values of land cover for providing bee forage and nesting habitats (Sharp et al., 2015). Additionally, there is inherent uncertainty in sampling and observation data, which often are used for validation of the model. Uncertainty in any of these components potentially affects both reliability and accuracy of InVEST model bee abundance predictions across the landscape.

We expected improved model performance with increased source data resolution (e.g., 5 m SPOT imagery in the *Eastern* extent) and spectral discrimination of the focal crop (blueberry), however, the model's explanatory power did not improve with these enhancements. We removed isolated pixels and changed the land cover map accuracy by resampling to 10 m pixels. This change in resolution may have compromised model prediction accuracy. Land cover represented in 10 m cells may be too coarse to accurately capture foraging behavior of bee species that meet their foraging and nesting requirements within the area represented by 3–4, 10 m pixels. Mean patch area in our study extents was 5.6 ha (*Blue Hill*), 10.1 ha (*Downeast*), and 11.0 ha (*Eastern*), however, even the smallest patch size may exceed the area to which bees in this system respond (e.g., those foraging within 3–4, 10 m pixels). Land cover resolution was implicated in poor model prediction accuracy of InVEST in New Jersey, where the 30 m pixel resolution land cover layer did not adequately capture the landscape heterogeneity where the bees foraged and nested (Lonsdorf et al., 2009, 2011). Our focal landscapes also differed in composition, with more extensive conifers in the *Downeast*. Conifers do not provide good bee nesting and foraging habitat (Droege, 2012; Bushmann and Drummond, 2015), and the reduced bee abundance and diversity in this extent may reflect the poor habitat quality of this cover type.

The InVEST model prediction accuracy was sensitive to changes in the suitability ranking of *deciduous/mixed forest* and *blueberries* land cover classes. *Deciduous/mixed forest* is a dominant land cover type surrounding blueberry fields, and proportions of the landscape in *conifer* and *deciduous/mixed forest* classes in buffers around the focal fields were more variable than other land cover classes. Model sensitivity to this class reflects the abundance of the land cover type. Sensitivity to the *blueberries* parameter can be attributed to the patchiness and local dominance (around focal fields) of this land cover class. The model also was sensitive to altering parameters for ground nesting bees, which accounted for the majority (11 of 14) of the modeled native bee species. This sensitivity emphasizes the need for bee species and land cover-specific nesting (and foraging) habitat information for increasing model prediction accuracy, especially for larger bees that encounter a variety of land cover as they venture farther into the landscape surrounding focal fields. Wild blueberry is managed in a biennial production cycle, in which the fruiting year provides more floral resources than are available in the non-fruiting, vegetative growth year (Yarborough, 2009). We did not vary our land cover map to capture this production cycle nor did we update the land cover data for each of the three years during which the bee abundance data were collected, although the annual variation in land cover during this period and over the modeled extent was minimal. Additional evaluation of effects of landscape composition, extent, data resolution, and year-to-year variation in land cover composition on InVEST model behavior would enhance our understanding about importance of these factors when applying the model in the Maine wild blueberry crop landscape.

Model prediction strength and reliability were affected by native bee foraging distance. Model prediction reliability was greatest for short-distance (<100 m) foragers. Smaller bees (i.e., those that forage < 100 m from the nesting location) are more strongly influenced by local, field-scale resources (Benjamin et al., 2014). The predominant land cover class within 100 m of our focal fields was *blueberries*, and we expected good model performance in this class owing to proximity to the field sites as well as because it was our focal crop. We also would expect increased diversity of bee species in the focal field as more fields are sampled, capturing larger bees that forage over longer distances where they encounter a greater variety of habitats among fields. Fields surrounded by greater diversity of land cover classes also would host a greater diversity of bees within the focal field, potentially increasing model prediction error. Bee abundance predictions across the entire *Downeast* extent varied little with increase in number of species modeled, reflecting the large number of fields across the region for which samples were composited.

4.2. Model sensitivity to parameterization approach

Expert opinion surveys often are used to parameterize models developed to facilitate conservation efforts (Compton et al., 2007; Lonsdorf et al., 2009; Spear et al., 2010; Kennedy et al., 2013) in two approaches: responses first are recorded independently and then combined, or the survey participants work together to arrive at a consensus (Martin et al., 2012). Our expert opinion survey did not allow for experts to reach consensus in land cover suitability assessments for nesting and foraging habitat, which may have increased variation in the parameter valuations. As an alternative to expert consensus, we parameterized the InVEST model with rescaled average response values (Martin et al., 2012) that relativized and generalized the values and thus may have increased parameter error. Between-expert uncertainty rarely is explored (Johnson and Gillingham, 2004), however, it may increase model prediction error. Independent expert parameter valuation provides an opportunity to examine effects of parameter uncertainty that can reduce bias in decision-making (Czembor et al., 2011). We selected experts familiar with Maine's landscape and native bees, however, they may not have accurately extrapolated their location-specific knowledge, resulting in poorly constructed predictive models (Murray et al., 2009). In addition to diversity in expert experience, variation in the responses could reflect true variation in the landscape, as many of the modeled land cover types provide naturally patchy floral and nesting resources (Cane, 2001). Improvement of the InVEST model performance in Maine may be gained with robust parameterization based on empirical data for bee abundance and diversity collected in a variety of land cover types in place of expert evaluation, as well as integrating an opportunity for expert consensus building for valuation of land cover for forage and nesting (Kennedy et al., 2013).

Expert-informed parameterization is typical for models used in conservation planning, and we used this approach as the baseline for comparison of the InVEST model pollinator abundance prediction in wild blueberries. The informed and uninformed optimized models performed better than the expert-informed model, however, this does not invalidate the expert informed model. The informed, optimized model used expert-derived parameter values optimized based on sensitivity analysis results; this model performed better than both the expert-opinion and the uninformed, optimized models. Parameter values assigned in the uninformed optimized model were very different from and less variable than those values assigned through expert opinion. Although methods used to obtain expert opinion and synthesis of the results can affect the soundness of models parameterized with those results (Charney, 2012), optimized models potentially over-fit the data. The same dataset is used to calibrate and validate the model, and both the signal and the noise are fitted within the model. A more rigorous approach would include validation with an additional dataset as well as out-of-area model evaluation.

There are few examples of comparisons between expert versus data driven model parameterization. Expert assignment of model parameter values has been found unreliable for complex models requiring valuation of numerous parameters (Charney, 2012). Our application of the InVEST model required suitability rankings for eight land cover classes, across three different seasons, and for two nesting guilds of bees. Application of the InVEST model in the Costa Rica coffee agroecosystem used expert-assigned suitably rankings for six land cover classes and one floral season and resulted in an $r^2 = 0.62$ (Lonsdorf et al., 2009). Simplification of the model was appropriate for coffee, however, wild blueberries are a complex crop system inadequately represented by a simplified model. Improved performance of the InVEST blueberry model instead may be gained by greater resolution land cover data and land cover class-specific forage and nesting habitat quality data for native bees.

4.3. Bee abundance predicted from landscape composition vs. the InVEST model

Proportions of both *deciduous/mixed forest* and *coniferous forest* in the 2000 m surrounding blueberry fields were significantly and orthogonally correlated with the number of bees found within Maine's wild blueberry fields. This simple model out-performed the InVEST model in the field perimeter. The proportion of deciduous and coniferous forest (combined) surrounding Wisconsin apple orchards was similarly correlated with bee abundance, while the proportion of developed land surrounding a field was negatively correlated with bee abundance (Watson et al., 2011). Although the proportional model is useful for evaluating near-farm pollinator habitat and bee abundance, the InVEST model provides a tool for conservation planning and bee abundance assessment beyond the field margin into the surrounding landscape. Reliability of InVEST model predictions will be increased with information about forage and nesting habitat quality data collected in the landscape outside the crop field and greater resolution land cover data, as well as validation of model predictions with independent datasets.

5. Conclusions

Spatial models can predict species distributions and abundances based on habitat conditions available across landscapes (Austin, 2002; Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Lonsdorf et al., 2011). Relationships between native bees and land cover have been documented worldwide, and landscape-scale predictive modeling, such as the InVEST Crop Pollination model, uses these relationships to predict bee abundance across the landscape (e.g., Kremen et al., 2004; Ricketts et al., 2008; Garibaldi et al., 2011). There are limitations to applying any tool, however, including those that inform conservation efforts, and understanding the limitations is critical to ensuring appropriate use of the tool (Johnson and Gillingham, 2004). The InVEST model prediction of native bees in Maine's wild blueberry crop landscape is sensitive to parameterization techniques and relationships among bee abundances, species assemblages, land cover type, and landscape pattern. Are the expert opinion derived parameters in error, or do parameters derived from fitting the model reflect the true nature of the relationship between the habitat and bee diversity and abundance? Our study does not evaluate these questions, however, additional information about how native bees use nesting and foraging resources in this landscape will enhance conservation of their populations and the pollination services they provide in this crop system.

Software and data availability

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.envsoft.2016.01.003.

References

Asher, J.S., Pickering, J., 2013. Discover Life Bee Species Guide and World Checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species.

Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecol. Model. 157 (2–3), 101–118.

Benjamin, F.E., Reilly, J.R., Winfree, R., 2014. Pollinator body size mediates the scale at which land use drives crop pollination services. J. Appl. Ecol. 51 (1), 1–10.

Beyer, H.L., 2012. Geospatial modelling environment (Version 0.6.0.0). (software). URL. http://www.spatialecology.com/gme.

Brosi, B., Armsworth, P., Daily, G., 2008. Optimal design of agricultural landscapes for pollination services. Conserv. Lett. 1, 26–27.

Bushmann, S., Drummond, F., 2015. Abundance and diversity of wild bees (Hymenoptera:Apoidea) found in lowbush blueberry growing regions of downeast Maine. Environ. Entomol. 44 (3), 1–15.

Cane, J.H., 1992. Soils of ground nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. J. Kans. Entomological Soc. 64, 406–413.

Cane, J.H., 2001. Habitat fragmentation and native bees: a premature verdict? Ecol. Soc. 5 (1), 3 [online] URL. http://www.consecol.org/vol5/iss1/art3/.

Cane, J.H., Payne, J.A., 1988. Foraging ecology of the bee Habropoda laboriosa (Hymenoptera: Anthophoridae), an oligolege of blueberries (Ericaceae: Vaccinium) in the southeastern USA. Ann. Entomological Soc. Am. 81, 419–427.

Charney, N.D., 2012. Evaluating expert opinion and spatial scale in an amphibian model. Ecol. Model. 242, 37–45.

Compton, B.W., McGarigal, K., Cushman, S.A., Gamble, L.R., 2007. A resistant-kernal model of connectivity for amphibians that breed in vernal pools. Conserv. Biol. 21 (3), 788–799.

Czembor, C.A., Morris, W.K., Wintle, B.A., Vesk, P.A., 2011. Quantifying variance components in ecological models based on expert opinion. J. Appl. Ecol. 48, 736–745.

Droege, S., 2012. The bees (Apoidea). In: Chandler, D.S., Manski, D., Donahue, C., Alyokhin, A. (Eds.), Biodiversity of the Schoodic Peninsula. 2012, pp. 36–42. Maine Agricultural and Forest Experiment Station Tech. Bull. 206, 210 pp.

Drummond, F.A., 2002. Honeybees and Lowbush Blueberry Pollination # 2079. University of Maine Cooperative Extension, Orono, Maine, USA.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual review of Ecology. Evol. Syst. 40, 677–697.

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhoffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyorgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol. Lett. 14, 1062–1072.

Goffe, W.L., Ferrier, G.D., Rogers, J., 1994. Global optimization of statistical functions with simulated annealing. J. Econ. 60, 65–99.

Greenleaf, S., Williams, N., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. Oecologia 153, 589–596.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009.

Hanes, S.P., Collum, K.K., Hoshide, A., Asare, E., 2013. “Grower perceptions of native pollinators and pollination strategies in Maine's lowbush blueberry industry”. Renew. Agric. Food Syst. 28 (4), 1–8.

Johnson, C.J., Gillingham, M.P., 2004. Mapping uncertainty: sensitivity of wildlife habitat ratings to expert opinion. J. Appl. Ecol. 41, 1032–1041.

Jones, M.S., Vanhanen, H., Peltola, R., Drummond, F.A., 2014. A global review of Arthropod-mediated ecosystem-services in *vaccinium* Berry agroecosystems. Terr. Arthropod Rev. 7, 41–78.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N.P., Cunningham, S.A., Danforth, B.N., Dudenhoffer, J., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S., Jha, S., Klein, A.M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlof, M., Saez, A., Steffan-Dewenter, I., Taki, H., Felipe Viana, B., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16 (5), 584–599.

Kirkpatrick, S., Gelatt, C.D., Vecchi, M.P., 1983. Optimization by simulated annealing. Science 220 (4598), 671–680.

Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Natl. Acad. Sci. 99 (26), 16812–16816.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P., Thorp, R.W., 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. Ecol. Lett. 7, 1109–1119.

Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol. Lett. 10, 299–314.

Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., Greenleaf, S., 2009.

Modeling pollination services across agricultural landscapes. Ann. Bot. 103, 1589–1600.
Lonsdorf, E., Ricketts, T., Kremen, C., Winfree, R., Greenleaf, S., Williams, N., 2011. Crop pollination services. In: Kareiva, P.H., Tallis, H., Ricketts, T.H., Daily, G.C., Polasky, S. (Eds.), Natural Capital: Theory and Practice of Mapping Ecosystem Services. Oxford University Press - USA, New York, USA, pp. 168–187.
Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., Mcbride, M., Mengersen, K., 2012. Eliciting expert knowledge in conservation science. Conserv. Biol. 26 (1), 29–38.
McGarigal, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. Computer Software Program Produced by the Authors at the University of Massachusetts, Amherst. Available at: the following web site. http://www.umass.edu/landeco/research/fragstats/fragstats.html.
Michener, C.D., 1966. The bionomics of a primitively social bee, *Lasioglossum Versatum*. J. Kans. Entomological Soc. 3, 193–217.
Michener, C.D., 2000. The Bees of the World. The John Hopkins University Press, Baltimore, Maryland, USA.
Murray, J.V., Goldizen, A.W., 'Leary, R.A.O., McAlpine, C.A., Possignham, H.P., Choy, S.L., 2009. How useful is expert opinion in predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. J. Appl. Ecol. 46 (4), 842–851.
Oliphant, T.E., 2007. Python for scientific computing. Comput. Sci. Eng. 9 (90), 27–29.
Osgood, E.A., 1972. Soil Characteristics of Nesting Sites of Solitary Bees Associated with the Low-bush Blueberry in Maine. The Life Sciences and Agriculture Experiment Station. University of Maine at Orono. Technical Bulletin 59.
Patricio-Roberto, G.B., Campos, M.J.O., 2014. Aspects of landscape and pollinators - what is important to bee conservation? Diversity 6, 158–175.
Pettis, J.S., Delaplane, K.S., 2010. Coordinated responses to honey bee decline in the USA. Apidologie 41 (3), 256–263.
Polce, C., Termansen, M., Aguirre-Gutierrez, J., Boatman, N.D., E Budge, G., Crowe, A., Garratt, M.P., Pietravalle, S., Potts, S.G., Ramirez, J.A., Somerwill, K.E., Biesmeijer, J.C., 2013. Species distribution models for crop pollination: a modellling framework applied to Great Britain. PLOS One 8 (10), 1–12.
Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25 (6), 245–353.
Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11, 499–515.
Sharp, R., Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Chaplin-Kramer, R., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D., Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Arkema, K., Lonsdorf, E., Kennedy, C., Verutes, G., Kim, C.K., Guannel, G., Papenfus, M., Toft, J., Marsik, M., Bernhardt, J., Griffin, R., Glowinski, K., Chaumont, N., Perelman, A., Lacayo, M., Mandle, L., Hamel, P., Vogl, A., 2015. InVEST 2.5.4 User's Guide. The Natural Capital Project, Stanford. University of Minnesota, The Nature Conservancy, and World Wildlife Fund.
Spear, S.F., Balkenhol, N., Fortin, M., Mcrae, B.H., Scribner, K., 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Mol. Ecol. 19, 3576–3591.
Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., Tscharntke, T., 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83 (5), 1421–1432.
Taki, H., Kevan, P., Ascher, J., 2007. Landscape effects of forest loss in a pollination system. Landsc. Ecol. 22, 1575–1587.
Watson, J.C., Wolf, A.T., Asher, J.S., 2011. Forested landscapes promote richness and abundance in native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin Apple Orchards. Environ. Entomol. 40 (3), 621–632.
Yarborough, D.E., 2009. Wild Blueberry Culture in Maine. Extension Bulletin # 2088. University of Maine Cooperative Extension, Orono, Maine, USA.
Zulian, G., Maes, J., Paracchini, M.L., 2013. Linking landcover data and crop yields for mapping and assessment of pollination services in Europe. Land 2, 472–492.