

**As the Bee Flies: Predicting Native Bee Diversity in Brentwood, CA
Using Landcover and Bee Life History**

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ABSTRACT

In the face of honeybee decline and rising colony costs, attention has turned to native bee health and their role as pollinators in the agricultural industry. I compiled information on landcover suitability and bee life history for use in the InVEST Crop Pollination Model. I used the model to predict bee abundance in Brentwood, California and validated the prediction using field-collected abundance data. I then conducted a sensitivity analysis to evaluate the impact of uncertainty on the model. The model predicted bee abundance with high significance, and the sensitivity analysis highlighted two landcover types that were highly sensitive to changes in model parameters: *grassland/herbaceous* and *cultivated crops*. These are the two most dominant land classes in the landscape, and contain important resources for native bee health.

KEYWORDS

native bee conservation, geospatial modeling, landuse change, life history, flight distance

INTRODUCTION

Native bees provide critical ecosystem services for California's agricultural industry. 1600 of the nation's 4000 native bee species occur in California, working in tandem with managed, non-native honeybees (*Apis mellifera*) to pollinate California's plants and crops (Frankie et al. 2009). In the last ten years, public and scientific attention has been brought to the drastic global decline in honeybee populations, even prompting a presidential memorandum aimed at evaluating and promoting pollinator health in the country (Obama 2014). The increased mortality rate in honeybees is attributed to factors such as land use change, the heavy use of neonicotinoids in agricultural and residential pesticides, and colony infestations by the Varroa mite, a honeybee pest (Frankie et al. 2009). The impacts of these factors on native pollinators is less understood (Hladik et al. 2016). Managed colonies are also becoming more expensive to purchase and maintain, with the detrimental effects of chemicals and biological pests combined with higher peak season demands resulting in per colony prices jumping almost three-fold between 2004 and 2006 (Sumner and Boriss 2006).

Native pollinators have always been important players in agricultural ecosystems, and studies are increasingly focused on quantifying and understanding their role in the industry (Foy 2011). For example, a more diverse and abundant native bee community increased crop yield in New York State's commercial apple orchards (Blitzer et al. 2016). Increasing floral diversity was more effective in supporting higher bee richness than increasing the quantity of semi-natural habitat near intensively managed agro-systems in western France (Rollin et al. 2019). Alternately tilled vineyards in Eastern Austria showed increased wild bee diversity and abundance than non-tilled vineyards (Kratschmer et al. 2018). Such studies focus on identifying and studying the key drivers of native bee diversity, thereby evaluating the robustness of the free and increasingly essential ecosystem service native pollinators provide in the face of declining honeybee populations.

Land use change is one of the most influential factors in native bee population health. Unlike honeybees, most natives are solitary and are either ground or wood dwelling, and thrive the most in natural habitats with minimal anthropogenic disturbance (Kremen et al. 2002). Urbanization, characterized by the conversion of land use from riparian and grassland to impervious surfaces, poses the most immediate threat to native bee populations as the habitat ideal

for nesting and foraging decreases and becomes increasingly disconnected. Although urban landscapes exhibit heterogeneity, they are generally associated with lower ecosystem complexity as a result of the reduction in natural vegetation cover (Zanette 2005). The expansion in paved areas that is characteristic of an urbanizing landscape also negatively impacts nesting densities of bumblebees in the Bay Area (Jha and Kremen 2013). In addition to land use change, the increased use of pesticides in both agricultural and urban settings negatively impact wild bee health, especially when bees are exposed to a cocktail of pesticide compounds over a long time period (Botías 2017).

However, there is still some uncertainty regarding the survivability of healthy bee assemblages in urban environments. Although urban environments have significantly higher percentages of impervious surfaces such as roads and buildings, the presence of residential gardens, green open spaces, and planted median strips provide essential floral and nesting resources (Frankie et al. 2009). Using an urbanization gradient in Eastern France, species abundance was negatively correlated with proportion of impervious surface, but species richness peaked at 50% impervious surface landscape composition (Fortel et al. 2014). The diversity of floral resources found in managed gardens as compared to unmanaged grassland or riparian areas likely has a positive impact on bee diversity in urban environments. Additionally, human-made nesting structures in urban parks and gardens can help support cavity-nesting native bee populations (Fortel 2016). In an agricultural area that is in close proximity to an urbanized landscape, the heterogeneity and diversity of floral resources along with available nesting habitat in the urbanized landscape might be sufficient to support native bee assemblages. Understanding how native bee resources vary across the intersection between urban and agriculture landscapes is an important aspect of determining the role and importance of native bees in the region's agricultural sector.

This study uses the InVEST Crop Pollination Model, developed by the Natural Capital Project (Lonsdorf et al. 2009), to examine the relationship between landscape composition and relative bee abundance in Brentwood, California (Frankie et al. 2018). The model predicts relative pollinator abundance by using life history tables, and maps of nesting and floral suitability across the landscape. By comparing the predicted values to field collected abundance measurements, I hope to understand how Brentwood's landscape influences the local bee assemblage, and to test the accuracy of the model parametrization. As such, there are two primary questions I attempt to

address in this study: (1) How well does the InVEST Model predict relative pollinator abundance across the landscape, and in which direction? And (2) how sensitive is the model to changes in the different landcover classes?

METHODS

Study site

The City of Brentwood (37.9319° N, 121.6958° W) lies 50 miles East of San Francisco (Figure 1) and has a warm, temperate summers and cold, wet winters suitable for crops such as corn, cherries, and stone fruit (City of Brentwood 2018). The city features a rapidly changing and heterogeneous landscape. Although the extent of its urban center has not grown significantly, the proportion of impervious surface within city limits has increased as more land is converted to housing and commercial space for the rapidly increasing population (US Census Bureau 2017). Still, the presence of residential gardens, riparian areas beside Marsh Creek, and managed pollinator gardens may provide beneficial habitat for bees in both the urban center and agricultural areas of Brentwood (Frankie et al. 2009).

The study population was native California bees collected across 8 farm sites in 2011 by members of the Urban Bee Lab at UC Berkeley, led by Dr. Gordon Frankie. As the baseline extent, I applied an 8000 m buffer on a point derived using the “Mean Median Spatial Statistics” tool in ArcGIS, with the goal that all sample points be at least 2000 m from the extent’s edge, and absence of gaps in the included extent (ArcGIS ® version 10.5.1; Environmental Systems Research Institute, Redlands, CA, United States). For the simple proportional landscape analysis, I also created 500, 1000, 1500, and 2000 m buffers from the collection points.

Data collection

Landcover dataset and parametrization

The National Landcover Dataset (NLCD 2011) provides nationwide landcover data at 30-meter resolution, and a 16-class legend based on a modified Anderson Level II classification

system (MRLC 2011). The most recent NLCD available from Multi-Resolution Land Characteristics Consortium was for 2011. There were 14 landcover classes in total after clipping to the baseline extent (Figure 4). I then used expert-opinion derived suitability indices from Koh et al. (2016) to rank floral and nesting resources for each class (Table 1).

Bee collection and parametrization

The closest year to 2011 for which complete field bee abundance data is available is 2012. I make the assumption that landcover has not changed significantly from the year it was collected, to the year the bee samples were collected. The sampling season occurred in the spring, coinciding with the period when bee abundance is highest. Approximately every month, members of the Urban Bee Lab conducted field sampling periods for approximately four hours. The lab utilized two primary collection methods: pan-trapping and net-sampling. For the first method, fifteen 29.6 mm diameter pans alternating between fluorescent yellow, plain white, and fluorescent blue were distributed approximately 8 m apart in sunny locations along a mostly linear transect of each of the 8 farms for each sampling period (Hall 2016). Bees and other flying insects are attracted to the pan trap colors and trapped in soapy water in the pans. Pan trap samples were collected at the end of the sampling period and subsequently processed in the lab (Frankie et al. 2018).

The second collection method was an active sampling approach that occurred simultaneously with the pan-trapping method, wherein two to four researchers swept nets to collect samples during the sampling period (Frankie et al. 2018). Net sampling potentially introduces collector bias as it is based on each researcher's ability to spot a bee and successfully trap it in the net. However, it is useful when attempting to link pollinators to specific flower visits because the researcher records information regarding what flower the bee was visiting at the time of collection (Popic et al. 2013). The samples were then identified and databased at the species level, and species abundance and richness were calculated by the lab (Frankie et al. 2018).

In addition to a spatial landcover dataset with indices of habitat suitability for each landcover type, the model requires information regarding interspecific variations in nesting behavior, optimal seasonal activity, and foraging distance, informing how different species access the resources that vary spatially and temporally. These values and parameters are informed by published values or expert opinion, with the latter being more common in related studies (Chapin

2014). To limit the number of focal species to model with InVEST, I selected all species that appeared in at least two of the three lists of recorded bee species by crop, for a total of 10 species in 4 families (Frankie et al. 2018). I then conducted a literature review and assigned each species life history parameters of nesting preference as either ground- or cavity-nesting, and flight seasonality as a range of months at which activity is highest (Table 2).

Body size can be used as an estimator for a particular species' foraging distance (Greenleaf et al. 2007). To estimate foraging distance for each focal species, I used published values of mean intertegular width, the distance between wing bases, for each of the 10 focal bee species (Table 3), and used the regression formulae developed by Greenleaf et al. (2007) to estimate the foraging ranges to be used in the model parametrization (Table 2).

Data analysis

I ran the model using these inputs on the 8000 m baseline extent and at the same 30 m resolution as the landcover dataset. To evaluate the relationship between the InVEST model output of predicted bee abundance and the field-collected bee abundance, I calculated the Pearson product moment correlation coefficients between the two (R 2.14.1, R Development Core Team 2011).

To test how sensitive the model was to changes in the suitability indices, I conducted a sensitivity analysis and compared the resulting correlation coefficients to that of the baseline (Chapin 2014). To determine how uncertainty in the suitability indices influenced the output, I individually changed each of the nesting and floral suitability indices by ± 0.1 ($\pm 10\%$). If the resulting value was smaller than 0 or larger than 1, I used those numbers respectively as the lower and upper bounds. I compared the output of each of these iterations to the field-collected abundance data using percent change in the Pearson product moment correlation coefficients (r), as compared to the baseline model.

RESULTS

Landcover parametrization

Using expert-derived values (Koh et al. 2016), I assigned suitability indices to each of the 14 landcover classifications. The indices range from 0 to 1, with values closer to 1 indicating high suitability, and values closer to 0 indicating low suitability (Table 1). As there was no singular value assigned to the *cultivated crops* class in Koh et al., I used the calculated average of values assigned to the following crop types instead: corns, beans, berries, strawberries, citrus, cucurbits, melons, orchard, solanums, vegetables, and olives. I only included crops that are commonly grown in the Brentwood study sites from which bee samples were collected (Frankie et al. 2018), and that rely “heavily” or “essentially” on flower visitors for production (Guerrero et al. 2017). In general, landcover types with high amounts of water, impervious surfaces, or agriculture were ranked poorly for nesting and floral resources, while shrubland, grassland, and forests were ranked more favorably. Across all landcover types, the *ground* type generally had higher nesting suitability, while the *spring* and *summer* seasons generally had higher floral resource suitability.

Bee life history and foraging distance

I selected a total of 10 focal species, belonging to 4 families that exhibit a variety of life history strategies (Table 2) (Frankie et al. 2018). 3 of the 4 families (*Andrenidae*, *Apidae*, and *Halictidae*) generally exhibit ground-nesting behavior, with the remaining family (*Colletidae*) exhibiting cavity-nesting behavior. In the case that a genera has been recorded exhibiting both behaviors (e.g. *Bombus*), I assigned it as such. Flight seasonality begins as early as February, and ends as late as October. For foraging distance, the Greenleaf et al. (2007) regression formula (Figure 2) evidently overestimated foraging distances for the largest bee (*Xylocopa varipuncta*), and I chose to use published values of foraging distance for this genera (Zurbuchen et al. 2010) instead of the calculated value (Table 3).

Analysis

Baseline Model

The model's predictions of bee abundance were significantly correlated with field-collected abundances. I calculated a Pearson's r of 0.366, with a significance value of 4.779×10^{-9} (Figure 3).

Sensitivity Analysis

Altering the model parameters by $\pm 10\%$ resulted in a change in correlation coefficient values of -6.43% to $+7.92\%$ (Table 4). The model is most sensitive to changes in the *grassland/herbaceous* and *cultivated crops* landcover classes, with percent changes ranging from -6.43% to $+7.92\%$ and -6.29% to $+7.52\%$ respectively for those classes. Decreasing all indices resulted in an increase in correlations for the following classes: *evergreen forest*, *pasture/hay*, and *developed, medium intensity*.

DISCUSSION

My findings indicate that the InVEST Model is a useful tool to predict native bee abundance across a landscape. Given the availability of accurate and adequate input data, it is easily adapted to my study site, its unique landscape characteristics, and the specific species present. However, *grassland/herbaceous* and *cultivated crops* are most sensitive to changes in suitability parameters, and the result is susceptible to uncertainty from subjective suitability indices and the landcover map's 30 m resolution. The model's simplicity and lack of supplementary data prevents the accounting of certain complexities and nuances in bee life history and landscape suitability.

Baseline model

The model's prediction of native bee abundance in Brentwood was highly significant, making the results an insightful starting point for understanding how Brentwood's landscape influences the local bee assemblage. Similar studies conducted in study sites across the country also generally found the model to be a good predictor of abundance (Chapin 2014, Cunningham et al. 2018, Lonsdorf et al. 2009, and Davis et al. 2017). However, they also unanimously emphasize the importance of correctly calibrating the model's input parameters. While all previous studies used some version of the 30 m resolution National Landcover Database for the map input, suitability indices were informed both by literature review and by local expert opinion. Expert opinion is subjective and potentially conflicting, but it can fill in gaps in the literature for locally specific empirical data, and variation in responses can reflect true diversity in landscape suitability (Chapin 2014). Although the Koh et al. (2016) values I used for nesting and floral suitability were expert-derived, they were intended for a nation-wide analysis of native bee health, and the average indices might not reflect the needs of the specific bees found in Brentwood. However, I decided that the standardization of the landcover classes was still useful to utilize in my analysis.

Additionally, although landcover data at 30 m resolution was standard for previous studies, authors acknowledge a pixel size of 30 m is potentially too large to capture the movement of smaller bees (Lonsdorf et al. 2009). Even in my estimation of foraging distance using IT width (Table 3), *Hylaeus mesillae* and *Halictus tripartitus* have distances just under and just above 30 m, respectively. Again, because of the standardization afforded by the landcover dataset and lack of finer spatial data available at the time of sample collection, I chose to utilize the NLCD data. Another source of uncertainty is that even at finer spatial scales, landcover datasets rarely reflect additional class details such as whether a farm is organically or conventionally managed, or whether the landscape has undergone drought or flooding, unless the data is initially collected with those variables in mind (Davis et al. 2017). This detail can be important if attempting to quantify the role of pesticide use in land suitability for bees, or the availability of floral resources after a weather event.

Despite these limitations, my result of a statistically significant prediction matched the results of most similar studies. While not perfect, the output maps of predicted species richness

can identify areas in a landscape that can benefit from implemented pollinator habitat to help maintain pollinator health, and aid their travel between nesting and foraging sites.

Sensitivity analysis

By conducting a sensitivity analysis, I found the *grassland/herbaceous* and *cultivated crops* classes were most sensitive to changes in the nesting and floral resources parameters. As all the bees in my study were collected on or near a farm, I expected *cultivated crops* would exhibit the most sensitivity as the dominant land cover type surrounding the sample sites holds more weight in the model (Chapin 2014). Because a small change to a dominant landcover type has a significant effect on the output result, this emphasizes for future studies that the suitability indices for that landcover type must be assigned carefully so that the prediction is not skewed by a wrongly-weighted class. While the *grassland/herbaceous* class does not immediately surround the sample points, it is a significant portion of the study extent, and so exhibits the same sensitivity (Figure 4).

Grassland/herbaceous was ranked highest of all landcover types for ground nesting suitability. As most of the focal bee species are ground nesting, the availability and distribution of this land type is important to ensure native bees can get from their nests to the floral resources or crops for foraging and pollination. Unfortunately, this is also one of the first classes to decrease in size in an urbanizing environment, to be replaced with housing or transportation infrastructure (Kremen et al. 2002), and in Brentwood, most of the grassland lies within city limits (Figure 1). While urban areas might still have adequate resources for nesting and foraging, it is unlikely to be as suitable as grassland habitat. By showing that even a small change in the proportion and availability of grassland habitat will have a large impact on bee health, such research can help spur more comprehensive pollinator protection plans and holistic city planning.

Limitations and future directions

Beyond the limitations inherent in landcover resolution, and uncertain suitability indices, one of the main limitations with my study design is the use of field-collected data from 2012 and a landcover map from 2011. My assumption that landcover did not change from 2011 to 2012 is

probably not true. However, it is highly unlikely that any small changes would have been reflected on a 2012 landcover map because of the 30 m pixel size. Ground truthing the landcover map, or checking for any misclassifications in the map, would also improved accuracy.

Secondly, while the images of bees on online databases were of high quality (Figure 2), my foraging distance estimates would benefit from manual IT width measurements of a sample of the collected specimens from Brentwood, as there might be slight variation in species size based on the location at which specimens were collected.

As native pollinator research progresses, a long term application of this model could test if the implementation of native pollinator habitat in areas highlighted as resource-poor in an initial survey will eventually help diversify and increase the local pollinator community. By identifying a few key spaces for habitat in a city, city planners and landscape architects can have a more targeted, efficient, and cheap approach to greening their city and supporting native pollinators at the same time. The model can eventually be used as a monitoring tool to test if the pollinator community is doing as well as is expected with the new habitat.

Broader implications

Evaluating the reliability of tools such as the InVEST Model can help better inform parametrization for future studies on bee abundance and pollinator health. By understanding the scenarios under which the model performs most accurately, changes and adjustments can be made for application in other ecosystems, cities, and countries. As the predictive power of the model improves, it can be used to promote policies and initiatives aimed at protecting native pollinators in urban environments. There is also an economic benefit to protecting native bees, and the model has the capability to measure and predict the economic value of their free service. By putting a money value on their presence, big agricultural corporations might be convinced to invest in pollinator research and protection.

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APPENDIX

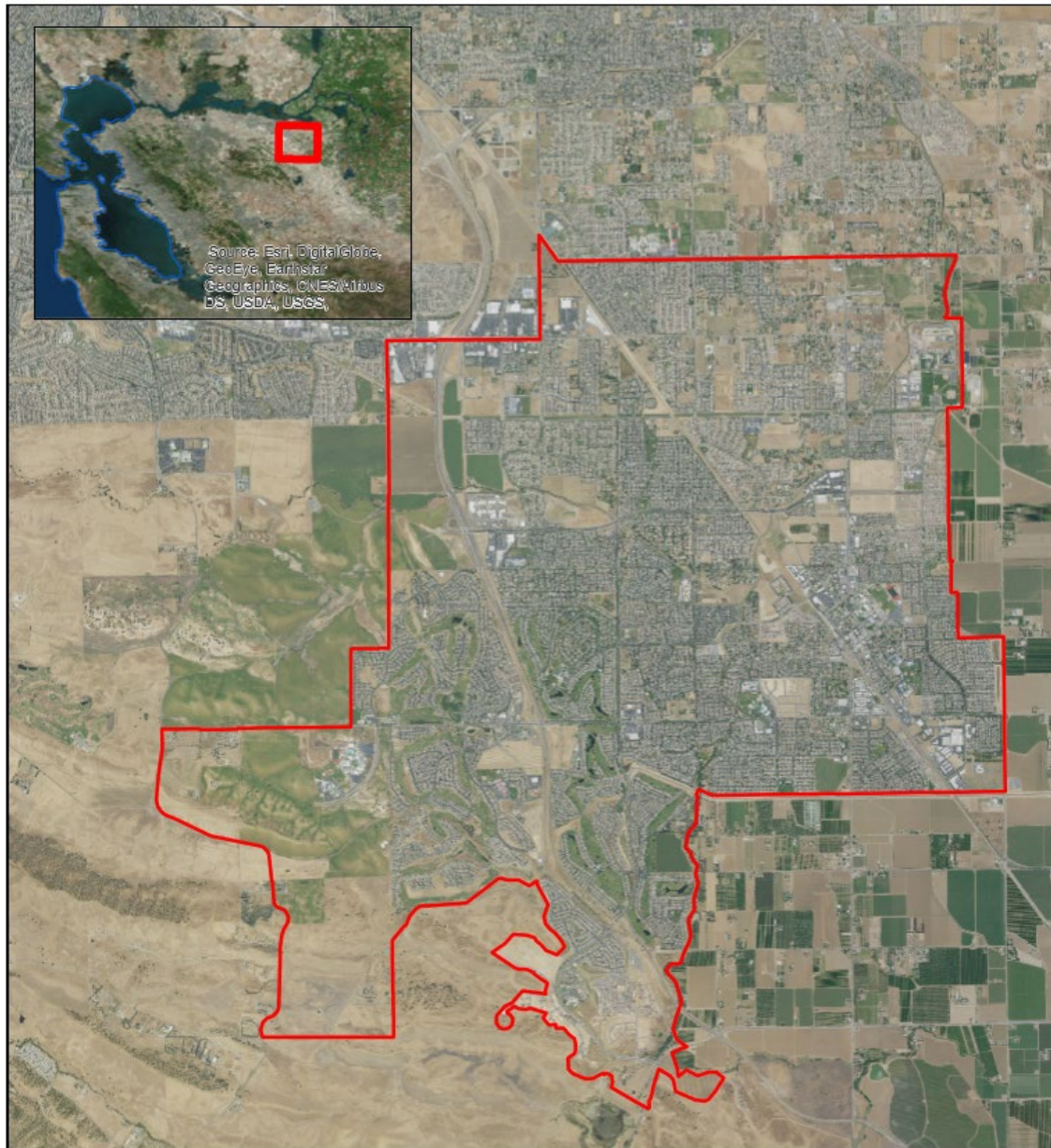


Figure 1. City of Brentwood study site. The City limit is highlighted in red.

(a) $\log(D) = -1.643 + 3.242 \log(IT)$



Figure 2. Greenleaf et al. 2017 regression formula. This variation of the equation uses the intertegular width (IT) of each focal species to calculate the mean typical homing distance (D). I used images with reference scale bars (b) to determine an IT width representative of each species (Table 3) (SCAN 2018).

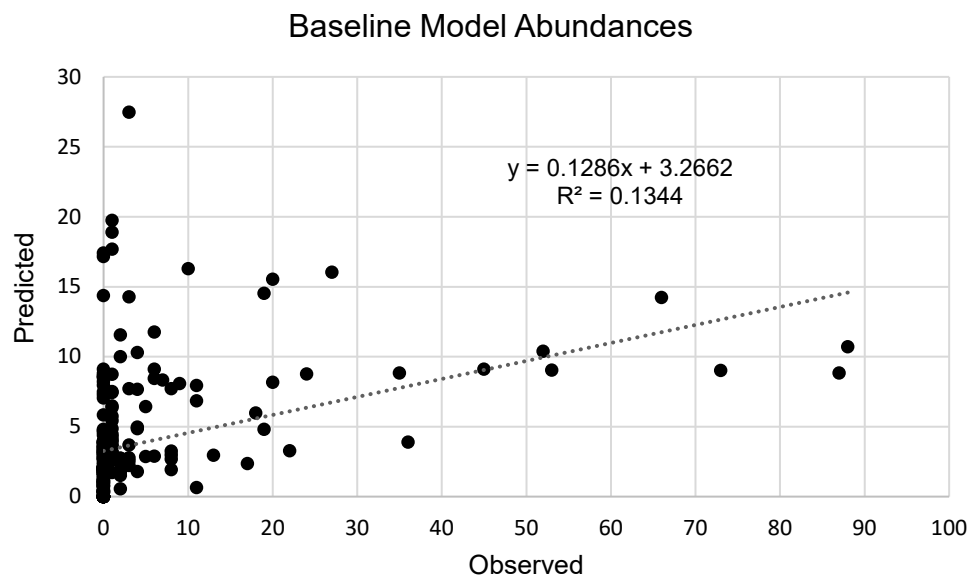


Figure 3. Baseline correlation analysis. At the 8000 m extent, there was significant correlation ($r = 0.366$, $P = 4.779 \times 10^{-9}$) between the model's prediction of bee abundance and the observed values at the 8 farm sites.

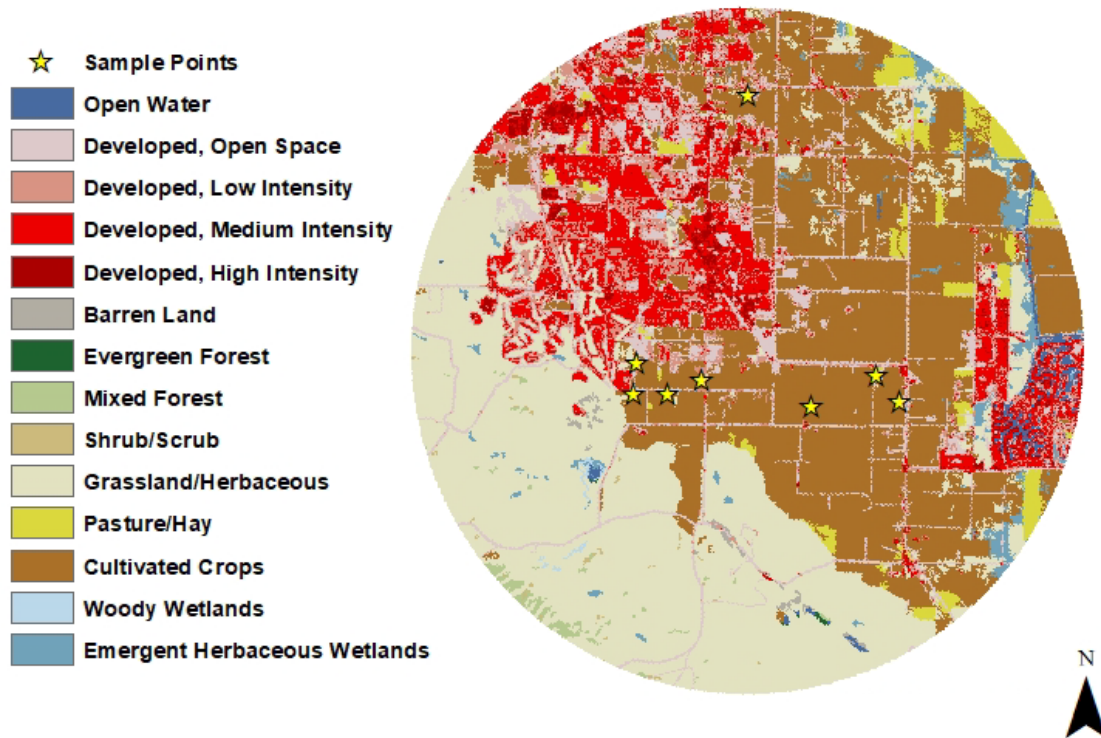


Figure 4. Landcover map. 8000 m study extent is shown. The two classes most sensitive to changes in suitability indices are *grassland/herbaceous* (most of the southeastern quarter of the extent) and *cultivated crops* (most of the northeastern half of the extent). Most sample points are on or very close to land classified as *cultivated crops*.

Table 1. Landcover classifications and assigned suitability indices. Values range from 0 to 1, with lower values representing low suitability and higher values representing high suitability.

Landcover	Ground Nesting	Cavity Nesting	Spring	Summer	Fall
Open Water	0.00	0.00	0.00	0.00	0.00
Developed, Open Space	0.36	0.24	0.46	0.55	0.46
Developed, Low Intensity	0.36	0.21	0.53	0.60	0.48
Developed, Medium Intensity	0.19	0.19	0.41	0.53	0.39
Developed, High Intensity	0.08	0.14	0.32	0.45	0.26
Barren Land	0.27	0.08	0.25	0.28	0.22
Evergreen Forest	0.44	0.51	0.43	0.44	0.36
Mixed Forest	0.66	0.68	0.58	0.46	0.40
Shrub/Scrub	0.76	0.67	0.70	0.58	0.45
Grassland/Herbaceous	0.81	0.58	0.57	0.63	0.48
Pasture/Hay	0.31	0.25	0.29	0.42	0.37
Cultivated Crops*	0.27	0.17	0.33	0.40	0.21
Woody Wetlands	0.14	0.34	0.60	0.53	0.43
Emergent Herbaceous Wetlands	0.16	0.15	0.46	0.54	0.44

Sources: Koh et al. 2016,

*Values are a calculated average of selected classes: corns, beans, berries, strawberries, citrus, cucurbits, melons, orchard, solanums, vegetables, and olives.

Table 2. Life history traits of focal bee species. Values were derived using literature-review.

Species	Nest Substrate	Flight Season	Typical homing distance (m)
<i>Andrena miserabilis</i>	ground	Feb – Jun	215
<i>Andrena sola</i>	ground	Feb – Jun	444
<i>Bombus melanopygus</i>	both	Apr – Jul	2983
<i>Bombus vosnesenskii</i>	both	Apr – Sep	2036
<i>Xylocopa varipuncta</i>	cavity	Mar – Aug	6040*
<i>Hylaeus mesillae</i>	cavity	Jun – Oct	96
<i>Agapostemon texanus</i>	ground	Mar – Oct	1202
<i>Halictus tripartitus</i>	ground	Mar – Oct	31
<i>Halictus ligatus</i>	ground	Mar – Oct	148
<i>Lasioglossum (Dialictus)</i> <i>sp. B</i>	ground	Mar – Aug	31

Sources: Cane 2015, Common Bee Groups of California 2019, Environment and Natural Resources 2017, Greenleaf et al. 2007, Guerrero et al. 2017, Sardiñas and Kremen 2014, Youssef and Bohart 1968.

*Refer to Table 3

Table 3. IT widths and the corresponding typical homing distances. Multiple images across multiple online databases were used to find a representative IT width for each species. The formula overestimates distance for larger bees such as *Xylocopa varipuncta*.

Species	IT width (mm)	Typical homing distance (m)
<i>Andrena miserabilis</i>	2.0	215
<i>Andrena sola</i>	2.5	444
<i>Bombus melanopygus</i>	4.5	2983
<i>Bombus vosnesenskii</i>	4.0	2036
<i>Xylocopa varipuncta</i>	7.3	14318 (6040)*
<i>Hylaeus mesillae</i>	0.9	16
<i>Agapostemon texanus</i>	2.0	215
<i>Halictus tripartitus</i>	1.2	41
<i>Halictus ligatus</i>	1.5	85
<i>Lasioglossum (Dialictus)</i> <i>sp. B</i>	1.7	127

Sources: SCAN 2018, Discover Life 2019, Zurbuchen et al. 2010

*The overestimated calculation is replaced by the literature-derived value in parentheses for the model.

Table 4a. Sensitivity analysis. Values are shown as the percent change in correlation coefficients. I did not adjust values for the “Open Water” class.

Change	Open Water	D, Open Space	D, L Intensity	D, M Intensity	D, H Intensity	Barren Land	Evergreen Forest
Cavity (-)	0.00	-0.87	-0.78	3.34	-0.90	-3.45	0.50
Cavity (+)	0.00	0.85	0.80	-3.52	0.92	3.50	-0.49
Ground (-)	0.00	-2.45	-3.51	6.04	-1.09	-1.90	1.93
Ground (+)	0.00	2.60	3.42	-5.95	0.99	2.00	-1.87
Spring (-)	0.00	-1.16	-2.16	5.53	-2.00	-3.00	1.30
Spring (+)	0.00	1.21	2.18	-5.21	1.90	2.56	-1.21
Summer (-)	0.00	-0.87	-0.18	5.32	-5.00	-1.01	2.00
Summer (+)	0.00	0.59	0.23	-4.54	4.21	1.19	-2.19
Fall (-)	0.00	-3.56	-4.34	4.95	-1.09	-0.34	0.73
Fall (+)	0.00	4.01	4.36	-2.40	1.05	1.02	-0.81

Table 4b. Sensitivity analysis (continued). Values are shown as the percent change in correlation coefficients after a 10% change in suitability value from the baseline model.

Change	Mixed Forest	Shrub/Scrub	Grassland/Herbaceous	Pasture/Hay	Cultivated Crops	Woody Wetlands	Emergent Wetlands
Cavity (-)	-1.03	-0.09	-0.39	0.11	-4.56	0.15	0.13
Cavity (+)	1.19	0.08	0.45	-0.13	4.60	-0.11	-0.15
Ground (-)	-3.40	-1.23	-0.92	0.54	-6.29	-0.34	-0.23
Ground (+)	3.49	1.37	1.08	-0.72	7.52	-0.29	-0.41
Spring (-)	0.07	0.07	-2.03	0.97	-3.45	0.56	0.07
Spring (+)	-0.04	-0.06	2.09	-0.76	3.50	-0.48	-0.09
Summer (-)	0.02	-0.06	-6.43	0.39	-2.35	-0.13	-0.06
Summer (+)	-0.05	0.05	7.92	-0.44	2.00	0.09	0.04
Fall (-)	-0.15	0.07	-5.20	0.64	-0.05	0.24	0.13
Fall (+)	0.23	0.13	3.24	-0.71	0.09	-0.15	-0.11