



The application of semantic modelling to map pollination service provisioning at large landscape scales

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ABSTRACT

Mapping ecosystem services (ES), including crop pollination by wild insect pollinators, is challenging due to the number of variables involved and the spatial-temporal dimensions of their interactions. To enhance the synergistic relationship between pollination service and crop yield in agricultural landscapes, a better appreciation of the spatial dynamics of pollination service provisioning is needed. Spatially explicit modelling approaches have been used to investigate how different land cover types influence the distribution and abundance of wild bee pollinators in agricultural landscapes. However, an integrated dynamic and spatial modelling framework is needed to address the complexities of pollination supply mapping at the landscape scale. The Artificial Intelligence for Environment and Sustainability (ARIES) framework is a collaborative, spatially explicit and integrated tool for ES assessment. We applied a set of high-resolution process-based pollination models within ARIES to represent landscape capacity to supply pollination by wild bees at the local scale in the Canadian prairies. We also developed a systematic approach to perform a global sensitivity analysis by using a surrogate model (Gaussian Process Regression) and variance-based sensitivity analysis for the selected uncertain key parameters of the model. We modelled pollination dynamics through the mechanistic behavior of native bee guilds, including foraging distance, nesting ability, flight activity, the relative importance of bee guilds, and seasonal variation of floral resources. We focused on three guilds, bumblebees, sweat bees and mining bees, which differed by their nesting habits, floral preferences, and flight distances. We found that over 45% of pollination-dependent croplands in our study area lack wild pollination. The global sensitivity analysis revealed the significance of all key parameters, with seasonal activity across guilds identified as the key driving factors. Our results highlight the significance of the ecological role of wild bees in agricultural landscapes and the sensitivity analysis underscores the importance of temporal dynamics in ecological modeling and pollination.

1. Introduction

Pollination by wild bees as an important ecosystem service (ES) plays a crucial role in the sustainability of many agricultural landscapes worldwide. It is estimated that 10% (€153 billion) of the global economic value of food production depends on insect pollination (Gallai et al. 2009). Pollination improves yields and leads to higher quality crops (Stein et al. 2017), diversifies nutrition (Ellis, Myers, and Ricketts 2015; Hünicken et al. 2020), and conserves wild plant populations in natural landscapes (Blaauw and Isaacs 2014). The dramatic decline in wild pollinator populations is due to habitat loss and fragmentation, agricultural intensification, and changes in landcover patterns (Potts et al. 2010). There is a growing concern about how to manage, protect

and restore the natural ecosystem services of pollination in modern agriculture (Raderschall et al. 2021; Vickruck et al. 2019, 2021) — especially in light of increasing demand for food and a resulting increased production through agriculture intensification.

Despite the importance of crop pollination by managed honeybees, wild bees can also pollinate crops if sufficient natural habitat is available on farms (Kline and Joshi 2020; Perennes et al. 2021; Potts et al. 2016; Purvis et al. 2020; Vaughan and Black 2007). In Canada, the estimated total annual economic value of honeybee pollination was \$2.57 billion in 2017 (Agriculture and Agri-Food Canada 2021). In addition, the number of beekeepers was recorded to be over 11,700 in 2020 (Agriculture and Agri-Food Canada 2021). In the Southern prairies of Alberta, honeybee pollination accounted for about 50% of seed canola

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production with the remaining half attributed to wild bees (Agriculture and Agri-Food Canada 2017). As native species are, by definition, adapted to local environmental conditions, they may perform better than introduced species. Furthermore, research has demonstrated that wild bees are more efficient pollinators than honeybees (Vaughan et al. 2007). For example, a global meta-analysis by (Garibaldi et al. 2013) found a positive association between wild insect visitation rates and enhanced fruit sets. In light of these findings, there is an increasing concern to conserve native bees and their habitats (Potts et al. 2016). By doing so, dependence on commercial honeybees for crop pollination could be reduced. However, a limitation to preserving and managing wild bee communities is the scarcity of their habitat in agricultural landscapes, thereby limiting the flow of this beneficial ES to farms.

Investigating the relative potential pollination by different bee guilds demonstrates their ecological function in the agricultural landscapes. Pollination services by various bee guilds, thus, may vary according to their behavior and their interactions with landscape structure. For instance, a comparative study of five bee species (Andrikopoulos and Cane 2018) on pollination efficacy on raspberry production found managed honeybees are the most cost-effective pollinator, while bumblebees and mason bees could be beneficial for protected cultivation systems. Given that various bee guilds have unique nesting and foraging behaviours, addressing the scale at which they forage has significant ecological implications in agricultural landscapes. For example, most native bees in Canada are solitary bees that live only for one year and are active for a short time during summer and fall (Agriculture and Agri-Food Canada 2013). However, some species like bumblebees are social bees and live in relatively large colonies. In addition, bumblebees have a longer lifetime than other native bees, and their activity continues until early fall (Agriculture and Agri-Food Canada 2013). Considering pollinator behavior in pollination mapping is one way to engage with the spatial dynamics of various bee guilds to identify pollination-deficient areas that illustrate where pollination service provision has not yet met the demand of nearby cropland.

Mapping pollination is challenging due to the complexities of real-world landscapes and their influence on pollinator populations, which unlike other ES cannot be directly observed at large scales by remote sensing or in situ sensors (Ramirez-Reyes et al. 2019). Presently, a set of spatially explicit tools such as Artificial Intelligence for Environment and Sustainability (ARIES Villa et al. 2014), Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST, Sharp et al. 2014), Ecosystem Services Mapping Tool (ESTIMAP, Zulian et al., 2013b) and more recently, PollMap (Rahimi et al., 2021) have been developed to address some of these pollination mapping challenges. Such tools have been used to develop strategies to prevent and alleviate the effects of pollinator declines on crop production across landscapes, by generating spatial data at appropriate scales. Regarding these mapping tools, ARIES is based on integrated ES modelling methodology (Villa et al. 2014), and integrates existing ecosystem service models such as pollination using a tier-based approach (Martínez-López et al. 2019). Notably, the ARIES project is based on a semantic-meta modelling paradigm (Villa et al. 2017) that by design adheres to the FAIR principles (The four FAIR principles: Findable, Accessible, Interoperable, Reusable were introduced by Wilkinson et al. (2016) to advance open science through improved infrastructure for reusability of scientific data by both people and computers.), where semantics provide consistent labeling of multidisciplinary data and model elements that are recognizable by the computer, while a machine reasoner navigates data and models on linked repositories, selects the ones best suited to the given context, after which the models are executed and results and provenance information returned to the user (Villa et al. 2017).

The innovative integrated modelling worldview and machine reasoning feature in ARIES privilege the interoperability of ecosystem service models and datasets through observables, e.g., physical objects (a farm), their qualities (crop yield per hectare), the processes (crop growth) and events (crop flowering/blooming) which can be directly

observed in the ARIES modelling platform called K.LAB (a software stack for semantic modelling - the process of creating meaning from data and computation using a shared worldview- to support users in model-data integration through a series of client and server components) (The Integrated Modelling Partnership 2021). After semantic annotation of datasets, the modelling process in K.LAB begins with observing a concept in a user-defined context that requires spatial and temporal declaration. K.LAB supports various models from simple functions to complex stochastic simulations and GIS raster geoprocessing. For example, a model in K.LAB can be a simple land cover classification, look-up tables or a complex simulation model. In addition, ARIES provides complex scientific computation, such as through scientific workflows, thereby increasing the speed, reliability, and customizability of the ES assessment process (Torres, Balbi, and Villa 2021; Villa et al. 2014).

The novelty of this research lies in its spatially explicit modeling of pollination services by different bee guilds, taking into account pollinator behavior and interactions with landscape structures. Our approach considers the nesting and foraging behaviors of various bee guilds, rarely considered in most pollination frameworks. We integrate these factors within a high-resolution pollinator species model developed within the Artificial Intelligence for Environment and Sustainability (ARIES) platform with the goal of evaluating the capacity of agricultural landscapes to supply wild pollination services. The model captures spatial and temporal pollination dynamics that govern complex relationships between the landscape and different bee guilds, including nesting ability, flight activity throughout the year, seasonal variation of floral resources, and relative importance of bee species in a landscape. We demonstrate this approach in an agricultural region in the Canadian prairies of Manitoba. Our results highlight the importance of addressing the scale at which guilds forage and their ecological implications in agricultural landscapes.

2. Methods

2.1. Study area

The widespread agricultural intensification in the Canadian prairies has posed a significant risk for floral resource diversity and suitable nesting habitat for native bee species (Vickruck et al. 2019). We selected a sample crop statistical region in the Southern prairies of Manitoba (Fig. 1) known as crops Small Area Data (SAD) to test our integrated pollination mapping approach at the local landscape scale. SAD in Canada subdivides the country's agricultural regions to provide coherent agricultural statistics at the local scale. Manitoba is divided into 12 SAD regions. This study is conducted in SAD number 7, corresponding to Manitoba's Census Agriculture Region number 7 with a 10,905 km² area. The average farm size in Manitoba was about 4.8 km² in 2016 (Statistics Canada 2016). There are over 1700 farms in SAD 7, and oilseed and grain farming (859 farms, 49.5 %) are the most prevalent farming type (Statistics Canada 2016). According to the census of agriculture in 2016 by Statistics Canada, the major crops grown in this region are canola (42.7 %), wheat (38.10%), oat (34.60 %), barley (13.5 %), and flaxseed (9 %). Canola and flaxseed are the most important pollination-dependent crops on the landscape; however, scattered sunflower and corn farms are also evident and are greatly pollination-dependent (Fig. 1).

2.2. Selecting key pollinators

Agriculture and Agri-Food Canada (AAFC) (2013) has divided Canadian native bees in agricultural landscapes into different guilds according to their body size and the foraging distance to collect pollen and nectar in nearby landscapes. We conceptualized our model and selected three different bee guilds (Bumblebees, Mining bees, and Sweat bees, respectively, representing large, medium-sized, and small bees) based

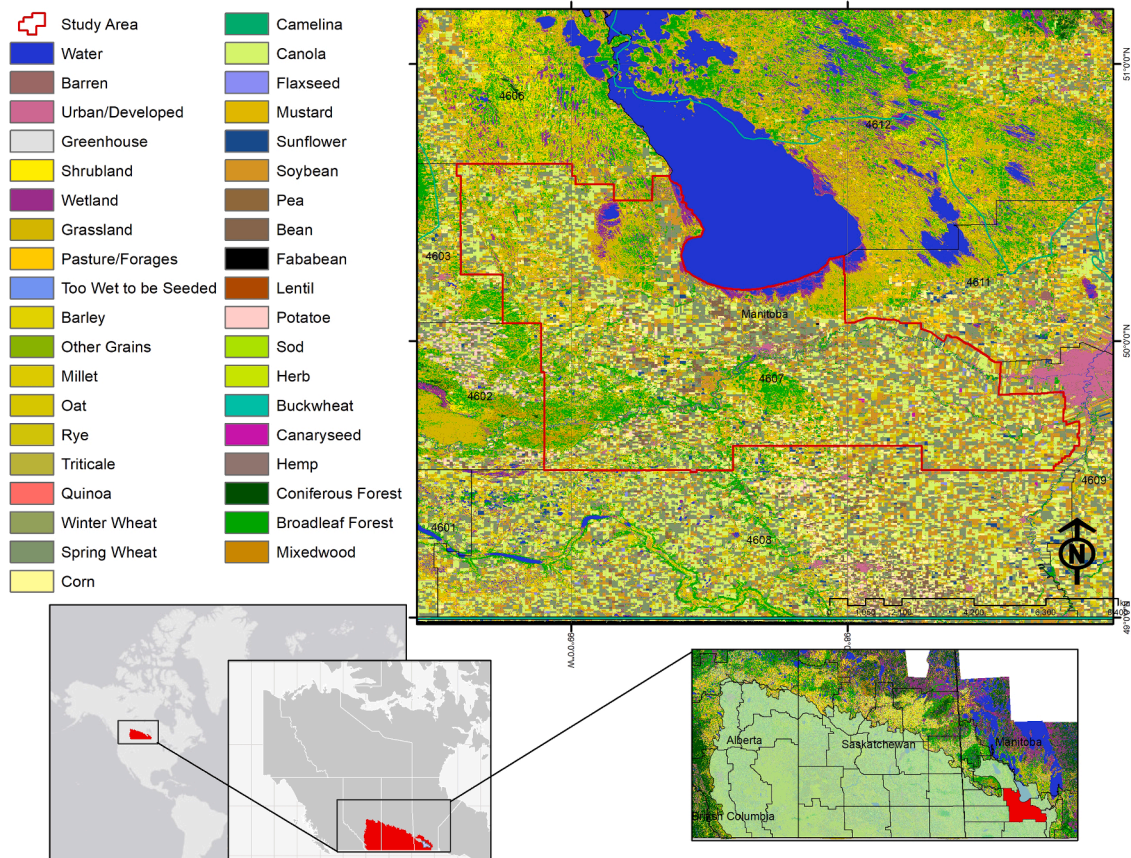


Fig. 1. The location of the study area, SAD number 7 in Manitoba, Canada is dominated by annual croplands. wheat, canola, soybean, flaxseed, oat and rye are the dominant cover types in the landscape (Supplementary Materials, Table 1). The landscape structure in this region is heterogeneous, with much of the remaining landcover classified as broadleaf forest distributed mainly in the southern part. Pollination-dependent crops are annotated with an asterisk symbol. The color code shows the pollination dependency rate (green: high pollination dependent, orange: moderate pollination dependent, black: little pollination dependent).

on AAFC’s guideline and guild behavior.

Table 1 shows the parameters used to represent the three major bee guilds that we selected to model. We modelled the following behavior mechanisms: flight distance, nesting ability in various nesting sites, and flight activity throughout the year. We compiled the data for different guilds from multiple technical reports for agriculture and pollination in Canada and North America (Agriculture and Agri-Food Canada 2013; Agriculture and Agri-Food Canada, 2020; Vaughan et al. 2015).

2.3. Model design within ARIES

Our guild-based pollination model builds from the mechanistic pollination model of Lonsdorf et al (2009) and the ecological production function framework (Kremen et al. 2007). The base methodology uses landcover data to estimate pollinator nesting suitability and probability of floral resources in a landscape by remapping landcover classes. Fig. 2 demonstrates model steps and provides a general overview of the model framework. We used five look-up tables, (1) floral resources, (2) nesting

suitability, (3) foraging distance, (4) nesting ability, and (5) guild importance through the modelling process to map pollination complexities resulting from pollinator diversity. A common assumption in most current pollination models (Kremen et al. 2007; Lonsdorf et al. 2009; Schulp, Lautenbach, and Verburg 2014; Zulian, Paracchini, et al. 2013) is to use landscape suitability to represent pollinator abundance and diversity. These models generate a pollinator abundance index and a pollinator visitation rate by using landcover data to represent landscape suitability for the pollination service (Perennes et al. 2021). The modeled species richness of pollinators thus may represent a general and quantifiable indicator of the potential value of pollination supply for crop production.

Step 1. Landcover Classification: We use high-resolution data of landscape context variables, including crop cover types at 30 m resolution and run the model with the same spatial resolution. We retrieved the annual crop inventory for 2020 from the Open Government data portal on the Government of Canada’s website (https://agriculture.

Table 1
Different selected bee guilds and their behavior components in the pollination model.

Guilds/ body size and species	Relative Importance in Pollination Supply	Flight Distance/ Foraging Distance (m)	Nesting Ability				Seasonal Relative Importance of Flight Activity		
			Ground	Wood	Stem	Cavity	Spring	Summer	Fall
Large bee (Bumblebees)	0.5	1500	1	1	0.2	0.3	0.3	0.6	0.1
Medium-sized (Mining bees)	0.3	400	1	1	0.5	0.2	0.2	0.8	0
Small bee (Sweat bees)	0.2	200	1	1	0.5	0.2	0.2	0.8	0

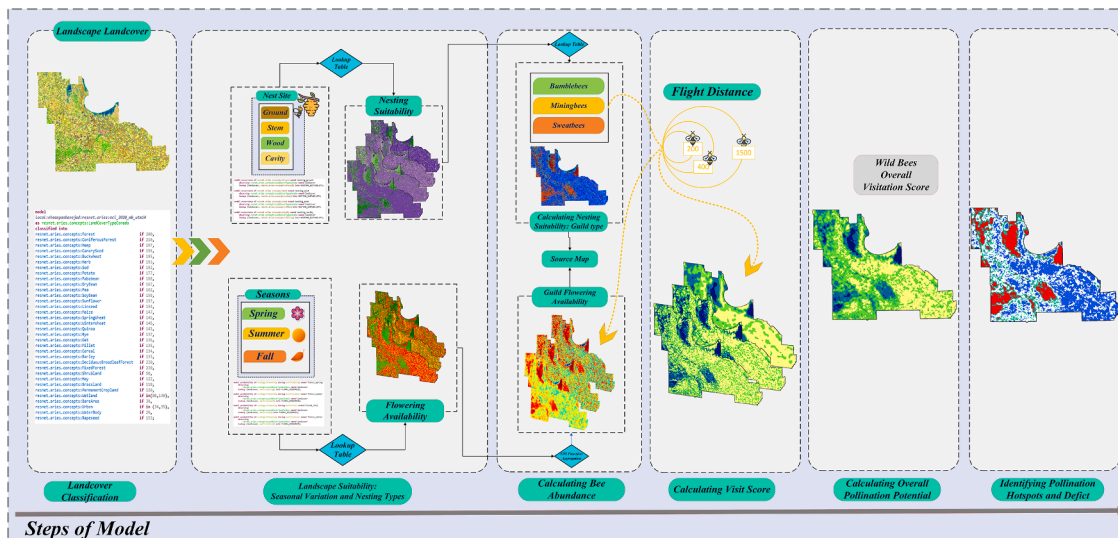


Fig. 2. Pollination model framework.

canada.ca/atlas/data_donnees/agr/annualCropInventory/tif/2020/) for Manitoba. Agriculture and Agri-Food Canada (AAFC) has been using Landsat satellite images since 2009 to produce annual national crop inventory (Agriculture and Agri-Food Canada 2020), which also maps non-crop landcover types (Fig. 1). The modelling process in the ARIES platform begins by making all data sources, including landcover, (1) machine actionable, by hosting them on a GeoServer and importing them as resources available to ARIES, during which the data are validated and a Uniform Resource Name is generated for each resource and (2) semantically annotated, by providing a consistent and unambiguous definition of the data content, which allows ARIES to navigate data and models to assemble and execute computational workflows (Villa et al. 2017).

Step 2. Landscape Suitability: According to the base model (Lonsdorf et al. 2009), we assigned two landscape suitability indicators, (1) to map floral resource availability and (2) nesting suitability based on expert knowledge (Supplementary Materials, Tables 2 and 3). We calculated landscape suitability for pollinators (nesting suitability and floral availability) based on these two composite indicators. In this study, we modified model coefficients of floral resources and nesting suitability from the Canadian context according to the literature and a similar study conducted in the US (Koh et al. 2016) and consulted with pollination experts in Canada. We used new values for non-crop cover types based on expert elicitation for Canadian prairies, close to Koh et al. (2016)’s numbers (Supplementary Materials, Tables 2 and 3). However, we did

Table 2
Key uncertain parameters for sensitivity analysis.

Category	Parameter	Range	
Foraging distance for each guild	Bumblebees	1000 – 2000 m	
	Mining bees	350 – 450 m	
	Sweat bees	100 – 200 m	
Seasonal relative importance of flight activity	Bumblebees	Spring	0.24 – 0.36
		Summer	0.48 – 0.72
		Fall	0.08 – 0.12
	Mining bees	Spring	0.16 – 0.24
		Summer	0.64 – 0.96
		Fall*	0 (Fixed value for all combination)
Sweat bees	Spring	0.16 – 0.24	
	Summer	0.64 – 0.96	
	Fall*	0 (Fixed value for all combination)	

*excluded parameters from sensitivity analysis

not change the weights of crop types from Koh et al. (2016) for nesting sites and floral resources availability. To benchmark regional-level model performance, Koh et al. (2016) did not find much difference between regional coefficients as compared to a model with a single national-level set of coefficients. The base model computes pollination potential according to the foraging distance of pollinators (Table 1) using a decay function. This means that foraging distances of the desired pollinator species decline exponentially with distance (Ricketts et al. 2008). Finally, the model calculates a score for pollinator visits between 0–1 for a given landscape, where 0 represents the minimum visitation rate and 1 shows the maximum visitation rate.

Step 2.1. Seasonal and Guild Floral Resources Availability: Seasonal variation is an important factor in producing a floral resource map as flowering resources vary among seasons. Thus, we calculated overall flowering availability as a weighted sum across seasons from 0–1 (i.e., spring, summer, fall) for various species (Lonsdorf et al. 2009, Table 1). We then computed guild-based floral resource maps. Based on the availability of floral resources in different seasons and using a look-up table (flight activity, Section 2.2), the floral resource map for each guild is produced. To consider guild foraging distance in the landscape, we used the neighbourhood of each pixel using a GIS function within ARIES to aggregate the mean value of floral resources for each guild according to their foraging distance (Table 1).

We first calculate guild floral resource maps by considering guild foraging distance using the neighbourhood of each pixel according to Eq. 1, where floral resources vary among K seasons. Therefore, the overall floral resource maps are calculated as the weighted sum across K seasons where the weight (w_{sk}) $\in [0, 1]$ shows the relative importance of floral resources in season k for species s (Lonsdorf et al. 2009). According to pollinator foraging distance, the base model uses a decay function to produce floral resource maps. However, we implemented the mean value of each cell in the neighbourhood instead of the Euclidean distance based on Eq. 1 where FA_{ijsk} is the floral resource availability in cell i, j for species s in season k (FA_{ijs}) $\in [0, 1]$:

$$FA_{ijs} = \frac{1}{N} \sum_{k=1}^K w_{sk} \sum_{(i,j) \in \Lambda} FA_{ijsk} \tag{1}$$

where Λ is a set N of cells located inside the radius of R_s of cell i, j and R_s is foraging distance for species s . We conceptualized foraging distance for three guilds in the Canadian prairies according to their body size. Therefore, R_s in Eq. 1, respectively for large bees (Bumblebees),

Table 3
Spatial distribution and comparison of pollination-dependent crops in the landscape and pollination deficit area.

Crop type	Total Area Km ² (in the landscape)	Percentage	Area in pollination deficit		Average Yield (Kilograms per hectare)	Production (Metric tonnes)
			km ²	Percentage of total cropland		
Canola***	2002	18.36	630.88	31.51	2341	424,900
Corn**	418.49	3.84	249.35	59.58	n/a	n/a
Flaxseed*	20.26	0.19	11.9	58.74	2091	6200
Soybean *	1130.64	10.37	781.34	69.11	2529	236,000
Sunflower***	60.39	0.55	6.53	10.81	1853	7400
Total (pollination dependent crops)	3631.78	33.3	1680	46.26	-	-
Other crops and natural landcover	7273.22	66.7	2823	38.81	-	-
Total	10,905	-	4503	-	-	-

* little pollination dependent

** moderately pollination dependent

*** highly pollination dependent. The calculated area is based on pollination model output and landcover distribution. Yield and production data is derived from (Statistics Canada 2022).

medium-sized bees (Mining bees), and small bees (Sweat bees) is considered 1500 m, 400 m, and 200 m (Agriculture and Agri-Food Canada 2013).

Step 2.2. Guild Nesting Suitability Map: First, landscape suitability for different nesting sites (ground, wood, stem, and cavity) is calculated using coefficients from the nesting suitability look-up table (Supplementary Materials, Table 3). Then, using the guild-specific nesting ability look-up table (derived from Table 1), we produced guild nesting ability maps as a function of nesting suitability (see Section 2.2 and Table 1) in the landscape. Finally, we applied a simple deterministic model to normalize landscape suitability values to produce the nesting suitability for each guild.

Step 3. Calculating Guild Bee Abundance: The base model (Lonsdorf et al. 2009) combines the floral resource map and nesting suitability map to produce the pollinator abundance map. We calculated the bee abundance for each guild by multiplying the guild-specific floral resource and nesting suitability maps and then normalizing the values using a deterministic model. The relative pollinator abundance in each nest site is thus estimated between nesting suitability (NS_{ijs}) and floral resource availability (FA_{ijs}):

$$PA_{ijs} = NS_{ijs} \times FA_{ijs} \quad (2)$$

Step 4. Calculating Pollination Supply Map: To produce the final pollination supply map for each guild, we first model the probability of visitation by each guild in the landscape according to guild foraging range (similar to step 2.1, a mean aggregation of each neighbourhood is calculated). Since each guild has different ecological functionality in a landscape, we then combine the visitation rate for all guilds considering their relative importance in pollination provisioning (Table 1). Finally, an overall bee visitation score for wild bees is calculated (Eq. 3) and accordingly, the pollination potential hotspots and cold spots are identified by reclassifying in ArcGIS (Fig. 2). We used an area-based approach using very high and high classes of final pollination service map as hotspots and very low areas as pollination cold spots.

We calculated pollinator abundance for each guild, and then the visitation probability for each guild is computed using Eq. 3 ($VS_{ijs} \in [0, 1]$):

$$VS_{ijs} = \frac{1}{N} \sum_{(ij \in \Lambda)} PA_{ijs} \quad (3)$$

where VS_{ijs} is the visitation score for species s . We based the provisioning of the pollination service on bee visitation probability according to the maximum value of their foraging distance in the landscape. Thus, the total pollination potential is the sum of the weighted guild visitation

score maps. The distance decay function is applied a second time in the base model to provide the bee abundance visiting each cell to represent pollination supply. Similar to calculating floral resource maps (Eq. 1), we modified the base model using an aggregation method to calculate guild visitation probability. We based the importance of bee guilds (bumblebees: 0.5, mining bees: 0.3 and sweat bees: 0.2) on their foraging distance and then multiplied their weight to the guild visit score maps (guild pollination supply maps) and normalized the values using a deterministic model within ARIES.

The underlying conceptual structure of the pollination model is illustrated in Fig. 2. The final output of the mechanistic pollination model quantifies pollination service supply for a given landscape among different bee guilds. In this study, we selected three bee guilds (bumblebees, mining bees, and sweat bees), each with varying foraging distances (Table 1).

2.4. Sensitivity analysis

We performed a global sensitivity analysis to identify the key input parameters of the pollination model applied in this study. Pollination as an ecological process is non-linear inherently. Therefore, we applied variance-based sensitivity analysis to capture the nonlinearity of model outputs and to further identify influential model parameters in the model outputs as well as the interactions among model parameters. A variance-based sensitivity analysis usually provides the first-order sensitivity indices S_i and the total-effect sensitivity indices T_i for the uncertain factors of the mathematical model under analysis (Lo Piano et al. 2021). As discussed in the literature, computational cost of sensitivity analysis is crucial and greatly depends on the number of parameters and model evaluations. Various techniques exist for estimating sensitivity indices, ranging from sample-based approaches to meta-modelling methods, such as employing surrogate models (Lo Piano et al. 2021). In this study, we utilized a surrogate statistical model to predict the pollination model output based on a set of 40 model observations. More specifically, we employed Gaussian Process Regression (GPR; discussed in the subsequent section) to interpolate and predict data generated by the pollination model from ARIES. GPR is particularly effective when the response surface of interest smoothly maps onto the parameter space (Dancik and Dorman 2008). By leveraging GPR, we aim to provide a robust, data-driven approximation of the pollination model response, thereby enhancing the accuracy of our sensitivity analysis.

We did not run a sensitivity analysis for the coefficients used from Koh et al (2016) for floral resources and nesting suitability indices of different land cover types since in their study, as mentioned in the previous section, they did not find much difference of regional variability in the model coefficients when compared to national-level coefficients.

The sensitivity analysis was thus performed on a selected group of 10 parameters, as presented in Table 2. These parameters were defined within a range of $\pm 20\%$ of their original values (sourced from Table 1), an approach informed by relevant literature and expert opinion. To generate diverse sets of parameter combinations, we employed the Latin Hypercube Sampling (LHS) method, resulting in a total of 40 combinations (see supplementary information 2).

The appropriate sample size for sensitivity analysis depends on the complexity of the model and the number of input parameters being considered (Sheikholeslami and Razavi 2017). In general, a larger sample size provides a more accurate assessment of parameter sensitivity, but also requires more computational resources and time. However, due to nature of our pollination model and computation time, we selected 40 samples with the LHS method to run the model in the sample areas (SI2).

For the implementation of the LHS method, we used the pyDOE (Design of Experiments for Python; <https://pythonhosted.org/pyDOE/>) package and for variance-bases sensitivity analysis we used the SALib-Sensitivity Analysis Library in Python (Iwanaga, Usher, and Herman 2022). LHS is a stratified random sampling method ensuring a uniform distribution of input combinations across the range of input parameters. This method requires several considerations, including the listing of the model's parameters and their corresponding values, along with the identification of uncertain parameters (Gomero 2012). From our initial list of 19 parameters (based on Table 1), we filtered the most uncertain parameters, focusing particularly on those related to bee behavior, such as foraging distances and seasonal activity. We omitted the nesting ability of different nesting sites for the guilds of interest from the list of uncertain parameters. This decision was guided by the minimal differences identified in Table 1 and corresponding literature regarding the different nesting sites for wild bee guilds in the study area. Table 2 presents the list of key uncertain parameters and their defined range for sensitivity analysis. A preliminary correlation analysis conducted

between input parameters revealed weak or non-existent correlations among input features for the selected parameters, as depicted in Fig. 3. However, these weak relationships could be influential in variance decompositions of model output when two or more input features interact together.

Given the computational demands associated with running the model at a 30 m resolution with ARIES for the entire study area, we adopted a strategic approach to reduce computation time. We elected to operate the model across 40 distinct parameter combinations within selected sample areas from the study area. The initial step involved ranking the geographical limits of the study areas based on the diversity of land cover and crop types. We subsequently identified each unique type and partitioned these coordinates into clusters using the K-means algorithm. These clusters informed the definition of sample areas for executing the sensitivity analysis. We established a 3 km buffer around these areas, a distance that is roughly twice the foraging range of a bumblebee ($\alpha = 1.5$ km). To further refine the selection, we applied the Shannon Diversity index to each of these sample areas. This measure quantified the diversity of land cover types within each area, facilitating an effective ranking system. Based on this ranking, we chose five areas for subsequent analysis: two areas with the highest diversity, two with the lowest, and one median (Fig. 4). Subsequent to running the model 40 times, each with a different parameter combination, we extracted the raster values based on random points ($n=20$ in each landscape, yielding a total of 100 points). This approach allowed us to generate a comprehensive yet manageable dataset for our sensitivity analysis, effectively balancing computational demands with the need for diverse and representative sample areas.

2.4.1. Variance-based sensitivity analysis

Variance-based sensitivity analysis quantifies the contribution of each input parameter to the output variance. This contribution can be from a single parameter or from interactions among two or more

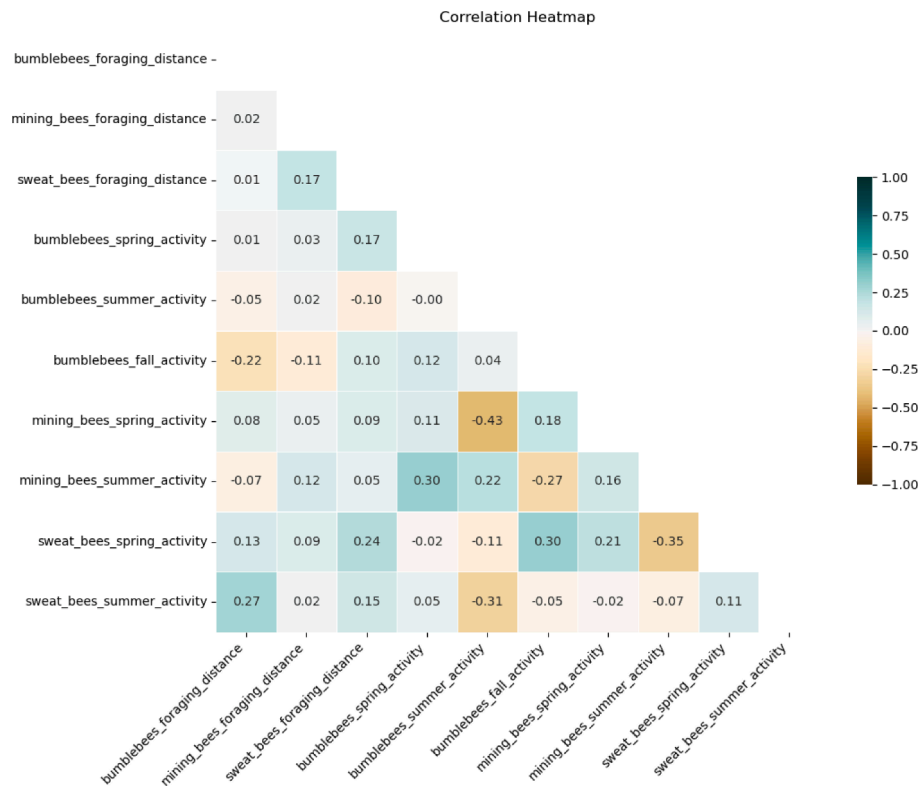


Fig. 3. Heatmap correlation of input parameters considered in the sensitivity analysis. There is a weak correlation between some of input parameters and no relationship in most of the time as shown in the heatmap. For example there is a mild negative correlation between summer activity in miningbees and bumblebees ($r = -0.43$).

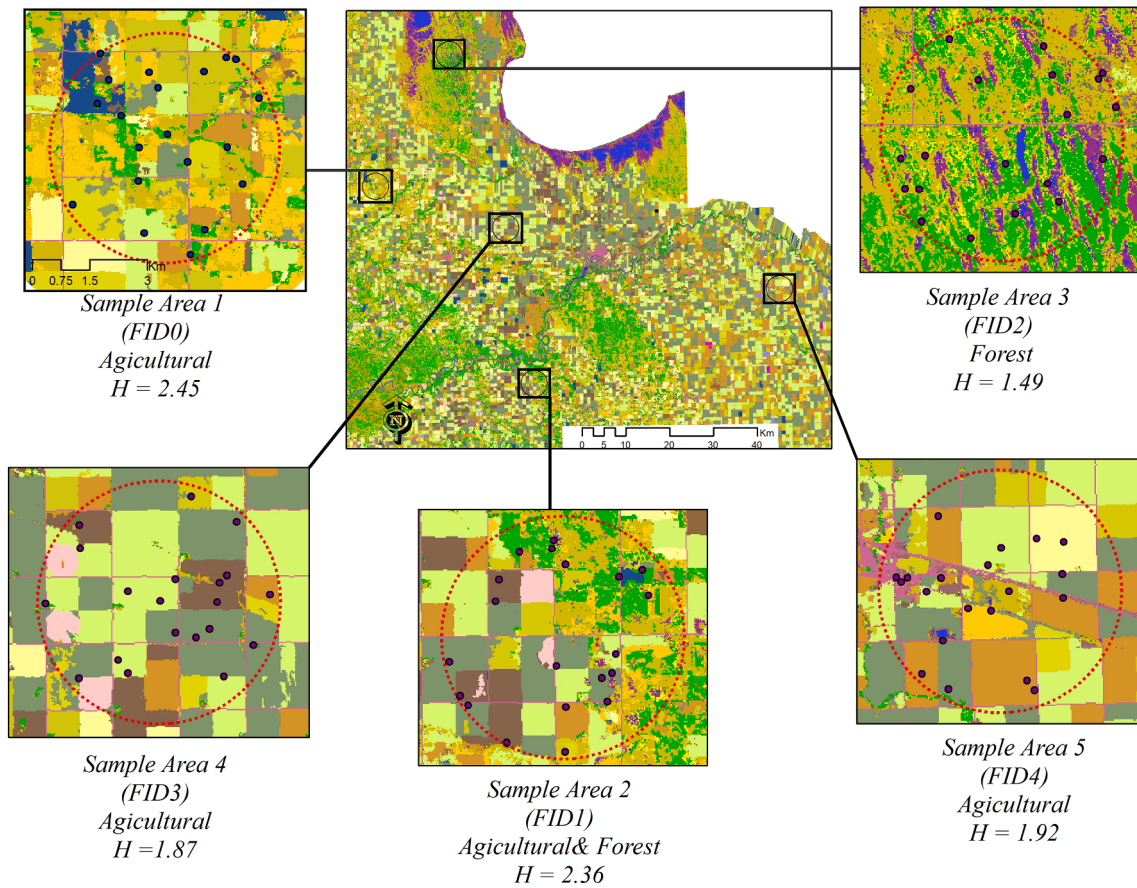


Fig. 4. Spatial distribution and location of selected sample areas and random points for sensitivity analysis. Landscape diversity is calculated for each landscape based on Shannon landscape diversity(H). As shown in the figure sample areas 1 and 2 is a mixed landscape of cropland and forest types while sample area 3 is mostly dominated by forest types and grassland. Whereas sample area 4 and 5 is dominated by cropland with sample patches of forest.

parameters, leading to what is known as first-order and higher-order sensitivity indices, respectively (Pianosi et al. 2016). The Sobol sensitivity analysis technique (Sobol 1993) calculates these contributions, known as Sobol SI's indices, by taking into account both the impact of individual parameters and the interactions between two or more parameters. The Sobol method provides a robust framework for understanding mathematical models and can handle non-linear and non-monotonic functions and relationships.

The Sobol indices are essential in determining which parameters are most impactful and, therefore, should be the focus of further research and refinement. This form of sensitivity analysis is instrumental in determining how much the uncertainty in the output of a mathematical model or system can be attributed to different sources of uncertainty in its inputs.

In the context of the Sobol method, a model is represented by a function, $Y = f(X)$, where Y is the model output and X is the set of parameters, denoted as $X = (X_1, X_2, \dots, X_k)$. The Sobol method recommends decomposing this function, f , into summands of increasing dimensionality (Pianosi et al. 2016). This approach simplifies complex models into more manageable and analyzable components, making it a popular tool in the modeling of complex environmental systems.

Following the model function defined above, the first-order indices, or main effects, measure the direct contribution of individual input features to the model output variance. Essentially, by fixing a specific input feature, we can estimate the expected reduction in the output variance (Nossent, Elsen, and Bauwens 2011; Pianosi et al. 2016).

$$S_i^F = \frac{V_{X_i}[E_{X_{\sim i}}(y|x_i)]}{V(y)} = \frac{V(y) - V_{X_i}[E_{X_{\sim i}}(y|x_i)]}{V(y)} \quad (4)$$

where:

- S_i^F is the first-order sensitivity index for the i -th input parameter. This index quantifies the proportion of the total output variance that is due to the i -th input factor alone.
- E is the expected value,
- V is the total variance or the output y
- $X_{\sim i}$ denotes all input factors except the i -th one.

The total-order or total effect indices is another index introduced by (Homma and Saltelli 1996) to measure the contribution to the output variance caused by an input factor including both its first-order effects and its interaction with all the other factors known as higher-order interactions. While the first-order effect provides a valuable means of ranking the individual influence of each factor, particularly in scenarios where interaction effects are negligible or non-existent in their contribution to output variance, the Total-Order Index offers a more holistic view. It is particularly well-suited for preliminary screening purposes, as it provides a robust mechanism to identify influential and non-influential factors (Pianosi et al. 2016). Accordingly, the total-order index can be written as:

$$S_i^T = \frac{E_{X_{\sim i}}[V_{X_i}(y|x_{\sim i})]}{V(y)} = 1 - \frac{V_{X_{\sim i}}[E_{X_i}(y|x_{\sim i})]}{V(y)} \quad (5)$$

Second-order indices or intermediate order can also be defined that is the measure of the contribution to the model variance caused by the interaction of two model inputs.

2.4.2. Gaussian process model to interpolate the pollination model output

Gaussian process regression (GPR) is a non-parametric Bayesian inference. This approach initially proposed in statistics by (O’Hagan 1978) is also known as kriging in geostatistics. Essentially, Gaussian Processes (GPs) are a type of kernel method that uniquely provides a thorough, conditional statistical representation of the predicted variable. This ability is particularly useful in defining hyperparameters and establishing confidence intervals, contributing to more precise and interpretable model outcomes (Camps-Valls et al. 2016). A Gaussian process function can be defined as a stochastic process where each point, denoted by X , in the continuous domain is associated with a random variable, represented as $f(x)$. The essential characteristic of this process is that the joint distribution of a finite number of these variables $p(f(x_1), \dots, f(x_n))$ follows a Gaussian distribution:

$$p(f|X) \sim N(f|\mu, K) \tag{6}$$

where $f = (f(x_1), \dots, f(x_n))$, $\mu = (m(x_1), \dots, m(x_n))$ and $K_{ij} = k(x_i, x_j)$. In this equation, the mean function m represents the prior mean of the Gaussian process. It is common to set the mean function to zero due to the flexibility of the Gaussian process which allows it to model the mean even when assigned an arbitrary beginning value (Schulz, Speekenbrink, and Krause 2018).

Assuming we have the values of a noise-free function f at certain inputs x , we can transition a Gaussian Process (GP) from a prior state to a posterior one. This transition enables us to generate predictions for new inputs. By the nature of a GP, the joint distribution of observed values and predictive values adheres to a Gaussian distribution (Schulz et al. 2018). This distribution can be partitioned as follows:

$$\begin{pmatrix} f \\ f^* \end{pmatrix} \sim N, \begin{pmatrix} K & K^* \\ K^{*T} & K^{**} \end{pmatrix} \tag{7}$$

in which $K^* = k(X, X^*)$ and $K^{**} = k(X^*, X^*)$.

Given m training data points and n new observations (test data points), K is an $m \times m$ matrix, K^* in an $m \times n$ matrix, and K^{**} is an $n \times n$ matrix.

According to the properties of Gaussian distribution, the predictive distribution also known as posterior is defined as follows:

$$p(f^*|X^*, X, f) \sim N(f^*|\mu^*, \Sigma^*) \tag{8}$$

where $\mu^* = K^{*T}K^{-1}f$

$$\Sigma^* = K^{**} - K^{*T}K^{-1}K^* \tag{9}$$

Suppose we introduce noise into objective function, such that $y = f + \epsilon$, where the noise follows a normal distribution

$$\epsilon \sim N(0, \sigma_y^2 I) \tag{10}$$

is independently and identically distributed. Under this condition, the posterior can then be depicted as:

$$p(f^*|X^*, X, y) \sim N(y^*|\mu^*, \Sigma^*) \tag{11}$$

where $\mu^* = K^{*T}K_y^{-1}y$

$$\Sigma^* = K^{**} - K^{*T}K_y^{-1}K^* \tag{12}$$

where $k_y = K + \sigma_y^2 I$

Finally, to account for the noise σ into prediction, it is incorporated by adding it to the diagonal of the covariance matrix.

$$p(f^*|X^*, X, y) \sim N(y^*|\mu^*, \Sigma^* + \sigma_y^2 I) \tag{13}$$

The subsequent steps provide a summary of the Gaussian Process Regression (GPR) implementation for training the model outputs:

- **Data preprocessing:** before training the model, a consistent scale of input features is required. Since all the input parameters were between the range of 0–1 except the foraging distances of bee guilds, we normalized this parameter using the Min/Max scaler scale. This transformation is given by:

$$X' = \frac{(X - X_{min})}{(X_{max} - X_{min})} \tag{14}$$

- **Kernel selection:** There are infinite numbers of kernel functions that can be selected. To identify the optimal kernel for the Gaussian process regression model, which is critical for accurate and robust predictions, we considered an array of kernels, including RBF, Matern, Rational Quadratic, and White Kernel, both individually and in combination, thereby exploring the potential advantages of composite kernels. To ensure the model was not limited by local minima in the optimization process, we implemented multiple restarts for the optimizer. We assessed the performance of each kernel function based on Normalized Mean Squared Error (NMSE) between predicted and actual values. The lowest NMSE was selected as best kernel.
- **Hyperparameter optimization:** The hyperparameter optimization is performed by comparing the performance of the several different kernels on the given dataset.
- **Kernel selection criterion and model performance evaluation:** The optimal kernel was chosen based on its performance, as measured by the smallest Normalized Mean Squared Error (NMSE) on the test set as a widely accepted measure of predictive performance. The NMSE is defined as:

$$NMSE = \frac{1}{n} \sum_{i=1}^n \frac{(y_{pred,i} - y_{true,i})^2}{y_{true,i}^2} \tag{15}$$

where n is the number of samples, $y_{pred,i}$ is the predicted value for the i -th sample, and $y_{true,i}$ is the true value for the i -th sample.

- **Model training and validation:** after preprocessing and kernel selection, the dataset is trained with the optimized kernel. Model performance is evaluated using the test set and quantified in terms of NMSE. To ensure the model was not limited by local minima during optimization, we implemented multiple restarts.

3. Results

3.1. Landscape suitability: floral resource availability (seasonal variation) and nesting suitability (nesting sites)

Fig. 5 shows seasonal variation in flowering availability (panel A) and different nesting types (panel B) for wild bees in the study area. A value of 0 means that a given cover type has no capacity to provide floral resources or nesting sites for wild bees, while 1 refers to the highest capacity of a specific cover type to provide floral resources and nesting habitat. Fig. 5 shows consistent associations between land cover types, floral resources, and suitable nesting sites. There are notable differences in floral resources values for different forest classes, grassland, wetlands, and some crop types such as sunflower, canola, and flaxseed (Supplementary Materials, Table 2). High-value floral resources and nesting habitat are typically distributed in natural and semi-natural patches among croplands. In addition, flowering differs by season and landcover type. The model addressed this seasonal variation using a look-up table for different seasons. For example, the yellow color in the summer floral resource map indicates the flowering period of different crops in the landscape, which disappears in other seasons (panel A Fig. 5).

Pollinator Abundance (guild source maps) and Pollination Supply

The resulting total pollinator abundance and pollination supply for each guild, shown in Fig. 6, reflects guild abundance and pollination

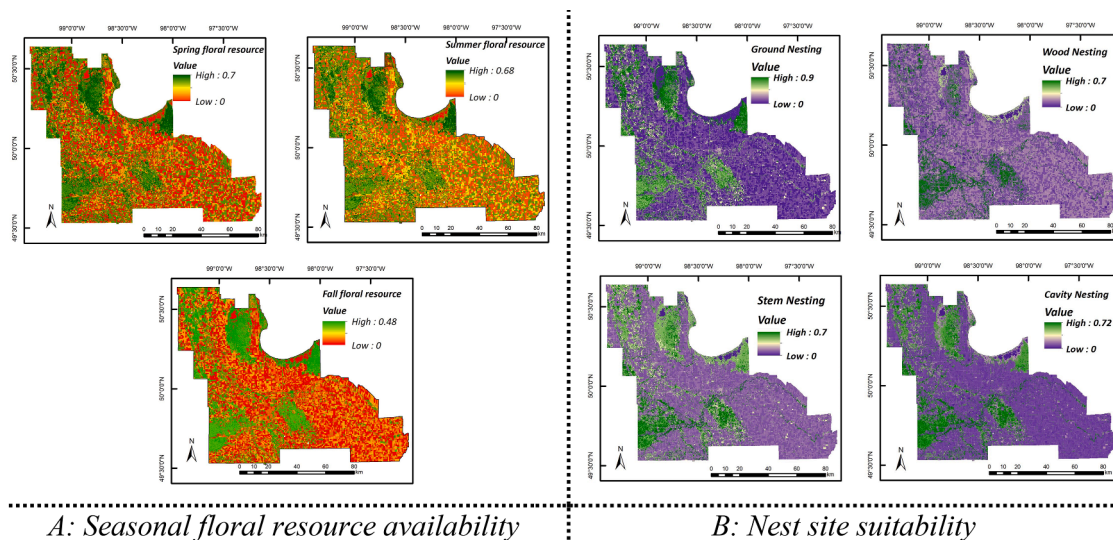


Fig. 5. Seasonal variation in floral resource availability (panel A) and landscape suitability of different nesting types (panel B). A: Seasonal floral resource availability. B: Nest site suitability.

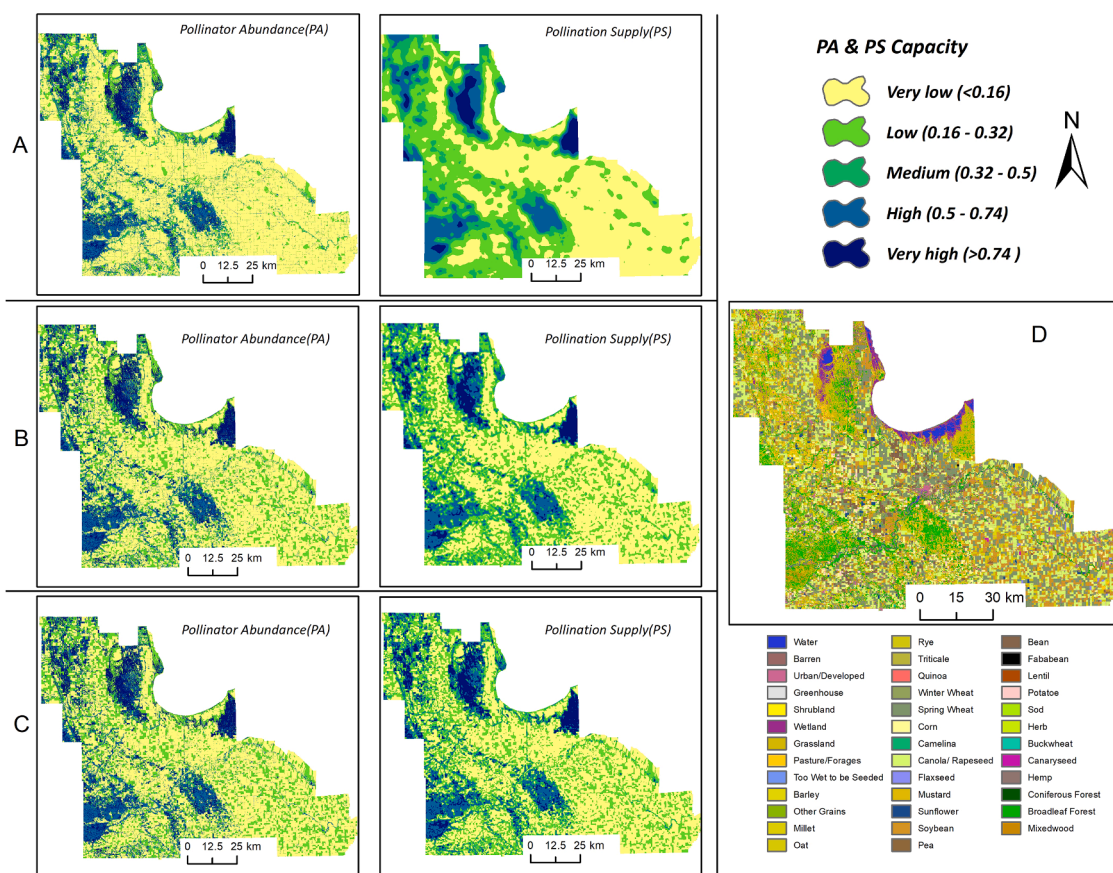


Fig. 6. Pollinator abundance and pollination supply model output of each guild. Panel A: Bumblebees (foraging distance = 1500 m), Panel B: Mining bees (foraging distance = 400 m) and Panel C: Sweat bees (foraging = 200 m). Panel D, the crop type and landcover map, is a key input to the model. The model reflects the significance of landscape structure in providing floral resources, suitable nesting habitat, and pollination service supply areas.

supply areas in the landscape. Fig. 6 shows how guilds vary spatially across landscape with different flight distances for foraging and nesting requirements.

Due to the higher availability of floral resources and nesting habitat in natural areas, greater pollinator abundance is estimated in these areas. However, inside the agriculture matrixes, high abundance values

are present, yet limited to natural patches and small fragmented habitats such as hedgerows and roadside vegetation that connect nesting sites and foraging destinations. As expected, the abundance of pollinators in the surrounding cropland is considerably lower than in semi-natural areas.

In addition to pollination potential for each guild, we also considered

the relative importance of guilds to model their proportional representation in the final pollination service map. Pollination potential supply in this model is equivalent to visitation probabilities of guilds in the landscape. Fig. 7 (Panel A) illustrates the predicted pollination service potential (the weighted sum of visitation probability for all target bee guilds). Overall, visitation probabilities by guilds tend to decrease with increasing cropland cover (Fig. 6 illustrates the landscape structure and pollination potential for each guild). In other words, pollination potential is significantly associated with natural and semi-natural patches in the landscape. Recent studies have found a strong relationship between enhanced bee abundance and semi-natural habitats with increased crop diversity (e.g., Raderschall et al. 2021). This is due to the availability of prolonged flowering periods in matrices with mixed crops and semi-natural habitats.

The total pollination supply classification depicts that almost 14.67% of the study area is spotted as pollination hotspots, while 41% of this landscape lacks potential wild pollination service, mainly inside cropland (Fig. 7, panel C). We also conducted a spatial autocorrelation analysis using the Moran's I index in ArcGIS to test the likelihood of clustering patterns of total guild pollination supply classes. The result shows that the clustering is not random and supports the hypothesis of an association between landscape structure and pollination service

capacity (Moran's Index: 0.517, z-score: 22.595, p-value: 0.00).

Fig. 8 illustrates the spatial distribution of pollination-dependent crops in the identified pollination deficit clusters, and Table 3 provides an in-depth comparison of the area these crops occupy in the landscape. As discussed in the study area section, canola is the most important pollination-dependent crop in this landscape. Canola covers 18.36% of the study area (2002 km²) and according to our model, 31.51% of canola farmlands are located in the pollination deficit area, meaning these farms do not meet the demand by wild pollination. While corn field spatial distribution is about 3.84%, this cover type suffers from pollination deficit as well (almost 59.85% of the total corn area is located in pollination deficit areas). Soybean is also a dominant crop type (with 236 thousand metric tonnes production in 2020) in the landscape with a low insect pollination dependency rate (Robinson, Nowofrodski, and Morse 1989). Soybean farm fields occupy 10.37% (1130.64 km²) of the study area and 781.34 km² (69.11%) of this cover type lacks wild pollination service on the farm. Among the pollination-dependent crop types, canola and soybean rank the first and second top significant crop by production in this landscape (Table 3).

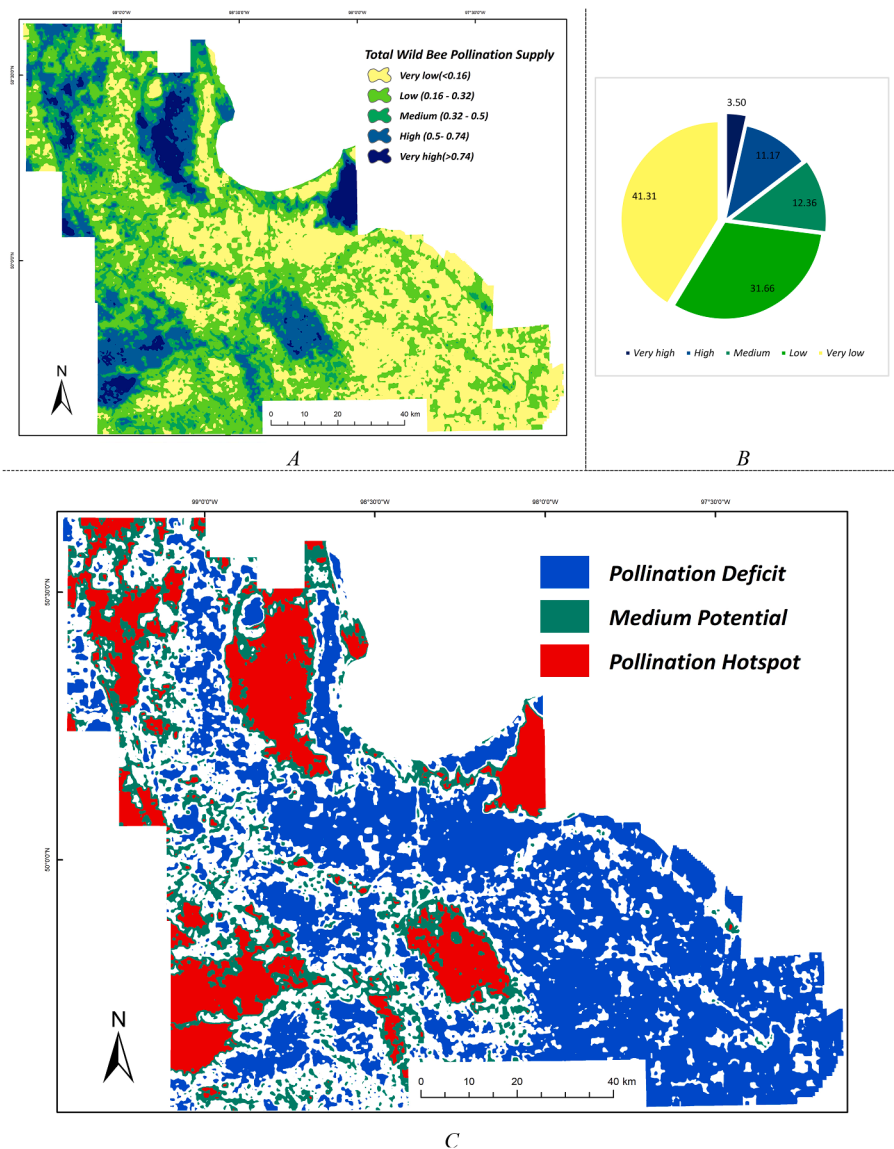


Fig. 7. Panel A: Total pollination potential supply. The color intensity represents the level of the potential pollination supply. Panel B: distribution of potential pollination supply area among different classes. Panel C: Pollination hotspots and pollination deficit areas. Medium potential is mainly identified as edge areas of natural habitat such as forest edges and this means demand for pollination is met in these patches. Pollination deficit areas are mainly identified inside larger patches of cropland, while hotspots are associated with natural patches.

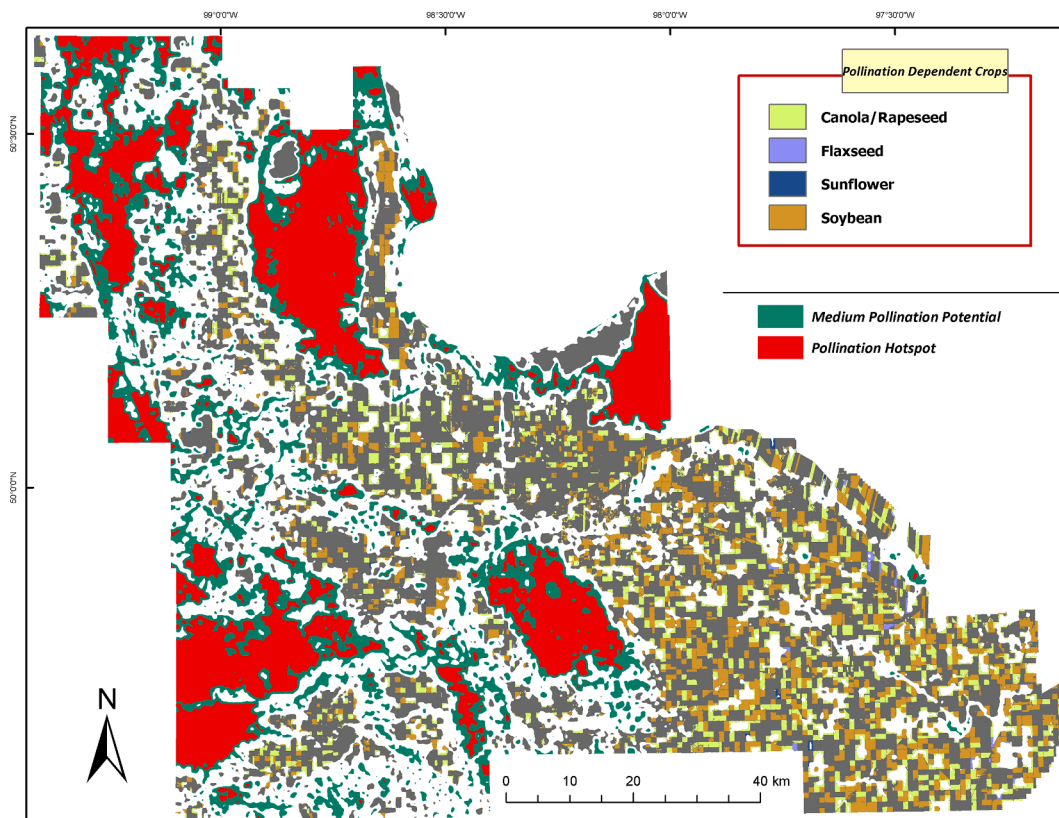


Fig. 8. Spatial distribution of pollination-dependent crops in the identified pollination deficit areas.

3.2. Guild comparison

The relative values of floral resources, pollinator abundance, and pollination supply for a selected part of the study area are shown in Fig. 9. This figure reflects how guilds with different foraging ranges and resource requirements are distributed in the landscape. Floral availability at the landscape scale, for example, is of special importance for bumblebees, as they are generalist pollinators that collect pollen in a broader range of floral resources (Fernandes et al. 2020). In comparison, solitary bees (such as sweat bees and mining bees) rely on a small portion of the nearby landscape, which can be at farm-scale if suitable on-farm habitats exist. Hence, the presence of solitary bees may be strongly related to native floral resources and habitat structure.

The availability of floral resources and seasonal variability of the flowering period within each guild predicts the spatial pattern of bee habitat. For example, guilds with smaller foraging ranges (200 m like sweat bees) will be less likely to encounter all bloom stages, whereas guilds with longer flight distance (1500 m like bumblebees) have access to floral resources over a larger portion of the landscape (Fig. 9, floral availability of different guilds). However, such patterns do not necessarily reflect the total bee abundance in the landscape or the actual pollination supply since other factors such as habitat structure and rewarding floral resource patches (Lihoreau, Chittka, and Raine 2011) could make actual bee abundance patterns more complex. In areas where the distribution of different guilds overlaps (e.g., in areas of high floral resources values), the landscape may experience a spillover of pollination supply in some areas; by contrast pollination deficits due to bee abundance imbalance in other areas of the landscape. This is not an actual indication of bee overabundance or bee scarcity in the landscape but rather the influence of landscape structure that may cause pollination hotspots and pollination deficient areas. We can therefore assume that the model effectively quantifies spatial heterogeneity of cropland and natural habitats; increasing this heterogeneity would be expected to

increase pollination service provision.

3.3. Sensitivity analysis

Scatter plots of model outputs against each input feature based on sample areas are shown in Fig. 10. In Fig. 10, each facet represents a parameter space on the x-axis, and the model output (visit score of bee guilds, the visit score is used as a proxy for pollination service supply), on the y-axis. In this context, a high visit score signifies areas where pollination services are abundant, whereas a lower score suggests less supply. Spatial replicates extend this analysis across multiple areas within the study site, revealing the impact of different landscapes on pollination. Variations in parameters are shown by the spread of data points, informing on model sensitivity to parameter changes. This integrated approach provides a thorough understanding of the link between landscape structure and pollination service.

Overall, Fig. 10 reveals little to no correlation between input features and model outputs. The only strong negative correlation is found in sample area 2 (Fig. 10.b, a mixed landscape of croplands and forest) for sweat bees foraging distance. These plots depict that high values of pollination supply (visit score) occur when foraging distances are between 100 to 140 m for sweat bees. A similar pattern with weak correlation in the same landscape is also found for mining bees foraging distance with an exception that visit score values increase when the foraging distance of mining bees increases. Based on the visual inspection of the scatter plots, overall no single parameter significantly or consistently affects the model outputs. However, landscape composition does seem to play a role in the model's behavior. Even so, model outputs remain relatively consistent across different parameter value combinations. Further, for any given sampling point in the landscape, the rank related to various parameter combination were overwhelmingly consistent. This indicates that the resulting maps produced by the model would have (nearly) identical patterns, regardless of the specific

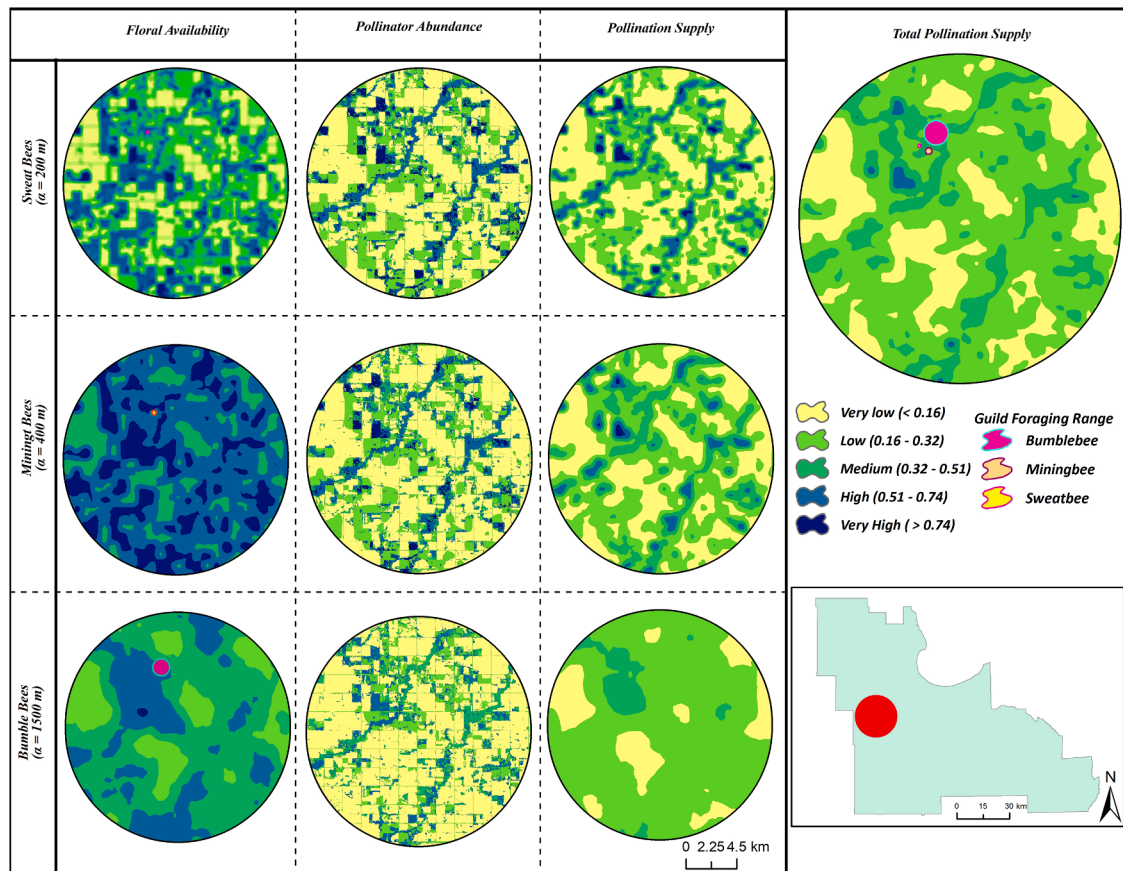


Fig. 9. Guild floral availability, pollinator abundance and pollination supply in a selected sample area of the landscape. The first row is sweat bees, the second is mining bees, and the third is bumblebees. Accordingly, guild foraging ranges are included in floral availability maps and the total pollination supply map (upper right corner). A comparison between these maps highlights the role of flight distance in the spatial representation of pollination supply. There is a relatively higher abundance of solitary bees (sweat bees and mining bees) than bumblebees. Indeed, bumblebees have a larger neighbourhood matrix to forage and this leads to a relatively large spatial coverage of this guild over landscape. However, despite the higher abundance of other guilds, their pollination service is limited to their foraging distance vicinity.

parameter combination used. In general, the results based on variance of model parameters show our results are quite stable to various parameter combinations. To further explore the role of input features in the model outputs we used a variance decomposition approach (see section below; Sobol sensitivity indices).

3.3.1. Variance-based sensitivity analysis by fitting a Gaussian process model

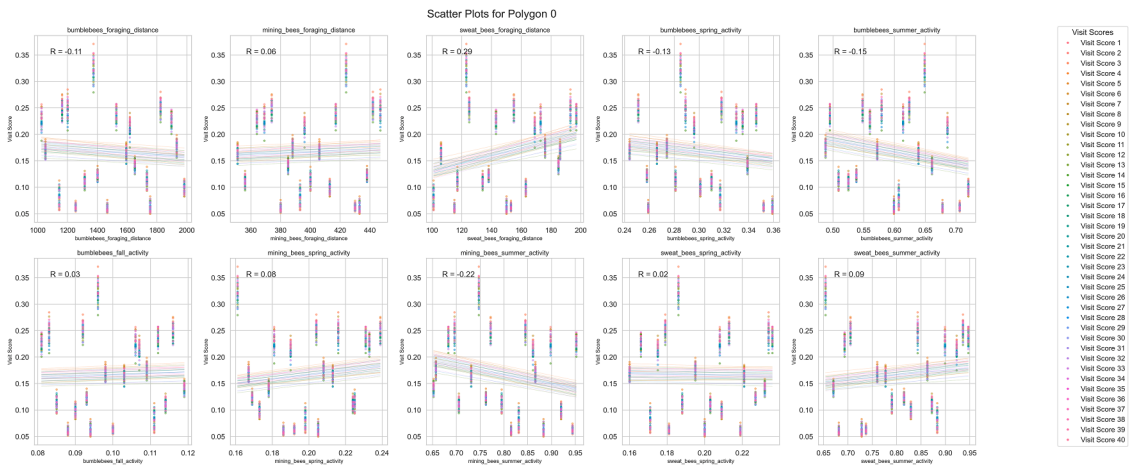
We applied a 100-fold shuffle split technique to the limited number of models runs (40). This approach randomizes the dataset and generates multiple train-test splits, enabling a evaluation of the model's predictive performance. The Normalized Mean Squared Error (NMSE) is used as an evaluation metric to assess the performance of Gaussian process regression model. The average NMSE on both training and test sets represents the mean of the squared differences between the predicted and actual values, adjusted by the scale of the actual values. A lower value suggests better performance of the model on the data. The normalized means squared error for both train and test set of the data is calculated in each shuffle and the average is reported in Fig. 11 which demonstrates the capacity of the model to capture underlying patterns and relationships in the data. In addition to the overall performance of the model the CDF plots of predicted versus actual values against some selective parameters is provided in SII (Supplementary information1, Fig. 1).

3.3.2. Sobol sensitivity indices

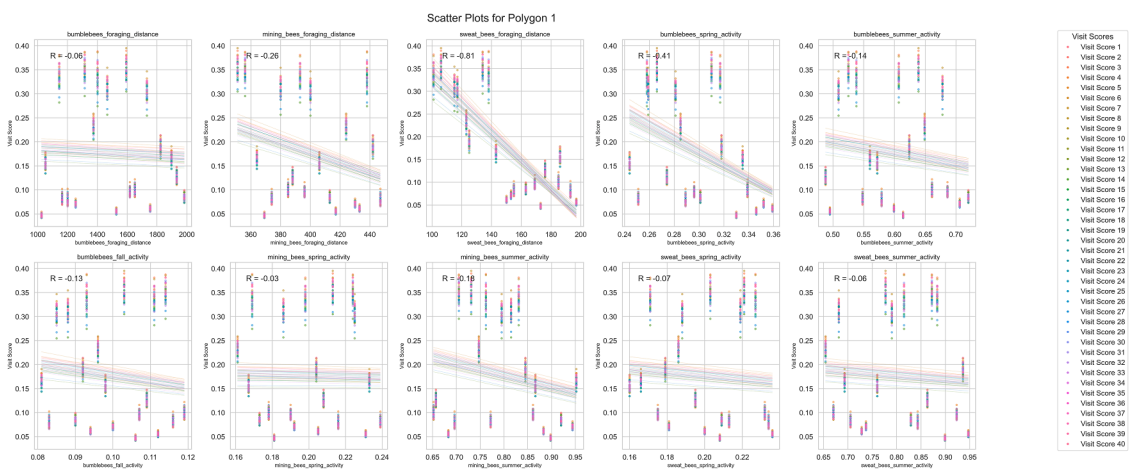
At this stage, we have developed a functional surrogate model, which

is a simplified representation of the complex pollination model previously discussed. This surrogate model allows us to predict new outputs of the pollination model for any new set of input parameters efficiently. Post-training, we conducted a global sensitivity analysis using Gaussian process model. According to the Sobol sensitivity analysis, first-order indices (S1) represent the main effect of each input feature on the model output. Indeed, S1 is an indication of uncertainty of model output that is attributed to an individual input feature. Total-order (ST) effect on the other hand, accounts for the effect of each parameter on the output, including both its individual effect and its interactions with all other parameters. Based on the first-order and total effect results in Table 4, the foraging distance input features of bumblebees and sweat bees displayed a negative first-order effect. This implies that these two parameters do not contribute to the model output individually but their relative impact is substantial when interacting with other parameters. Interestingly, these negative valued parameters contributed positively to the overall model output variance when interactions effects were considered (ST). For bumblebees, the activity during different seasons illustrated positive first-order and total indices. This indicates the seasonal activity of bumblebees is a significant driver of the model output variance. A similar pattern was observed for mining bees and sweat bees (Fig. 12). These results suggest that seasonal activities of all guilds have considerable influence on the model output variance.

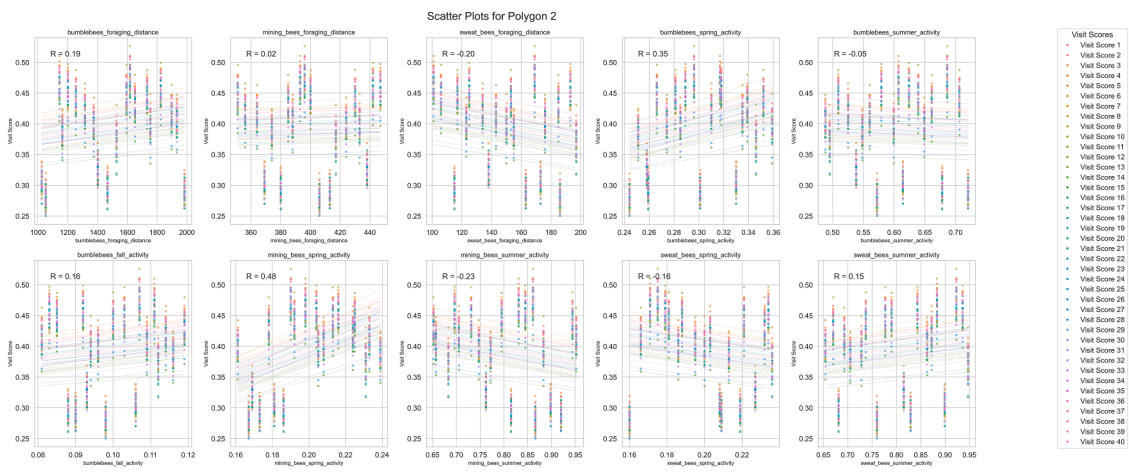
A parameter that demonstrates a high ST value and a low S1 value suggests its primary impact on the output is derived through its interactions with other parameters, with minimal or no individual effect. Although Sobol indices theoretically range between 0 and 1, it is



a. sample area 1 (polygon FID0), an agricultural landscape with low forest density.

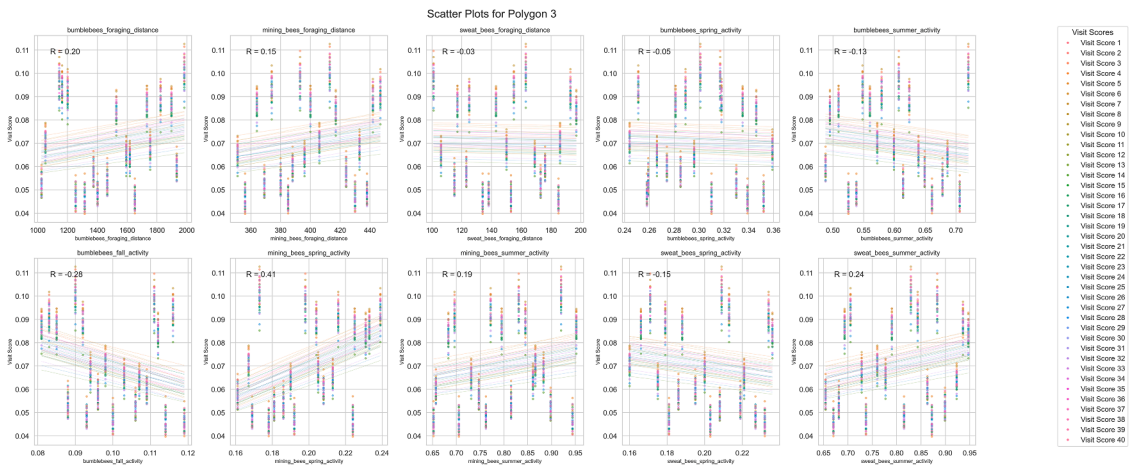


b. sample area 2 (polygon FID1), a mixed agricultural and forest landscape.

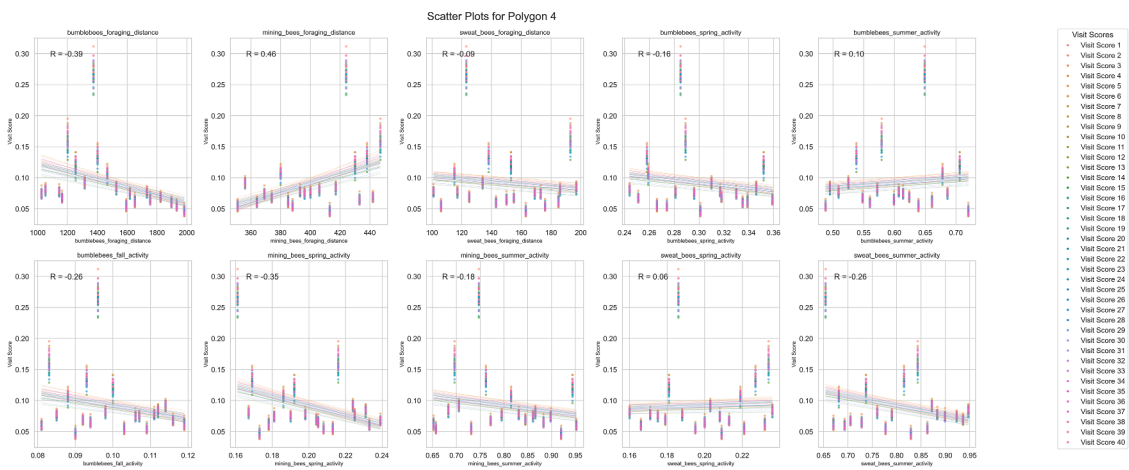


c. in sample area 3 (polygon FID2), a forest dominated landscape with grassland

Fig. 10. Scatter plot of model outputs against input parameters for each sample area. a. sample area 1 (polygon FID0), an agricultural landscape with low forest density. . b. sample area 2 (polygon FID1), a mixed agricultural and forest landscape. . c. in sample area 3 (polygon FID2), a forest dominated landscape with grassland. d. sample area 4 (polygon FID3), an agricultural landscape with low patches of forest. e. sample areas 5 (polygon FID4), an agricultural landscape with low patches of forest.



d. sample area 4 (polygon FID 3), an agricultural landscape with low patches of forest



e. sample areas 5 (polygon FID4), an agricultural landscape with low patches of forest

Fig. 10. (continued).

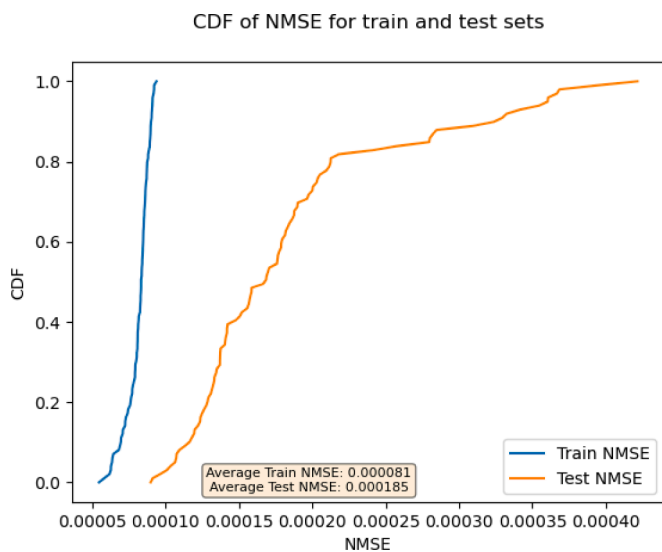


Fig. 11. Cumulative Distribution Function (CDF) plot of normalized mean squared errors for both training and testing sets. The plot demonstrates that the average NMSE values for both sets are negligible, indicating a well-fitted model to the dataset.

possible to observe negative values in certain situations when the sample size is not enough.

4. Discussion

The framework developed in this study to represent the complexities of pollination service provisioning by different guilds of wild bees provides an application of a holistic spatial dynamic model within the ARIES integrated and spatially explicit modelling framework (Gimenez-Garcia et al. in review). Our approach allows assessment of pollination service provision to simultaneously inform decision-making on ecosystem management and stimulate conservation strategies for native bee species and their habitat. The importance of wild bee species for crop pollination has been addressed in previous research and can be beneficial on an individual farm basis (Lonsdorf, Koh, and Ricketts 2020). While some have considered bumblebees to be the most critical wild pollinators (Cameron et al. 2011; Colla et al. 2012) for crop pollination, our mapping results showed that small and medium-sized bee species (sweat bees and mining bees) with lower foraging ranges (less than 500 m) could help pollination service at the local farm scale, assuming adequate habitat is located close enough to crop fields. Our results benefit landscape managers and farmers to identify pollination service potential by wild bees. Accordingly, this will also provide supportive actions for wild bee conservation and their habitat at the farm

Table 4
First-order and total effect sensitivity indices obtained with N = 3072 for the key pollination parameters.

Input parameters	S1	S1 CI	ST	ST CI
Bumblebees foraging distance	-0.120676*	0.003691	0.251855	0.001466
Mining bees foraging distance	0.094865	0.003640	0.343937	0.002405
Sweat bees foraging distance	-0.023717 *	0.002271	0.228140	0.001825
Bumblebees spring activity	0.200225	0.003792	0.473447	0.003113
Bumblebees summer activity	0.135755	0.004403	0.474305	0.003195
Bumblebees fall activity	0.239663	0.003811	0.627181	0.003095
Mining bees spring activity	0.281127	0.003887	0.506383	0.002624
Mining bees summer activity	0.377566	0.003484	0.608468	0.002848
Sweat bees spring activity	0.399421	0.003874	0.675718	0.003654
Sweat bees summer activity	0.371500	0.003719	0.624239	0.003252

*The negative values in the table are attributed to numerical inaccuracies in the Sobol estimations. It is common practice to interpret such values as zero, particularly for insignificant (non-influential) factors in the model output (Wang et al. 2020). These numerical errors can be minimized by enhancing the sample size. For this analysis, we initiated our model evaluation at a sample size of 1024, incrementing it by 1000 until we reached 14,336. Despite employing a large sample size for model evaluation, exceeding 100,000 (N= 128,000), we continued to encounter negative values. This suggests that the sensitivity indices for the less significant parameters failed to achieve ideal convergence.

scale.

Our results show that understanding how semi-natural landscape diversity promotes bee abundance in agricultural landscapes is essential (high and very high classes in Fig. 7, panel A near cropland). Previous research indicates that agricultural management practices, especially high diversity mixed crops with semi-natural patches, can provide abundant floral resources (Martins et al. 2018) and essential nesting habitat for native bees. However, to enhance the pollination service supply in the landscape, we also need to consider the capacity of small habitats (Rahimi, Barghjelveh, and Dong 2021). This highlights the role of habitat structure and habitat quality in pollination mapping practice.

Pollination-dependent crops (canola, corn, flaxseed, soybean, and sunflower) cover 33.3% (3631.78 km²) of the landscape area (Table 3). Our model output delineated the pollination hotspots and deficit areas, and we found that 46.26% (1680 km²) of pollination-dependent crop areas encountered wild pollination deficit (considering all guilds). This

highlights the value of pollination flowing to agricultural landscapes and the necessity of replacing it with managed honeybees. However, studies have shown that beekeeping in farmlands negatively affects plant-pollinator networks (Hung et al. 2019; Huryñ 1997). For example (Valido, Rodríguez-Rodríguez, and Jordano 2019) found that establishing high-density beehives on agricultural landscapes reduces the reproductivity of native plants, which are highly visited by managed honeybees. We conclude that preserving solitary bees and wild bees generally on farms could be a viable alternative to improve pollination flow to farmland and accordingly enhance crop yield and surrounding native plant communities.

Our modelling finds that landscape structure and guild behavior are associated with pollination hotspots and deficit areas. Landscape composition is essential to support habitat and provide sufficient floral resources for pollinators. Recent research argues that landscape configuration is critical in the most rewarding foraging habitat patches. For example, a study of *Bombus terrestris* (Maurer et al. 2020) in managed vineyards found that foraging behavior varied based on habitat fragmentation. In addition, a recent study (Clake, Rogers, and Galpern 2022) found that positive effects of habitat fragmentation could predict bumblebee abundance more accurately than relying on habitat amount (landscape composition as a proxy to indicate bee abundance). There is evidence in the literature that even small patches provide supporting habitat for some bee guilds (Kremen et al. 2004). Therefore, mapping complexities of pollination at a fine spatial grain requires taking landscape configuration into account and not just relying on total landcover type amounts in the landscape. However, a full exploration of fragmentation effects on habitat patches in the pollination mapping process is beyond the scope of this study.

4.1. Model evaluation and limitation

The mechanistic pollination model applied in this paper within the ARIES framework has two significant advances. First, the mechanistic perspective of this model allows us to characterize the expected behavior of different pollinator guilds, such as considering foraging ranges of different native bees, flight activity in different seasons, and guild nesting ability in different habitats. An earlier pollination model in the ARIES repository developed by (Martínez-López et al. 2019) lacks some of the above-mentioned features of the Lonsdorf base model, which have more recently been added by Gimenez-Garcia et al. (in review). Our approach demonstrates how to account for multiple guilds

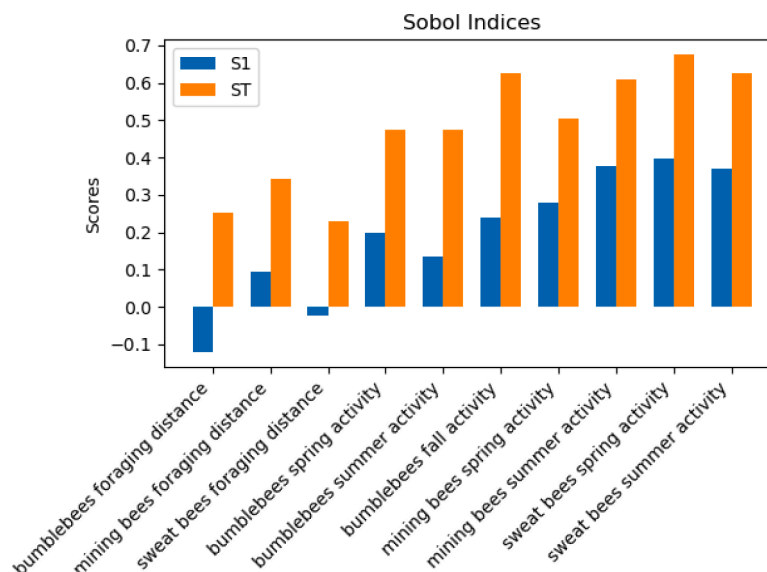


Fig. 12. Sensitivity indices versus input parameters. The first order index and total effect index are represented by S1 and ST, respectively.

with complex behavior since pollinators do not have uniform behavior and resource needs. Our paper and the recent work it builds from (Gimenez-Garcia et al. in review) improve conceptual coherence of the Lonsdorf pollination base model that has been scattered in the literature and allows us to build a more complex and dynamic pollination model within ARIES.

Second, our result highlights the significance of pollination supply by wild bee species and the ecological implication of native bees inside the cropland matrix. As shown in Fig. 9, the scale that pollinators fly is critical, and guilds have a different response to landscape composition, meaning in the absence of longer-distance pollinators like bumblebees, other guilds can provide pollination service at the smaller farm scale. In addition, identifying crop types and their attractiveness to bee species could be a synergistic management action to enhance bee abundance in the landscape. Studies (e.g., Schulp, Lautenbach, and Verburg 2014) have shown that the presence of wild bees is correlated with higher visitation rates to certain crop types. For example, sweat bees are frequent and important pollinators for wildflowers and sunflowers (Mallinger et al. 2019).

In our model, we considered the biotic influences on pollination service. However, abiotic factors can potentially improve pollination mapping practice. Previous studies have shown that in some cases, semi-natural areas with abiotic conditions adjacent to agricultural landscapes (e.g., roadsides, hedgerows and utility corridors) provide pollinator-friendly habitat. An example of abiotic factors in the pollination model is the ESTIMAP model (Zulian, Maes, and Paracchini 2013). This study added abiotic components into the model, such as the proximity of roadsides, and other biotic factors such as forest edges and bioclimatic factors (the latter is also included in Martínez-López et al. (2019)). In addition, pollination is an inherently complex ecological process, shaped by non-linear interactions between plants and their pollinators. These interactions can be affected by various landscape processes, including habitat fragmentation, land use change, and geomorphic features such as the configuration of drainage networks. Apart from the factors we considered, other spatial and environmental features significantly impact model outputs. For instance, a drainage network can shape the distribution and movement of organisms and nutrients within an ecosystem, thereby affecting local climate conditions, species distribution, and population dynamics (Fantinato et al. 2018; Rudi, Bailly, and Vinatier 2018). Further studies are needed to augment our existing pollination framework with abiotic factors, management interventions such as pesticide effects (Douglas et al. 2021), and human-induced air pollutants impacts (Ryalls et al. 2022) on pollination mapping. The integration of both biotic and abiotic influences, alongside other spatial and environmental factors, offer a more nuanced understanding of pollination service.

The application of variance-based global sensitivity analysis provides critical insights into the relative importance of different input parameters within our pollination model. The total-order indices (ST) for all factors are substantial and, in several instances, exceed 0.5, specifically the seasonal activities of all guilds. Interestingly, we observed negative first-order indices in the Sobol analysis, although such indices, lying outside the interval [0,1], can make interpretation more challenging, they can provide valuable insights, as discussed in previous studies like (Esward et al. 2010). Notably, the high sensitivity indices associated with the spring and summer activities of all guilds underscore the importance of seasonal variation in floral resources, a key aspect represented in our pollination model. Furthermore, the analysis reveals the significance of higher-order interactions, which capture complex dependencies. The influence of a variable might be accentuated or mitigated based on its interactions with other variables, as pointed out by Nossent et al. (2011). These interactions play a critical role in the Sobol sensitivity analysis, where first-order indices are often employed for factor ranking when interaction effects contribute insignificantly to the output variance.

The presence of negative first-order indices in our variance-based

sensitivity analysis may initially seem counterintuitive. However, within complex ecological models such as the pollination model, these negative indices could potentially indicate the presence of non-linear interactions between input parameters. Previous studies (Qian and Mahdi 2020; Sarrazin, Pianosi, and Wagener 2016; Wang et al. 2020) demonstrated that negative first-order effects may appear when indices are estimated with finite, and sometimes small, samples of model evaluation, pointing to potential numerical errors in the Sobol indices. While it may be interpreted as the parameters being non-influential and treating their value to be zero, this seems not the case in our complex pollination model as the total effect of parameters are relatively significant. Instead, this suggests that output depicts a nonmonotonic relationship as shown in scatter plots in Fig. 11. Therefore, there is no single parameter that significantly influence model outputs, but the interactions among parameters are more influential.

Complex ecological systems such as the pollination model in this study, are influenced by a number of factors including floral resources, foraging distance, nesting suitability, nesting ability, seasonal variations and ecological functionality of different bee guilds. All these factors interact in complex ways to shape the pollination potential of a landscape and could act to stabilize the ecological system under varying conditions. Floral resources and nesting suitability are fundamental to the survival and productivity of pollinators. When floral resources and nesting suitability are high, it is generally expected that pollinator abundance will increase (Affek et al. 2021; Fowler, Rotheray, and Goulson 2016). However, when floral resources and nesting suitability in a landscape is low, pollinator might still be able to sustain themselves, albeit at reduced level, due to their ability to forage over longer distances (Rands and Whitney 2011) or utilize alternative nesting sites. Foraging distances of bee guilds is another crucial variable in the model even if the sensitivity analysis of first-order effects demonstrated non-influential effects for two bee guilds. Bees with larger foraging distances can access floral resource farther away from their nesting sites, which can help maintain pollination service even when local floral resources are scarce. This ability to forage larger distances and adapt to fluctuations in floral resources availability can enhance the stability of the system. The model also accounts for seasonal variation in floral resource availability. Seasonality offers varying level of resources, and different bees might have varying adaptabilities and preferences to these changes. For example, bumblebees are the only active wild bees during the fall among the guilds under study. Thus, the ability of different bee guilds to shift their activity patterns in response to these seasonal variations can contribute to the stability of the pollination system. These stability factors might be particularly important in the face of disturbances or environmental changes, helping to maintain pollination service provisioning and flowing in the landscape.

At a large landscape scale, considering cropland as pollination coldspots and semi-natural habitats as hotspots may be an oversimplification in part due to using classification methods, landscape composition and the aggregation algorithm in the model. Previous studies such as (Bagstad et al. 2017) found that using different clustering methods for ES hot/coldspots delineation produced different spatial patterns. For example, area-based and quantile classification use high and low values for clustering spatial patterns. We used the neighbourhood of each pixel to compute the seasonal floral resource maps for each guild according to their foraging distance. However, pollinators are central place foragers (Olsson, Brown, and Helf 2008), meaning that they can accurately distinguish rewarding patches from non-rewarding ones, which influences their nest-site selection decisions (Fernandes et al. 2020). This interplay between landscape pattern and complex pollinator behavior is an important one; although our current model lacks such complexity, future modeling efforts within ARIES could fill this gap. Hence, integrating more complex foraging mechanisms may provide added value for the existing modelling framework.

A final drawback of our approach, which is common to pollination modeling, is the lack of the model validation process, which requires

further effort, such as field observation and experimental analysis in the landscape. One way to address this gap is to engage with the species distribution model and use species occurrence data from the Global Biodiversity Information Facility (<https://www.gbif.org/>). Recently, an important study by (Perennes et al. 2021) has developed a robust pollination mapping approach using pollinator species distribution predictions and knowledge on bee species life history.

5. Conclusion

There are currently several different spatial-based ES mapping tools available. Different models are developed for a specific context, use different approaches, and produce different output metrics (Bagstad et al. 2018), while ARIES is designed to integrate multiple model types of varying complexity, using artificial intelligence to guide model selection. As more varied models become available in ARIES, the system will have greater flexibility to answer more diverse ES modeling problems (Martínez-López et al. 2019). The mechanistic pollination model applied within the ARIES framework highlights the significance of pollination supply by various wild bee guilds and the ecological implication of native bees inside the cropland matrix in the Canadian prairies. A global sensitivity analysis based on variance decomposition on key input parameters showed that while there is no single parameter influencing model variance, all parameters are representative of complex ecological model of pollination service by wild bees. Even though the total effect of all parameters is fairly significant, seasonal activity across all guilds was identified as the key driving factor within our pollination model. As native bee guilds in agricultural landscapes could be a viable alternative for crop pollination and management purposes, these results could further support wild bee conservation actions in agriculture matrices in the Canadian prairies.

CRedit authorship contribution statement

Ehsan Pashanejad: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Project administration. **Hugo Thierry:** Software, Validation, Writing – review & editing. **Brian E. Robinson:** Writing – review & editing, Supervision, Funding acquisition. **Lael Parrott:** Writing – review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2023.110452](https://doi.org/10.1016/j.ecolmodel.2023.110452).

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