

# A field-validated species distribution model to support management of the critically endangered Poweshiek skipperling (*Oarisma poweshiek*) butterfly in Canada

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## Abstract

The Poweshiek skipperling (*Oarisma poweshiek*) is a critically endangered grassland butterfly with six populations remaining in the United States and Canada. The single Canadian population, with the largest remaining contiguous habitat, includes less than ~50 observed individuals and extirpation is potentially imminent. Captive breeding is underway and there is a need to locate suitable sites for reintroduction and habitat management. Species distribution models (SDMs) predict habitat quality and guide management decisions. Most SDMs rely on statistical validation as a surrogate metric for accuracy, with presence-only SDMs usually reporting area under the curve (AUC). Although experts have long cautioned against relying on statistical validation alone, accuracy is rarely field-validated. We developed a presence-only SDM using the maximum entropy (Maxent) method to predict probability of occurrence for the Poweshiek skipperling and determine environmental covariates associated with high probability of occurrence. We collected two independent datasets to (a) calibrate our model to predict categories of habitat quality (using factor analysis) and (b) compare expected and observed habitat quality to calculate model accuracy. Statistical validation showed that we predicted presence-absence of training data with high accuracy (AUC = 0.98). Covariates responsible for most of the variation in probability of occurrence included soil drainage, habitat patch size, and land use type. Only 0.4% of the study area was expected to represent good-excellent habitat with the remaining 99.6% medium-poor. Our model predicted novel habitat quality with 81% accuracy (better than chance). Poor-medium habitat was predicted more accurately (92%) than good-excellent habitat (54%). Our model showed better accuracy than most other field-validated SDMs reviewed. We reiterate calls for greater field-validation of SDMs: if we had relied on statistical validation alone, perceived accuracy of our model would be inflated. Finally, managers can use our

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results to reliably exclude predicted poor-medium habitats as candidates for Poweshiek skipperling habitat management or reintroduction.

#### KEYWORDS

field-validation, Maxent, species at risk

## 1 | INTRODUCTION

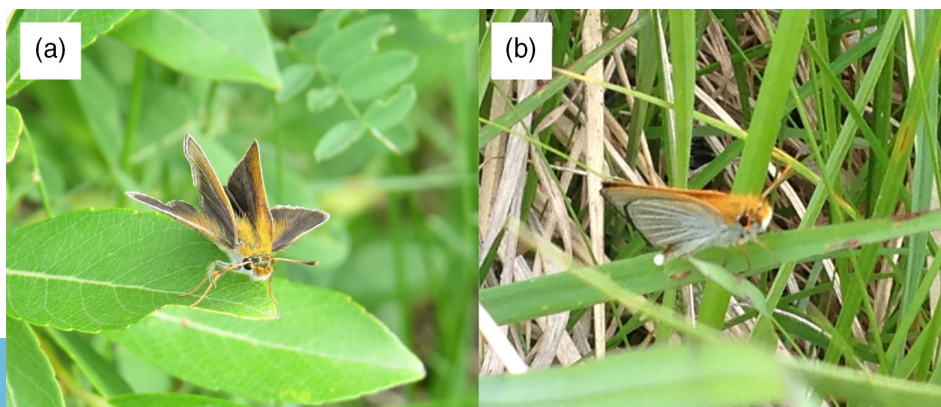
The Poweshiek skipperling (*Oarisma poweshiek*; Lepidoptera: Hesperidae; Figure 1) is a small, obligate tall grass prairie-dwelling butterfly listed as endangered in both Canada and the United States (Government of Canada, 2002; Government of the United States of America, 1973) and considered critically imperiled in Canada (Canadian Endangered Species Conservation Council, 2015). Despite being historically common, sharp population declines have been observed since the 1990s (Swengel & Swengel, 2014). The Poweshiek skipperling is now found in less than 1% of the sites it has been previously known to occupy, with six known extant populations as of 2015, all occurring on the margins of its historical range (Belitz et al., 2018). Five populations are located in the United States (86 individuals observed using standardized timed surveys, Belitz et al., 2018; Pogue, Monfils, Cuthrell, Heumann, & Monfils, 2016) and one population in Canada (36 individuals observed using standardized timed surveys; Delphney et al., 2016; Grantham, Westwood, Becker, & Hamel, 2016).

Although Canada originally included ~1% of the global historical range, when considering only the known locations since 2013, the Canadian range of 40 km<sup>2</sup> constitutes the largest contiguously-occupied area for this species (COSEWIC, 2014). In Canada, the Poweshiek skipperling is reliant on dry to moist upland prairie sites located between wooded areas, or adjacent to swamps or marshy areas (Dearborn & Westwood, 2014; McAlpine, 1972). The habitat supply for Poweshiek skipperling in

Canada has remained stable due to the poor drainage and high water table of the area, which have prevented conversion to agriculture (Eilers, Lelyk, & Fraser, 2002). This area is protected by tall grass prairie preserve (TGPP), and has been surveyed for this species on an annual basis since 2007.

The Canadian population faces ongoing threats from fragmented habitat, natural, and anthropogenic disturbance, and the interaction of these threats with each other and their life history. Poweshiek skipperlings have over an 11-month immature stage and overwinter without a protective structure (Dana, 1991; Dearborn & Westwood, 2014; Dupont-Morozoff, 2013). Tall grass prairie ecosystems are frequently subjected to natural and anthropogenic fire, flooding, and grazing. The small area of the TGPP is highly susceptible to catastrophic disturbance, putting the entire Canadian population at immediate risk. The TGPP is managed via controlled grazing and burning to maintain habitat quality over time. However, prescribed management activities like burning could eliminate local populations if poorly planned (Panzer & Schwartz, 2000; Stuhldreher & Fartmann, 2014; Swengel & Swengel, 2014).

Identifying critical habitat on a rapid timeline is essential (COSEWIC, 2014; Partnership for Poweshiek Skipperling Conservation, 2018) but may not be enough to prevent extirpation (Saarinen, Reilly, Austin, & Packer, 2016). Preventing extirpation will require persistent additional populations to maintain genetic variability and allow for recolonization after disturbance (Ries & Debinski, 2001; Taylor, Fahrig, Henein, & Merriam,



**FIGURE 1** (a) Female Poweshiek skipperling at rest (M. Hooshmandi) and (b) female ovipositing (R. Westwood)

1993). Efforts are underway to restock wild populations from rearing programs at the Minnesota Zoo and Assiniboine Park Zoo (APZ, 2017; Runquist & Nordmeyer, 2017; Smith et al., 2016). Choosing sites for reintroduction and management is particularly challenging given the high threat of disturbance and lack of understanding of life history strategies. Measures of habitat quality are needed to target areas to restock and reintroduce populations to maximize recovery success.

## 1.1 | Practical applications of species distribution models

Species distribution models (SDMs) are commonly-used tools to predict the probability of occurrence, occupancy, or abundance of a species across the landscape (Franklin, 2009). Their results frequently guide conservation action for species at risk (e.g., Collier et al., 2012; Crawford & Hoagland, 2010). An SDM has been reported for Poweshiek skipperling inhabiting fen habitat in Michigan (Pogue et al., 2016) which is ecologically different than tall-grass prairie habitat in Canada. Furthermore, an SDM was used to identify potential reintroduction for a similar species in England (Maes et al., 2019).

Although the only way to truly validate the accuracy of an SDM is with independent field-collected data (Araújo, Pearson, Thuiller, & Erhard, 2005; Franklin, 2013; Yates et al., 2018), in reality, this is rarely done due to the time and expense of collecting and processing such data (Anderson et al., 2016; Araújo & Guisan, 2006). Most SDMs are only validated statistically by withholding part of the original dataset and applying it as “test” data in a random or stratified fashion (Crawford & Hoagland, 2010; Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009; Roberts et al., 2017). Most SDMs show low model transferability (ability to make accurate predictions in other times or locations; Wenger & Olden, 2012). Despite thousands of published SDMs in the past two decades, there are very few examples validated by an independently collected dataset (but see Section 4).

We developed and field-validated an SDM for the Poweshiek skipperling in Canada using the maximum entropy (Maxent) approach (Phillips, Dudík, & Schapire, 2004). Given imminent extirpation risk, this model may be one of few chances to guide recovery efforts for the Canadian population. Our objectives were to: (a) better understand landscape-level habitat associations of the Poweshiek skipperling in Canada; (b) calibrate probability of occurrence into habitat quality categories using an independent field-collected dataset; (c) use the calibrated model to generate a stratified random sampling scheme to collect another independent dataset for field-

validation; and (d) compare expected and observed habitat quality to calculate model accuracy. Our results can be used to identify sites of high habitat quality to manage or restock existing populations and introduce new populations to support the recovery of Poweshiek skipperling in Canada.

## 2 | METHODS

### 2.1 | Study area

All historical observations of the Poweshiek skipperling in Canada are limited to the 358,000 ha Steinbach ecodistrict in Manitoba (Figure 2). Dominant land use in the ecodistrict is a mixture of farmland and unmanaged deciduous forest (Smith et al., 1998). The boreal continental climate is characterized by short, warm summers and cold winters, with mean temperatures of  $-17.1$  and  $19.8^{\circ}\text{C}$  for January and July, respectively (Environment and Climate Change Canada, 2015), and average annual temperature of  $3.4^{\circ}\text{C}$  (Smith et al., 1998). The growing season averages 184 days with mean annual precipitation of 510 mm, 1/5th of which falls as snow (Smith et al., 1998). Mean elevation is 237 m asl, with slopes less than 5%, and drainage is generally poor with soil composed of lacustrine parent material (Smith et al., 1998). The TGPP, where the Poweshiek population occurs, is formally conserved and managed by the Nature Conservancy of Canada, Nature Manitoba, and Manitoba Conservation.

### 2.2 | Modelling method and covariate selection

Of the types of SDMs in common use, we selected maximum entropy (Maxent; Phillips et al., 2004). Maxent has a superior ability to handle observations collected using different protocols (presence-only data) and a relatively small dataset (Aguirre-Gutiérrez et al., 2013; Elith et al., 2006; Phillips et al., 2009). Although methods using presence-absence or count data are generally more accurate than presence-only data, for butterflies, presence data collected over repeated years are highly correlated with count data (Casner, Forister, Ram, & Shapiro, 2014).

Maxent relates presence data and environmental covariates using a machine-learning algorithm to predict probability of species occurrence across the landscape. More important than type of SDM is the choice of environmental covariates (Elith & Leathwick, 2009; Franklin, 2009). A rule of thumb is to choose no more than one covariate per 10 presence locations to avoid model overfitting (Harrell, 2001; McGill, 2013).



**FIGURE 2** Study area for species distribution modelling of Poweshiek skipperling in Canada, which includes one of six extant worldwide populations. The nearest adjacent population is 1,200 km southeast in Michigan, USA. Ecoregions are differentiated by shading, and individual ecodistricts with gray borders. Left inset, Steinbach Ecoregion. Tall Grass Prairie Preserve boundaries provided by the Nature Conservancy of Canada (personal communication), ecodistrict boundaries available from Agriculture and Agri-Food Canada (2013) and satellite imagery from Esri Inc., (2014)

The distribution of any species, including the Poweshiek skipperling, is controlled by its niche requirements (Hutchinson, 1957; Pulliam, 2000), which are determined by proximate factors (directly linked to life history needs, such as daytime temperature, precipitation, cloud conditions, availability, and condition of host plants, and so on) and ultimate factors (indirectly linked to life history needs, such as average annual temperature and precipitation, soil type, and so on). SDMs are often completed with little theoretical linkage between covariates and niche factors (Hirzel & Le Lay, 2008), so we explicitly modelled niche requirements as best as possible. As the Poweshiek skipperling spends the vast majority of its life cycle in only a few square meters (much smaller than the resolution of most spatial data products used in landscape-scale modelling), we postulated proxies between the fundamental niche requirements of food, shelter, reproduction and factors which can be captured at the landscape scale by available spatial data products (Table 1). As butterflies are known to select habitats based on both local and landscape factors, particularly habitat configuration (Davis, Debinski, &

Danielson, 2007; Soga et al., 2015), we captured factors related not only to microsite but also landscape matrix.

Five spatial data layers (Table 2) were used to extract seven covariates (Table 3). All analyses were completed in ArcGIS 10.2.2 (Esri Inc., 2014). Covariate rasters were scaled to 30 m × 30 m and clipped to the boundaries of the Steinbach ecodistrict. We identified three distinct covariate groups: landcover type and configuration (*land use, distance to deciduous stand, and patch size*), microclimate proxies such as energy input, substrate, and moisture (*solar insolation—seasonal, solar insolation—year, soil type, and soil drainage*), and a proxy for disturbance (flood risk via *distance to wetlands*). Four additional candidate covariates were excluded due to data limitations: vegetation height and flood risk (LiDAR imagery was only available for a portion of the study area), and years since graze and years since burn (data as available for the TGPP but not for the rest of the ecoregion).

After calculating correlation ratios for all covariates (1 = perfect correlation and 0 = no correlation; Snedecor & Cochran, 1968) we discarded *solar insolation—seasonal* due to high correlation with *solar*

**TABLE 1** Relationship between fundamental niche requirements and factors at microhabitat and landscape-scales for the Poweshiek Skipperling (information on flower and grass species from Dupont-Morozoff (2013) and Hooshmandi (2016))

Niche requirement	Proximate factor (microhabitat scale)	Ultimate factor (landscape scale)	Covariate group
Cover/shelter	Shrubs and tall grass species	Size, shape, and border of tall grass prairie ecosystem	Landcover
Adult food plant availability	Nectar flower species ( <i>Rudbeckia hirta</i> , <i>Solidago ptarmicoides</i> , and <i>Prunella vulgaris</i> )	Tall grass prairie ecosystem moisture and temperature regime	Microclimate
Larval host plants and reproduction in Canada	Grasses for egg-laying and larval feeding ( <i>Andropogon gerardii</i> , <i>Schizachyrium scoparium</i> , <i>Muhlenbergia richardsonis</i> and <i>Sporobolus heterolepis</i> )	Years postgraze and postburn; flood risk	Disturbance regime

**TABLE 2** Spatial data layers to extract covariates for Maxent modelling of the Poweshiek skipperling in Canada (all layers are available from Government of Manitoba (2014) or NASA (2014))

Layer	Description	Data year	Resolution (m)	Rights
Digital elevation model (DEM)	Shuttle radar topology Mission (SRTM) 1 arc sec digital elevation tiles	2000	30 m	United States geological survey
Manitoba Forest resource inventory (FRI)	Forest inventory based on 1:15,840 orthorectified aerial photography	1958-present	Vector	Manitoba land initiative
Land use classification (LUC)	Land use classified from 30 m LANDSAT thematic mapper imagery	2005	30 m	Manitoba sustainable development, Manitoba remote sensing Centre
Soils	Field-verified classification of type and drainage of soils using the soil agricultural interpretations database, mapped at scales ranging from 1:20,000 to 1:126,720	Unk.	Vector	Manitoba department of agriculture
Southern peatlands	Classification of wetland coverage in the Interlake and southern boreal regions of Manitoba from 30 m LANDSAT 8 imagery, minimum map unit = 1 ha	2013	Vector	Manitoba habitat heritage Corporation and ducks unlimited Canada

insolation—yearly (ratio = 0.99). All other covariates showed correlation ratios of  $\leq 1$  and were retained.

### 2.3 | Maxent modelling

We combined presence observations collected by various observers between 2002 and 2015 to produce a dataset of 272 unique Poweshiek skipperling presence locations. Most of these observations were collected by the laboratory of R. Westwood using standardized timed surveys (Grantham et al., 2016) with 10 observations from the

records of R. Webster (Webster, 2002). Each record included (at minimum) the location and date of the collection or observation, the name of the collector or the observer, and in some cases information about the observation (nectaring, flying, and so on). Observations were collected using standardized timed surveys, which count of the number of individuals observed per 60 min of survey time. Survey days were generally sunny with a daily high temperature range of 20–32°C, low winds, and little precipitation (Grantham et al., 2016).

To limit autocorrelation, we applied spatial filtering (Boria, Olson, Goodman, & Anderson, 2014) in Maxent

**TABLE 3** Covariates used in Maxent modelling of the Poweshiek skipperling

Covariate	Extraction method	Type	Source layer (see Table 2 for description)
Distance to deciduous	Euclidean distance to nearest polygon classified as deciduous	Continuous	FRI
Distance to wetlands	Euclidean distance to nearest polygon classified as any type of wetland	Continuous	Southern peatlands
Land use	Conversion of land use classification to raster	Categorical	LUC
Patch size	Size (in ha) of patch representing an area of contiguous land use	Continuous	LUC
Soil drainage	Conversion of stoniness group value to raster	Categorical	Soils
Soil type	Conversion of dominant soil type to raster	Categorical	Soils
Solar insolation—seasonal	Calculated on the study area + 1 km buffer using Solar Analyst, following Fu and Rich (2000). Sky size was set at 3,000 cells/hemisphere and 64 viewsheds. Zenith division = 1,440 and azimuth division = 160. Diffuse model type = uniform sky, diffuse proportion = 0.3, transmissivity = 0.5. Interval outputs at 15 min were averaged over the growing season, May–October.	Continuous	DEM
Solar insolation—yearly	Calculated on the study area plus a 1 km buffer using the Solar Analyst tool, following Fu and Rich (2000). Sky size was set at 3000 cells/hemisphere and 64 viewsheds. Zenith division = 1,440 and azimuth division = 160. Diffuse model type was uniform sky with diffuse proportion = 0.3 and transmissivity = 0.5. Interval outputs at 15 min were averaged over the entire year.	Continuous	DEM

to exclude observations within 30 m of each other, leaving 180 filtered presence locations. We ran 10 cross-validated model replicates with the maximum iterations at default (500), where a random subset of the data was chosen for each replicate and compared to the default number of background points (10,000). For each replicate, we used a jackknife approach to test model fit, whereby 10% of the data (18 presence locations) was retained and assessed against model prediction, expressed as the area under the curve (AUC). AUC was averaged for all 10 replicates. Each replicate produced a probability of occurrence raster in .asc format, the arithmetic mean of which was used to produce the final probability of occurrence map.

## 2.4 | Model calibration

To translate predicted probability of occurrence to habitat quality, the relationship between the two must be quantified. Mathematical calibration can be done using

the lowest presence threshold (Pearson, 2010), such as by Pogue et al. (2016), who calibrated their model threshold values in areas of known Poweshiek skipperling occupancy from their original dataset. As our model was intended for use to identify potential locations to reintroduce populations, we calibrated the model to represent *habitat quality* rather than *occupied areas*. Based on previous studies of larval host plants, nectar plants, and moisture and landcover regimes associated with abundance of Poweshiek skipperling (Dupont-Morozoff, 2013; Hooshmandi, 2016), we developed a rating system for experts to classify sites into four categories (1 = excellent, 2 = good, 3 = medium, 4 = poor; Appendix S1).

We collected an independent dataset of habitat quality by rating 24 sites (ranging from 3 to 20 ha) in the TGPP with both extant butterfly populations of skipperlings and observations pre-2010. Researchers were given maps superimposing a grid of 30 m × 30 m cells over a satellite image of each site and surveyed straight transects through all traversable areas, visually assessing

**TABLE 4** Probability of occurrence of Poweshiek skipperling using Maxent modelling as compared to field-assigned habitat quality classes in the Tall Grass Prairie Preserve, Manitoba

Field-assigned habitat quality class	Mean probability of occurrence (raw)	Probability of occurrence (factor analysis)		Expected habitat quality class threshold	Expected habitat quality class
		Mean	Standard deviation		
Excellent	0.75	0.73	0.26	$\geq 0.73$	Good-excellent
Good	0.72				
Medium	0.63	0.66	0.31	$< 0.73$	Poor-medium
Poor	0.54	0.54	0.33		

each cell and ranking it as habitat quality category 1–4. We surveyed ~250 ha and assigned a habitat quality class to 1,451 cells. After digitizing, we compared observed habitat quality class to probability of Poweshiek skipperling occurrence in each cell (Table 4). Factor analysis using a Chi-squared Automatic Interaction Detection growing method and cross-validation (SPSS 21.0; IBM Corporation, 2012) indicated that probability of occurrence could only be significantly split into three classes or less. As only a small portion of the ecodistrict fell within the value range for the “medium,” we divided expected habitat class into two classes (good-excellent, probability of occurrence  $\geq 0.73$ ; poor-medium, probability of occurrence  $< 0.73$ ).

## 2.5 | Field-validation with an independent dataset

To field-validate model accuracy on a landscape scale within the Steinbach ecodistrict, we randomly selected locations from the map of expected habitat class to be rated. We stratified sampling by accessibility (within 100 m of road or trail) and by expected habitat class. Of 227 generated locations (195 predicted as poor-medium and 32 as good-excellent), researchers visited 108 locations (86 predicted as poor-medium and 22 predicted as good-excellent) in August–September 2017. Researchers were blind to expected class and ranked each location in the field as habitat quality Class 1–4.

Model prediction accuracy was classified using an error matrix (Cihlar et al., 2003; Congalton & Mead, 1983) by comparing categorical spatial datasets with reference data collected on the ground (Hart, 2014; Naesset, 1995). Cohen's Kappa (Cohen, 1960) coefficient ( $k$ ) was used to measure how observed correspondence between expected and observed habitat quality classes compared to correspondence that would occur simply by chance (Congalton & Mead, 1983).

## 3 | RESULTS

### 3.1 | SDMs and habitat associations

Across all 10 replicates, probability of occurrence models showed high AUC for modelling both training (average 0.981, SD = 0.001) and test (average 0.978, SD = 0.006) data. Covariates with highest mean percent contribution to the training model included *soil drainage* (36%), *patch size* (25%), and *land use* (20%). Remaining covariates contributed less than 10% (Table 5). Despite not showing highest percent contribution, jackknife results showed *patch size* as contributing most strongly to both training and test gain. To understand the relationship of probability of occurrence and environmental factors, we examined species-environment response curves for each covariate in isolation from the total model (Figure 3). Predicted probability of occurrence was highest ~200 m from wetlands, <100 m from deciduous treed stands, and in land use categories 4 (grassland/rangeland) and 16 (roads/trails). Higher probability of occurrence also corresponded to a patch size of ~1000m<sup>2</sup>, soil types 42, 80, and 99 (Inwood Soil Series, Pelan Series, and Sprague Series, respectively), soil drainage class 2 (moderately stony, 1–3%), and total yearly solar insolation of ~257 kW/m<sup>2</sup>.

When predictions based on the final model were mapped, only 0.4% of the Steinbach ecodistrict showed a predicted probability of occurrence above  $\geq 0.73$  (expected habitat quality class good-excellent; Figure 4). These areas predominantly occurred within 35 km of the TGPP, with the largest clusters of highly-ranked areas within 20 km of the TGPP.

### 3.2 | Field validation

When comparing predicted probability of occurrence to four observed habitat quality classes at 108 locations (Figure 5), sites observed as “excellent” showed mean

**TABLE 5** Average contribution of covariates to model prediction, permutation importance, training gain, and test gain across 10 cross-validated Maxent model runs predicting probability of occurrence of the Poweshiek skipperling

Environmental variable	Average percent contribution	Average permutation importance	Average training gain contribution rank	Average test gain contribution rank
Soil drainage	36.1	24.0	2	3
Patch size	24.7	13.4	1	1
Land use	20.2	17.9	4	4
Distance to wetlands	9.6	30.4	5	5
Soil type	6.8	10.3	3	2
Distance to deciduous	1.5	1.7	6	6
Yearly solar insolation	1.2	2.4	7	7

predicted probability of occurrence = 0.81 ( $SD = 0.25$ ), with 83% of “excellent” sites showing a predicted probability of occurrence  $>0.73$ . There was more variation in sites observed as “good” (mean = 0.39,  $SD = 0.39$ ) and “medium” (mean = 0.27,  $SD = 0.31$ ). All sites observed as “poor” showed a probability of occurrence  $<0.73$  (mean = 0.12,  $SD = 0.22$ ). An error matrix was used to compare habitat quality class at the two-class level between expected (model-predicted) and observed (field-assigned) classes (Appendix S2). Observed accuracy for the two-class condition was 81% with Kappa = 0.48, indicating agreement better than expected by chance. Accuracy was higher for sites observed as medium-poor (92%) and lower for sites observed as good-excellent (52%).

## 4 | DISCUSSION

Our findings provide a tool to guide restocking and reintroduction of this critically endangered species. Our AUC value (0.98) was very high, and likely inflated due to spatial autocorrelation (Vierod, Guinotte, & Davies, 2014) due to the clustered nature of the presence points and low environmental variation across the TGPP (all Poweshiek skipperling presences occurred within a 14 km by 14 km area). Inflation may also be a result of too many included variables, and future iterations of this model should use a statistical variable-reduction method appropriate for Maxent (such as forward-stepwise variable selection, see (Bale, Beazley, Westwood, & Bush, in press; Halvorsen et al., 2016) to improve model parsimony.

### 4.1 | Habitat associations of the Poweshiek skipperling

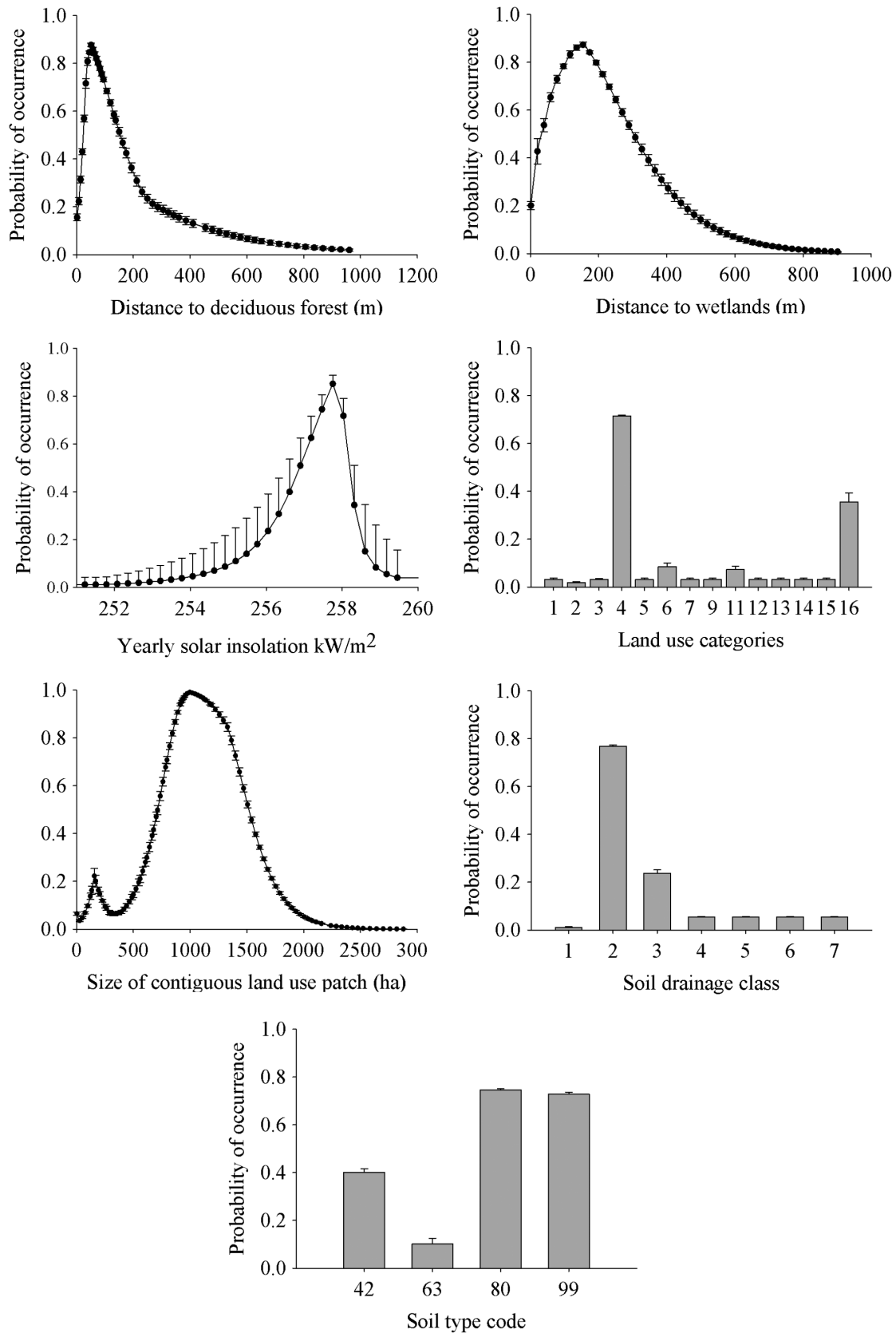
Due to short-lived adult stages and the cryptic nature of immatures, it is difficult to gather the life-history

information needed to identify critical habitat for many butterfly species. The habitat associations for the Canadian population derived from our model can guide future conservation efforts that are more reflective of known species' biology and ecology.

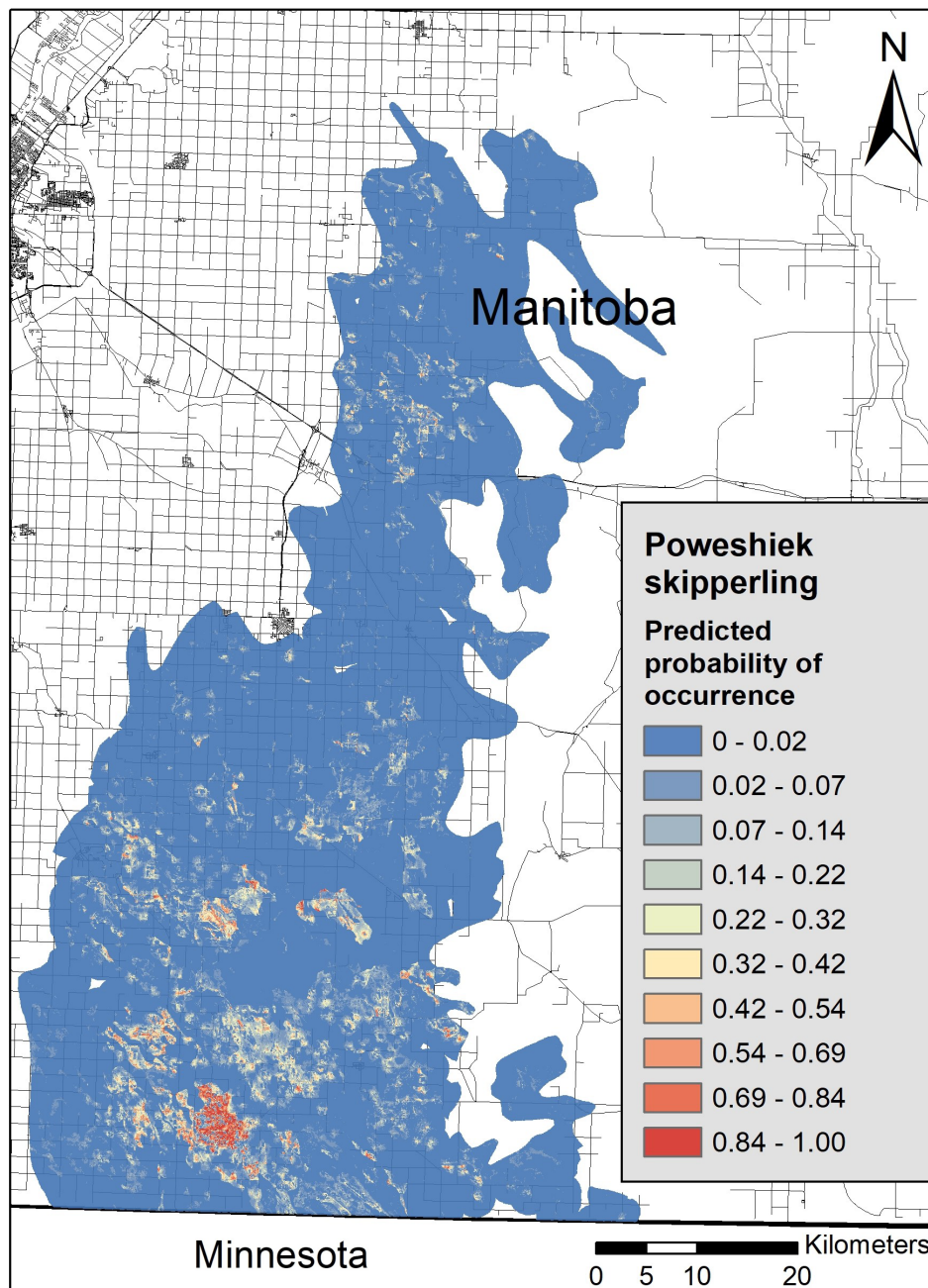
Though not directly transferable due to different covariates used and different aim, our results contrasted Pogue et al. (2016)'s Michigan-based model in some important ways. Pogue et al. (2016) found that probability of prairie fens favourable to Poweshiek skipperling occurrence decreased with higher densities of roads and developed areas (though with low contribution importance, 8%). We did not include road density as a covariate but found “roads/trails” was a cover type associated with high probability of occurrence of Poweshiek skipperling. This is likely because roadsides and trails in southern Manitoba are generally bordered by grassland and/or deciduous woodlands that are not subject to agriculture or grazing and may provide some buffering capacity from the effects of roads (Ries & Debinski, 2001). This also may be a factor of spatial autocorrelation as the entire Canadian population is found in an area of high road density, and all presence observations occur within 1,500 m of the nearest road.

Pogue et al. (2016)'s model was predominantly explained by area of prairie fen. In another study, meadow area alone was not positively correlated with butterfly abundance (Liivamägi, Kuusemets, Kaart, Luig, & Diaz-Forero, 2014). It is known that landscapes comprised of small, heterogenous patches support higher diversity, abundance, and species richness of butterflies in prairie-remnant communities (Davis et al., 2007; Slancarova, Benes, Kristynek, Kepka, & Konvicka, 2014; Weibull, Bengtsson, & Nohlgren, 2000). Our study supports the importance of landscape configuration with median patch sizes and proximity to deciduous forests. In Manitoba, the Poweshiek skipperling is most often located in connected small patches of open prairie near





**FIGURE 3** Species-response curves indicating the relationship between predicted probability of occurrence of the Poweshiek skipperling and covariates isolated from the total model. Error bars indicate standard deviation. \*only soil types with p.occ >0.01 are shown, all others are omitted

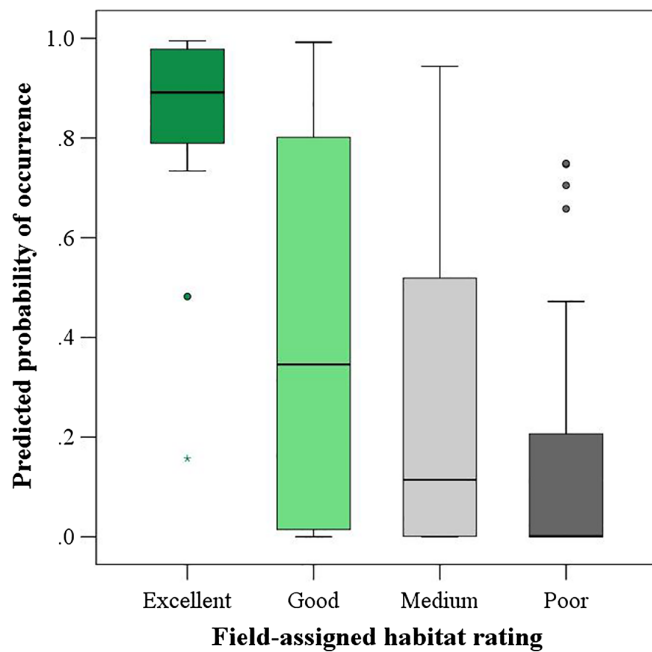


**FIGURE 4** Predicted probability of occurrence of Poweshiek skipperling using Maxent species distribution modelling in the Steinbach ecodistrict of Manitoba

small copses of trees and adults rarely enter areas with heavy shrubs or woodlands (Dupont-Morozoff, 2013; Hooshmandi, 2016; Semmler, 2010). It is unknown if trees provide a functional barrier to the movement of this species as documented for other butterflies (see Weibull et al., 2000). Future field or spatial analyses could be undertaken to help predict functional connectivity between discrete locations.

As all three soil types associated with high probability of occurrence are poorly drained and experience a water table at or near the surface during the growing season (Manitoba Agriculture Food and Rural Initiatives, 2010), our model suggests that soil type and drainage is an

important driver of distribution. This corresponds with Hooshmandi (2016), who found both composition and pH of soil to be an important predictor of abundance of Poweshiek skipperling. Although yearly solar insolation was not a meaningful predictor variable, the future availability of LiDAR-based DEMs may allow for a more precise examination of energy availability at the microsite level. As with many insects, the emergence period of Poweshiek skipperling is strongly predicted by number of growing degree days (Dearborn & Westwood, 2014), suggesting the importance of modelling energy availability and its relationship to structure or composition of habitat type. Microclimate effects including soil moisture



**FIGURE 5** Probability of occurrence for Poweshiek Skipperling, predicted by a Maxent model for the Steinbach ecodistrict of Manitoba, compared to field-observed classes of habitat quality

and solar insolation are important predictors of persistence for other lepidoptera species (Suggitt et al., 2015), and future modelling efforts for this species should consider the range-wide climatic envelope.

#### 4.2 | Limitations in model application

The Poweshiek skipperling faces other threats such as pesticides (Godfray et al., 2015) and pathogen and genetic impacts (Nice, Gompert, Forister, & Fordyce, 2009; Saarinen et al., 2016). Although our results can support ongoing identification of critical habitat for this species (Camaclang, Maron, Martin, & Possingham, 2015), further work is required to identify factors related to population persistence such as minimum area requirements (Baguette & Stevens, 2013) or mobility (Burke, Fitzsimmons, & Kerr, 2011). Furthermore, because of declines in number and additional pressures, it is possible that the Poweshiek skipperling is not occupying all available habitat (the problem of habitat saturation, see Whittaker, Willis, & Field, 2001) or that the habitat it does occupy is not ideal. Thus, predictions based on current populations may not reflect ideal reintroduction conditions. Indeed, with ~99% of the original tall grass prairie in North America having been lost since European settlement (Samson & Knopf, 1994), it may be impossible to understand ideal habitat

requirements for this species given high levels of disturbance.

This species is likely vulnerable to climate change due to phenological impacts (Westwood & Blair, 2010), particularly adult emergence and potential impacts on voltinism, as observed in similar species (Altermatt, 2010). The TGPP is expected to be strongly impacted by climate change by 2080 (Gerla, 2016). However, given the extremely low availability of native prairie, should the climate envelope move northward, there simply may not be any available habitat for dispersal unless restoration efforts begin immediately.

#### 4.3 | Model accuracy and implications for management

Field validation demonstrated that our model accurately predicted medium-poor habitat in almost all cases (92%). Thus, when using model results to identify locations for management, users can reliably exclude all areas with a predicted probability of occurrence  $\leq 0.73$  from search. Though, the model did not predict good-excellent habitat as accurately, the majority of field-identified excellent habitat (>80%) corresponded with a predicted probability of occurrence  $> 0.73$ . We suggest that candidate management or reintroduction areas ( $> 0.73$ ) should be searched for sufficient densities of host plants before reintroduction (Carleton & Schultz, 2013). Our Kappa value was likely artificially low as Kappa is intended to be used with categories of equal size, however, we had many more samples in medium-poor than good-excellent habitat.

Statistical validation of the model using AUC showed high accuracy of predicting presence-absence of test data (0.978), and most SDMs rely on statistical methods such as AUC alone as a surrogate for model accuracy. Given that field validation showed 81% accuracy, we echo recommendations of others to be cautious about interpreting model accuracy from statistical methods alone, particularly AUC (Drew, Wiersma, & Huettmann, 2011; El-Gabbas & Dormann, 2017). Of the few SDMs in the literature that have been field-verified, most show low accuracy. Anderson et al. (2016) found a correlation of only 10% between presence/absence of their predicted species and Maxent-predicted probability of occurrence and concluded that their model failed. Fois, Cuenca-Lombrana, Fenu, and Bacchetta (2018) tested Maxent models against independent datasets and concluded reliability was low. Although West, Kumar, Brown, Stohlgren, and Bromberg (2016) found that detection of their target species was more frequent in higher predicted habitat suitability classes, they did not statistically quantify prediction accuracy.

One study did find good agreement between predictions from four older SDM methods and independently-collected data (Spearman rank correlation .66–.94; Johnson & Gillingham, 2005), and Haughian, Clayden, and Cameron (2019) were able to find their target species in 13 of 22 (60%) of sites where predicted Maxent probability of occurrence was  $>0.50$ . We do note that other studies validated their models (which predicted probability of occurrence) against novel presence observations of species, whereas we predicted and validated habitat quality. Field-validating our model using novel presence observations is not possible in our situation, since the location of all individuals in the population was known and identical to the locations used to train the model.

In our case, we collected two independent datasets for model validation, which was partly facilitated by the small size of the study area. A recent aggregation of all known Poweshiek skipperling presence records from 1897 to 2018 (Belitz et al., 2018) may allow for the development of more accurate models across the species' range and offer new data to validate existing models. However, as has been recommended for over a decade (Araújo et al., 2005; Johnson & Gillingham, 2005), we reiterate a call for producers of SDMs to validate their models with an independent field-collected dataset, particularly where those SDMs are used to make management decisions. This caution is underscored in urgent cases like that of the critically endangered Poweshiek skipperling, where opportunities for model refinement may not be available if recovery actions are not implemented immediately.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHOR CONTRIBUTIONS

R.W. and M.H. conceived the study. Study design by R.W., M.H., A.R.W., and K.P. Field sampling conducted

by R.W., M.H., and K.L. Spatial analysis and modelling conducted by M.H., K.P., A.R.W., and C.M. Statistical analysis and visualization conducted by R.W. and A.R.W. Manuscript preparation and submission led by A.R.W. and R.W., with all coauthors providing editorial support.

## ETHICS STATEMENT

Provincial endangered species research permit was acquired for each year of noninvasive field sampling from the Government of Manitoba.

## DATA AVAILABILITY STATEMENT

Model results (predicted probability of occurrence of Poweshiek skipperlings) are available in Supporting Information. Survey data indicating presence locations and field-rated suitable habitat for Poweshiek skipperlings are not publicly available due to concerns about potential harm to a critically endangered, highly localized population. Please contact the laboratory of R.W., University of Winnipeg, for information about this dataset (r.westwood@uwinnipeg.ca).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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