


## SPECIAL ISSUE ARTICLE

# Landscape-level environmental stressors contributing to the decline of Poweshiek skipperling (*Oarisma poweshiek*)

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**Abstract.** 1. The Poweshiek skipperling [*Oarisma poweshiek* (Parker, 1870; Lepidoptera: HesperIIDae)] is a federally endangered butterfly that was historically common in prairies of the upper Midwestern United States and Southern Manitoba, Canada. Rapid declines over the last 20 years have reduced the population numbers to four verified extant sites. The causes of Poweshiek skipperling decline are unknown.

2. We aggregated all known Poweshiek skipperling occurrence records to examine the spatiotemporal patterns of Poweshiek skipperling decline. Ecological niche models were developed for five time frames (1985, 1990, 1995, 2000 and 2005) and three spatial extents (eastern occupied range, western occupied range and total occupied range). We used a backward elimination method to investigate the effects of climate and land use on the ecological niche of Poweshiek skipperling.

3. Predictors of occurrence changed over time and across the geographical extent of Poweshiek skipperling. Land use covariates were retained in east models. In the west and total extent, climate variables contributed the most to model predictive power for the 1985, 1990 and 1995 models; land use variables contributed the most to model predictive power in the 2000 and 2005 models.

4. During the rapid decline in Poweshiek skipperling population numbers occurring at the turn of the century, probability of Poweshiek skipperling presence was being driven by proportion of natural land cover and distance to nearest grassland/wetland. Our results suggest that these land use variables are important landscape-level variables to consider when developing risk assessments of extant populations and potential reintroduction sites.

**Key words.** Butterfly conservation, ecological niche modelling, endangered species, extinction, HesperIIDae, land use change, Maxent.

## Introduction

The Poweshiek skipperling [*Oarisma poweshiek* (Parker, 1870; Lepidoptera: HesperIIDae)] is a federally endangered butterfly that was historically common in prairies of the upper Midwestern United States and Southern Manitoba, Canada (Selby,

2005; Swengel *et al.*, 2011). Since the turn of the 20th century, a dramatic range-wide reduction in populations has occurred (Swengel *et al.*, 2011; Pogue *et al.*, 2016). This decline has been suggested to have proceeded from west to east (Dupont, 2011). As of 2019, there are four known extant Poweshiek skipperling sites occurring at the geographic edges of the historical range. Three sites are in Michigan prairie fens and one in a fragmented tallgrass prairie system in Manitoba, Canada (Delphey *et al.*, 2016; with updates from long-term Michigan surveys conducted with the Michigan Natural Features Inventory, and Wisconsin surveys by J. Zaspel, pers. comm., and Wisconsin Department

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of Natural Resources). In 2014, the United States and Canada classified the Poweshiek skipperling as federally endangered [US Endangered Species Act (ESA), 1973; SARA, 2002; Committee on the Status of Endangered Wildlife in Canada (COSEWIC), 2014; U.S. Fish and Wildlife Service (USFWS), 2014].

The Poweshiek skipperling is a small-bodied (wingspan 2.3–3.0 cm), univoltine butterfly (Selby, 2005) that has restricted dispersal ability and difficulty crossing dispersal barriers as it is rarely observed flying above 1.5 m. The adult flight period lasts from approximately late June to early July (Selby, 2005). McAlpine (1973) observed an egg stage that lasted approximately nine days, after which larvae feed until initiating diapause as a fifth instar in the latter part of September before resuming feeding in late March to early April. Overwintering Poweshiek skipperlings do not make shelters like many other skipper species and remain exposed at the base of grasses through winter, potentially leaving Poweshiek skipperling vulnerable to extreme weather conditions, dormant season fire, and other disturbances such as cattle grazing and pesticide drift (Runquist & Heimpel, 2017). Primary nectar sources of Poweshiek skipperling include *Rudbeckia hirta*, *Dasiphora fruticosa*, *Echinacea angustifolia*, and *Solidago ptarmicoides* (Swengel & Swengel, 1999; Semmler, 2010; Cuthrell & Slaughter, 2012; Belitz et al., 2019). Female Poweshiek skipperlings have been documented ovipositing on a variety of graminoid species, with larvae and ovipositing females appearing to prefer fine, thread-like structures (Selby, 2005; Belitz et al., 2019). Poweshiek skipperlings were historically documented in habitat that included wet-mesic prairie, dry prairie and prairie fen (Selby, 2005).

Immense land use change has occurred across the historic range of Poweshiek skipperling and populations exist in highly fragmented landscapes. Around 99% of tallgrass prairie in North America has been destroyed since 1830, with most former prairie habitat converted to agriculture by 1950 (Sampson & Knopf, 1994). Despite this widespread destruction of prairie habitat, Poweshiek skipperling was the prairie specialist butterfly most frequently observed in surveys conducted in the mid-1990s (Schlicht et al., 2009). These observations occurred in fragmented prairie patches, primarily concentrated in Western Minnesota and the Eastern North and South Dakota.

The recent and rapid decline in Poweshiek skipperling coincides with more recent changes in agricultural practices, particularly the introduction of neonicotinoids and the chemical response to the invasion of the soybean aphid (*Aphis glycines*; Runquist & Heimpel, 2017). Neonicotinoids were introduced in the 1990s and use rapidly increased in the United States between 2003 and 2011 (Douglas & Tooker, 2015). Between 2000 and 2006, there was a 130-fold increase in the use of insecticides on soybean fields, driven by documentation of the soybean aphid in 2000 and its rapid expansion to becoming the single-most important arthropod pest of soybeans (Ragsdale et al., 2011). The Poweshiek skipperling's historic range overlaps with the counties in the United States that produce the most corn ([https://www.nass.usda.gov/Charts\\_and\\_Maps/Crops\\_County/cr-pl.php](https://www.nass.usda.gov/Charts_and_Maps/Crops_County/cr-pl.php)) and soybeans ([https://www.nass.usda.gov/Charts\\_and\\_Maps/Crops\\_County/sb-pr.php](https://www.nass.usda.gov/Charts_and_Maps/Crops_County/sb-pr.php)), exposing Poweshiek skipperling sites to potential pesticide drift. Although

Poweshiek skipperling displayed the greatest decline, butterflies surveyed in Midwest prairies in general have shown declines (Swengel et al., 2011). Poweshiek skipperlings are particularly vulnerable to environmental perturbations because their short adult flight period, limited dispersal capability and specialization on prairie habitat limits their ability to recolonize vacant patches after local extinction (Thomas, 2016).

In addition to the wide-spread land use changes that have occurred across the historic range of Poweshiek skipperling, this species may also be negatively impacted by a changing climate. The Midwest has experienced an increase in minimum air temperature and precipitation from 1916 to 2007, a trend that is projected to continue (Mishra et al., 2010). Changes in mean climate parameters and the intensity of climatic extremes can impact butterfly physiology and fitness, making butterflies particularly sensitive to climate-related change (Boggs, 2016). Warming has led not only to milder winters in temperate zones but also to unpredictable extreme weather events (Jentsch et al., 2007). These extreme weather events, such as late spring frost, have led to dramatic short-term declines in Lepidoptera abundance (Greco et al., 2018).

Not being able to identify the factor(s) driving the decline of a species is a main reason conservation plans stay in the reactive stage (Worthington et al., 2014). To investigate the potential effects of climate and land-use changes on Poweshiek skipperling, we examined the spatiotemporal patterns of decline in the number of extant Poweshiek skipperling sites. We examined the presence of known Poweshiek skipperling sites in 5-year increments from 1985 to 2005. Using an ecological niche modeling (ENM) approach, we correlate the presence of Poweshiek skipperling to extreme temperature, extreme precipitation, proportion of land cover, fragmentation and agricultural chemical variables. This study aims to determine the effects of environmental variables on the ecological niche of Poweshiek skipperling through time and space to begin quantitatively assessing the influence of climate and land use variables on the range-wide decline of this species. Our goal was to contribute information on the impact of environmental stressors on Poweshiek skipperling to inform environmental risk assessments and conservation initiatives.

## Materials and methods

### Aggregating Poweshiek skipperling occurrence data

Poweshiek skipperling occurrence records were aggregated from observation and specimen-based records from natural heritage programs (e.g. Michigan Natural Features Inventory, Minnesota Department of Natural Resources), state conservation agencies (e.g. South Dakota Game, Fish and Parks), the USFWS, community scientists (e.g. iNaturalist, The Lepidopterists' Society), and natural history collections. Occurrence records were also gathered from the Global Biodiversity Information Facility and Lepidoptera of North America Network (LepNet). LepNet is a thematic collection network, whose data included human observations from community scientists and preserved specimens from natural history collections (Seltmann et al., 2017).

Extensive surveys have occurred in Western Minnesota, Eastern South Dakota, and Eastern Michigan to monitor Poweshiek skipperling population trends and determine if populations have been locally extirpated (Selby, 2005; Swengel *et al.*, 2011; USFWS, 2014; Swengel & Swengel, 2015; Pogue *et al.*, 2016). Our aggregated data set includes data collected from these surveys, along with occurrences documented through research vouchers and opportunistic observations and collections.

In the process of vetting the occurrence records and preparing the data for use in modelling, we georeferenced occurrences, removed duplicates and standardized formatting. Occurrence records were examined for inconsistencies with known Poweshiek skipperling biogeography and phenology, and we verified or removed inconsistencies by working with the original data providers. To ensure the correct identification of the specimen, images of specimens georeferenced outside the previously known range of the Poweshiek skipperling were obtained and checked by D.L. Cuthrell, a Poweshiek skipperling expert who has worked with this species for over 20 years. Additional information regarding our data aggregation methodology and a downloadable data set can be found in Belitz *et al.* (2018).

#### *Processing Poweshiek skipperling sites*

For the purpose of our analysis, occurrence records located within 1-km of other occurrence records were classified as a single site. Occurrence records that could not be accurately georeferenced with a 1-km or finer resolution were removed from the analysis. Sites, instead of individual occurrence records, were used in our analyses to limit the influence of potential spatiotemporal sampling biases (Yackulic *et al.*, 2013). All sites were overlaid in ArcMap 10.4.1 (Esri, 2016) with the World Imagery base map, which features 0.5-m resolution imagery in the continental United States, to verify locations were georeferenced in grasslands. The Poweshiek skipperling site in Manitoba, Canada was removed from our study because of the lack of inter-operability between the geographical information system (GIS) landscape data available for the United States and Canada.

#### *Geographic and temporal coverage of the study*

Our total study area consisted of all counties that were within 10-km of a site with a Poweshiek skipperling occurrence recorded in 1980 or later. We decided to include counties within 10-km because butterfly distributions are commonly mapped on a 10-km grid in northern Europe and have stimulated considerable research and conservation effort (Thomas & Abery, 1995). In addition to our total extent, we defined two additional extent windows that were determined based on the geographic separation of Poweshiek skipperling populations. The disjunct populations in Wisconsin and Michigan formed the east extent. States accommodating the core range of historic Poweshiek skipperling sites (North Dakota, South Dakota, Minnesota, and Iowa) were separated as the west extent (Fig. 1). ENMs may be skewed by species at the edge of their fundamental niche when environmental stressors lead a species to live in suboptimal conditions

(Braunisch *et al.*, 2008). To address this, we individually modelled east and west extents to examine differences in drivers of the ecological niche of Poweshiek skipperling between geographic locations.

We separated Poweshiek skipperling sites into data sets delineated by seven time frames separated by 5-year intervals: 1985, 1990, 1995, 2000, 2005, 2010 and 2015. These years were based on the temporal availability of Poweshiek skipperling occurrences, landscape data and climate data. All sites that had at least one Poweshiek skipperling occurrence recorded in or after the focal year were included in the respective data set. For example, the 1985 data set included all sites that had a Poweshiek skipperling occurrence after 1984. If Poweshiek skipperlings were observed in a site in 2016 (the last year of observations we included in our occurrence data set), that site was included in the data set for all seven time frames. Poweshiek skipperlings are poor dispersers that are rarely observed flying greater than chest height or flying over physical barriers. Due to the limited dispersal capacity of Poweshiek skipperling, combined with the extensive fragmentation of the prairies, occupied sites are expected to be closed populations. Therefore, we assumed that an occupied site in 2015 would also have been an occupied site in 1985. We did not develop ENMs for 2010 and 2015 because by 2010, Poweshiek skipperling were locally extinct in the west extent. We used all seven time frames to estimate apparent declines in occupied sites, but our ENMs were only developed for five time frames with sufficient data (1985, 1990, 1995, 2000 and 2005).

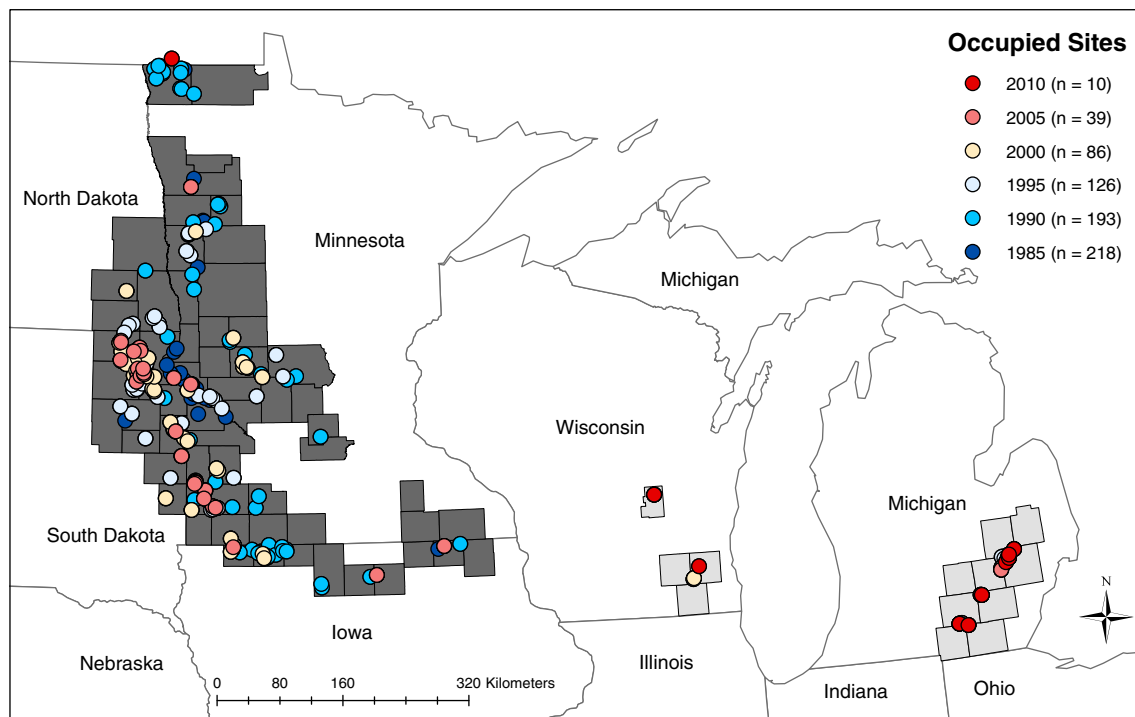
#### *Estimating apparent declines in occupied sites*

The site data sets were used to estimate the proportion of sites that went locally extinct between each time frame. The proportion of sites that went locally extinct between each time frame was determined by calculating  $1 - \frac{N_{t+1}}{N_t}$ , where  $N_t$  is the number of sites with Poweshiek skipperling at time frame  $t$ .

We recognize that we did not gather absence data and cannot explicitly determine when Poweshiek skipperling sites were extirpated, but the extensive surveys and inclusion of specimens from regional and major butterfly collections decreases the potential for false absences when determining site occupancy status at 5-year intervals.

#### *Lethal, lower threshold, and thaw degree days*

To assess the effect of extreme heat and extreme cold on the ecological niche of Poweshiek skipperling, we calculated lethal degree days (LDDs), lower threshold degree days (LTDDs) and thaw degree days (TDDs). These variables were calculated using daily surface weather data with a 1-km resolution downloaded from Daymet (Thornton *et al.*, 2017). Daily minimum temperature and maximum temperature data were downloaded for days in winter (December, January and February) and summer flight period (June and July; hereafter, summer) months between 1981 and 2005. Temperature data were not downloaded for any years after 2005, because we did not develop ENMs for



**Fig. 1.** Occupied Poweshiek skipperling sites over time. Points represent historical and extant Poweshiek skipperling sites. Points are coloured by the year that the last documented Poweshiek skipperling was observed. The number of sites occupied by Poweshiek skipperling in each year is listed in parentheses. The dark-shaded area represents the west extent of our study, while the lighter-shaded area represents the east extent of our study. The total extent includes both the west and east extents. This figure includes the Manitoba, Canada site as an occupied site to display all known historic occupied of Poweshiek skipperling from 1985 to 2010, but we do not include the Manitoba site in the analyses of this article. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

2010 and 2015 due to these years having too small of sample sizes. LDDs (Thogmartin *et al.*, 2017) count the degrees that are above an estimated upper threshold temperature to Poweshiek skipperling ( $\geq 32^\circ\text{C}$ , Dearborn & Westwood, 2014) during summer months. The sum of all LDDs across a summer was calculated for each cell in our study extent. The mean LDD was calculated by averaging the accumulated LDDs for the representative model year and the 4 years prior (i.e. 1985 models calculated mean LDDs from 1981 to 1985). Five-year averages were calculated for all climate variables to account for inter-annual variation. Similar to LDDs, LTDDs calculated the degrees during the summer months that are below an estimated lower temperature threshold to Poweshiek skipperling ( $\leq 6^\circ\text{C}$ , Dearborn & Westwood, 2014). The sum of all LTDD values across a summer was calculated for all cells in the study extent after which the mean of all 5 years making up a time frame was calculated. TDDs were calculated by counting the degrees greater than  $0^\circ\text{C}$  for winter months. The sum of all TDD values for a cell across a winter was calculated, and the mean of all 5 years representing a time frame was calculated.

#### Change in temperature

To investigate if changes in current temperature compared to historical (1895–1944) temperature impacted the ecological niche of Poweshiek skipperling, we calculated change in active

temperature and change in diapause temperature. McAlpine (1973) observed the active period of Poweshiek skipperling larvae and adults to be from April through September and the diapause period of larvae to be from October through March. These months were used to calculate our active and diapause variables. Monthly temperature data were downloaded for the historical years 1895–1944 and the present years 1981–2005 from PRISM Climate Group at a resolution of 5 km (PRISM Climate Group, 2017). We used the data from 1985 to 1944 to develop our historical temperature data set because these years represented a 50-year average of climate data prior to the largest increases in global surface temperature (Hansen *et al.*, 2006). The average active (April–September) and average diapause (October–March) temperatures for all years from 1895 to 1944 were calculated for each cell. Mean active and diapause temperature layers were also calculated for each 5-year interval modelled. The present mean temperature layers were then subtracted by the historical mean temperature layers to calculate the temperature change layers for the active and diapause seasons.

#### Change in precipitation

To investigate the influence of changes in current precipitation compared to historical precipitation (1895–1944) on the ecological niche of Poweshiek skipperling, we calculated change in precipitation for the active and diapause periods. Change in precipitation

was estimated using the change in temperature methodology, but instead of using monthly temperature data, we used monthly precipitation data (PRISM Climate Group, 2017).

#### *Extreme precipitation*

Extreme high winter precipitation, extreme low winter precipitation, extreme high summer and extreme low summer precipitation variables were calculated to investigate the influence of extreme precipitation on the ecological niche of Poweshiek skipperling. Extreme precipitation variables were calculated by downloading monthly winter (January, February and December) and flight period (June and July) precipitation data for the historical years 1895–1944 and the present years 1981–2005 from PRISM Climate Group at a 5-km resolution (PRISM Climate Group, 2017). We calculated historical mean monthly precipitation for every cell in our study extent during winter and summer from 1895 to 1944. Precipitation included total rain and melted snow. Next, we calculated the 10th and 90th percentiles of these mean historical precipitation layers. To derive the extreme high precipitation variables, we calculated the sum of all precipitation greater than the 90th percentiles (46 mm for winter and 101 mm for summer) and less than the 10th percentiles (14 mm for winter and 76 mm for summer) for each cell in our study extent over the 5-year time frames.

#### *Proportional land cover*

To assess the effect of proportional land cover on the ecological niche of Poweshiek skipperling, we calculated the proportion of developed, natural, open water and agricultural land cover surrounding a cell at 100-km<sup>2</sup>. Land cover data for the 1985 models were downloaded from an enhanced historical land use and land cover data set depicting land cover from the 1970s and 1980s (Price *et al.*, 2006). Land cover data for the 1990 and 1995 models were downloaded from the 1992 National Land Cover Database (NLCD; Vogelmann *et al.*, 2001). Land cover data for the 2000 and 2005 models were downloaded from the 2001 (Homer *et al.*, 2007) and 2006 (Fry *et al.*, 2011) NLCD, respectively. All land cover data were downloaded at 30-m resolution. We reclassified these data sets into five landscape categories: open water, developed, agriculture, natural and barren (Table S1). Using the focal statistics tool in ArcGis 10.4.1 (Esri, 2016), we calculated the proportion of natural, open water, developed and agriculture land use within a 10-km × 10-km focal area.

#### *Distance to nearest grassland/wetland*

The effect of fragmentation on the ecological niche of Poweshiek skipperling was investigated by calculating a distance to nearest grassland/wetland variable. Due to inconsistencies between the NLCD land cover classifications and the enhanced historical land use and land cover grassland classifications, the distance to nearest grassland/wetland variable calculated using the historical land use data was not comparable to our distance to nearest grassland/wetland variables calculated using the

NLCD data. We therefore used the 1992 NLCD data to calculate the 1985, 1990 and 1995 distance to nearest grassland/wetland variables. The 2001 NLCD data were used to calculate the 2000 nearest grassland/wetland variables, and the 2006 NLCD data were used to calculate the 2005 nearest grassland/wetland variables. After developing a grassland/wetland layer that only had cells that were classified as grassland/herbaceous, woody wetlands and emergent wetlands, we used the Euclidean Distance tool in ArcGis 10.4.1 (Esri, 2016) to calculate the distance from each cell in our study extent to the nearest cell with the grassland/wetland classification.

#### *Pesticide use*

To assess the influence of agricultural chemicals on the ecological niche of Poweshiek skipperling, we computed mean pesticide use, neonicotinoid use and soybean aphid pesticide use variables. The Pesticide National Synthesis Project of the U.S. Geological Survey (<https://water.usgs.gov/nawqa/pnsp/>) provided data sources of low and high pesticide use estimates for all counties within our study area. We used the low pesticide use estimates to calculate our pesticide variables, which treated missing values as zero, whereas the high estimates treated missing values as unsurveyed and extrapolated pesticide–crop use rates from nearby crop reporting districts (Thelin & Stone, 2013). Starting in 2015, the Pesticide National Synthesis project discontinued making estimates for seed treatment because of complexity and uncertainty. During the years covered by this study, however, the Pesticide National Synthesis Project of the U.S. Geological Survey captures all agricultural pesticide use, including seed treatments.

Total pesticide use per county was estimated by summing the pesticide use estimate (kg) of all chemicals reported for each county in the years 1992–2005. The 1985 and 1990 models did not include pesticide or neonicotinoid variables due to the lack of available broad-scale data. We calculated the mean pesticide use variable for 1995 by averaging the total pesticide use layers of 1992, 1993, 1994 and 1995. For the other two time frames, we averaged the 5 years making up their respective time frames to calculate total pesticide use.

The mean neonicotinoid use variables were created using a similar method to the total pesticide use variables, except these layers only summed the low estimates of the pesticides imidacloprid, clothianidin, thiamethoxam, acetamiprid, dinotefuran and thiacloprid. These six pesticides were chosen because they were the most widely used neonicotinoids during the duration of this study (Douglas & Tooker, 2015). The soybean aphid pesticide use variables summed the low estimates of the compounds chlorpyrifos, bifenthrin and cyhalothrin-lambda, which are the chemicals most frequently applied for soybean aphid control (Runquist & Heimpel, 2017). A summary of all variables prepared for our modelling approach is available (Table S2).

#### *Preparing data for Maxent and reducing variables*

All GIS data that were not originally downloaded in Albers equal-area conic projection were converted to this projection.

Additionally, GIS data that were not originally downloaded with a 1-km resolution were resampled to have a cell size of 1-km × 1-km using the bilinear resampling technique.

Correlation analyses were examined for all 19 variables for the total extent and for all model years using ENMTools (Warren *et al.*, 2010). We only included variables in our Maxent models with Pearson's correlation coefficients <0.60 for all five model years, a threshold below the one estimated to start distorting model predictions (Dormann *et al.*, 2013). We chose the variable to be removed from our models by choosing the variables that were estimated to have the most biological influence on the distribution of butterflies (e.g. those that capture extreme climatic conditions during a year), while also trying to keep a balance between the number of land use, precipitation, and temperature variables included as covariates. The overwintering stage of butterflies has been found to be particularly sensitive to extremes in temperature and precipitation (McDermott Long *et al.*, 2017). We therefore chose to keep variables relating to the larval overwintering stage over the active larval stage. Our final set of variables used in our modelling consisted of six land use and five climate variables (Table 1).

### Modelling procedure

We developed ENMs using maximum entropy modelling with Maxent 3.4.1 (Phillips *et al.*, 2017) for five different time frames at three different extents. ENMs offer a versatile tool to quantitatively correlate the presence of a species across a geographic extent with variation in environmental conditions at a landscape scale. These models can be useful in identifying likely drivers among many inter-connected stressors that may be contributing to decline in a species (Worthington *et al.*, 2014). Maxent is a machine learning technique that has been widely used to model presence-only data sets of species in areas with environmental heterogeneity (Elith & Leathwick, 2009). We selected Maxent

because it does not require absence data, has consistently outperformed other presence only methods (Elith *et al.*, 2006) and performs well for rare and cryptic species having few occurrence points (Ortega-Huerta & Peterson, 2008; Wisz *et al.*, 2008).

To account for the variation obtained when creating models with different sets of data, we computed ENMs using 100 repetitions with a bootstrap approach in which 80% of the data were used for training and 20% were used for model testing. We included a random seed to ensure random selection of Poweshiek skipperling sites in each model selection. We did not include threshold features, as including both threshold and hinge features can lead to complex and overfitted model responses that do not represent the biology of the system (Heumann *et al.*, 2013). We created species response curves, did jackknifing to measure variable importance and selected our output format to be cloglog to produce an estimate of occurrence probability (Phillips *et al.*, 2017).

### Model selection and evaluation

Starting with global models (9 variables for the 1985 and 1990 models; 11 variables for the 1995, 2000 and 2005 models), we used backward elimination to develop potential models (Parolo *et al.*, 2008; Bellamy *et al.*, 2013; Zlonis *et al.*, 2017). After a model was developed and ran, we removed the variable that contributed the least to the testing area under the curve (AUC) of the receiver operating characteristics until there was only a single variable model. AUC calculates a score from 0 to 1 that measures the model probability of correctly distinguishing presence from random locations (Phillips *et al.*, 2006). We used an information theoretic approach using Akaike's Information Criterion corrected for small sample size (AIC<sub>c</sub>) to rank models (Burnham & Anderson, 2002). ENMTools was used to calculate AIC<sub>c</sub> values of competing models (Warren *et al.*, 2010). The model with the lowest AIC<sub>c</sub> value per time frame and spatial

**Table 1.** Variables selected for Poweshiek skipperling ENMs after removing correlated variables.

Variable	Description	Environmental stressor
LDDs	Degrees above 32 °C throughout flight period	Extreme weather – summer temp.
Change in diapause temperature ( $\Delta$ temp)	Difference between present mean diapause temperature and historical mean diapause temperature	Change in temperature
Extreme high flight period precipitation (s90 ppt)	Monthly precipitation greater than the 90th percentile of historical flight period precipitation	Extreme weather – summer precipitation
Extreme low flight period precipitation (s10 ppt)	Monthly precipitation less than the 10th percentile of historical flight period precipitation	Extreme weather – summer precipitation
Extreme low winter precipitation (w10ppt)	Monthly precipitation less than the 10th percentile of historical January, February and December precipitation	Extreme weather – winter precipitation
Proportion of developed land cover (developed)	Percentage of developed land cover within 10 km	Habitat deterioration
Proportion of natural land cover (natural)	Percentage of Natural land cover within 10 km	Habitat deterioration
Proportion of open water land cover (water)	Percentage of open water land cover within 10 km	Habitat deterioration
Distance to nearest grassland/wetland (dis)	Euclidean distance of a cell to the nearest cell classified as grassland/wetland land cover	Fragmentation
Neonicotinoid use (neonics)	Low estimate of neonicotinoid usage	Agricultural practices
Soybean aphid chemical use (sba)	Low estimate of main chemicals used to control soybean aphids	Agricultural practices

**Table 2.** Proportion of Poweshiek skipperling sites that went locally extinct during five-year intervals from 1985 to 2015. Parentheses show the number of known extant sites at the end of the time period over the number of known extant sites at the beginning of the time period. Declines are shown for the total, east and west extents.

	1985–1990	1990–1995	1995–2000	2000–2005	2005–2010	2010–2015
Total	0.11 (192/217)	0.35 (125/192)	0.32 (85/125)	0.54 (39/85)	0.77 (9/39)	0.44 (5/9)
East	0.00 (17/17)	0.00 (17/17)	0.29 (12/17)	0.00 (12/12)	0.25 (9/12)	0.44 (5/9)
West	0.12 (175/200)	0.38 (108/175)	0.32 (73/108)	0.63 (27/73)	1.00 (0/27)	N/A (0/0)

**Table 3.** Top Poweshiek skipperling ENMs selected by AIC<sub>c</sub> values for each year and extent. The permutation importance of each variable to the model is displayed in parentheses. AUC of the receiver operating characteristics was used as a metric of model fit and was determined by averaging the 100 model iterations. See Table 1 for description of variables included in models.

	Year	Model	Sample size	AUC
Total	1985	s10 ppt (33.8%) + w10ppt (23.5%) + dis (21.8%) + water (21%)	217	0.766
	1990	LDD (51.5%) + water (48.5%)	192	0.742
	1995	water (41.1%) + s90 ppt (41%) + LDD (17.9%)	125	0.842
	2000	natural (52%) + LDD (36.7%) + dis (11.4%)	85	0.859
	2005	natural (100%)	39	0.824
East	1985	water (100%)	17	0.745
	1990	natural (100%)	17	0.787
	1995	natural (100%)	17	0.789
	2000	natural (100%)	12	0.855
	2005	natural (100%)	12	0.872
West	1985	Δ temp (24.6%) + dis (21.1%) + w10ppt (21%) + s10 ppt (19.4%) + water (13.9%)	200	0.808
	1990	w10ppt (24.7%) + natural (22%) + LDD (19.9%) + water (17.7%) + dis (15.7%)	175	0.806
	1995	s90 ppt (55%) + natural (24.2%) + water (20.8%)	108	0.849
	2000	natural (52.7%) + LDD (37.8%) + dis (9.6%)	73	0.877
	2005	dis (100%)	27	0.907

extent was selected as the best model and used for evaluation. Models that were a subset of another model examined were not considered the top model if their AIC<sub>c</sub> score was ≤2. We also used AIC<sub>c</sub> values to calculate Akaike weights ( $w_i$ ) of competing models, which can provide the probability of each model being the best model given the data and the set of candidate models (Wagenmakers & Farrell, 2004).

We interpreted our top ENMs by examining average model outputs. Outputs examined were permutation importance of the environmental variables, the species–environment response curves and the AUC of the receiver operating characteristics. Permutation importance quantifies the loss in model predictive power with the removal of a variable. The species–environment response curves represent the effect of an environmental variable on the predicted probability of Poweshiek skipperling occurrence (Phillips *et al.*, 2006).

## Results

We aggregated over 3600 Poweshiek skipperling occurrence records from 1872 to present. From 1985 forward, we documented occurrence records representing 217 individual sites in the United States and one site in Manitoba, Canada, which we did not include in our analyses due to lack of inter-operable spatial data. By 2015, there were only five sites in the United States with

documented occurrences. Across the total extent, the 5-year interval with the highest proportion of new extirpated sites was from 2005 to 2010, with 77% of previously occupied sites no longer having an occurrence record in or after 2010. The west extent first experienced a 50% decline in the number of occupied sites between 2000 and 2005. The east extent experienced the greatest decline (44%) in the number of occupied sites first in the 2010–2015 5-year interval (Table 2).

Backward selection and comparison of AIC<sub>c</sub> values produced best models with one to five variables. All models across the total, east, and west extents had AUC values greater than 0.7 and 10 of the 15 models had AUC values greater than 0.8, above the general recommendation that models useful in discriminating background environmental locations from presence locations have an AUC greater than 0.7 and models with an AUC value greater than 0.8 have good predictive accuracy (Araújo *et al.*, 2005). The AUC values for the total extent models ranged from 0.742 to 0.859. The AUC values for the five models in the east extent ranged from 0.745 to 0.872, and the AUC values of the west extent ranged from 0.806 to 0.907 (Table 3).

### Variable contribution: Total extent

For the total extent, climate variables contributed the most to model predictive power for the 1985, 1990, and 1995 models.

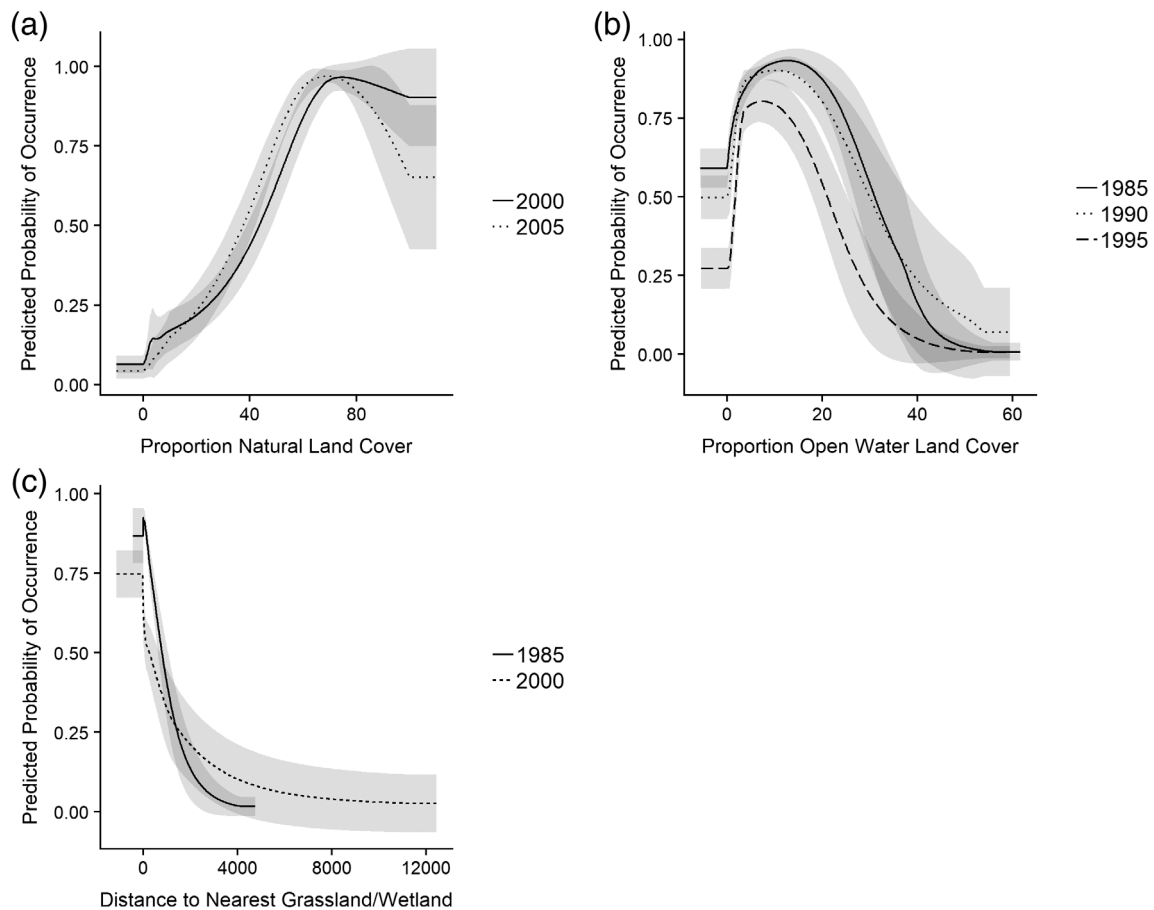
Land use variables contributed the most to model predictive power for the 2000 and 2005 models (Table 3). The only top model for the total extent that did not have an Akaike weight ( $w_i$ ) of one was the 2000 model. For this year, the top model had an Akaike weight of 0.88, and the next competing model had an additional land use variable (water) and an Akaike weight of 0.11 (Table S3). Response curves of the land use variables retained in the top models were consistent across the five time frames (Fig. 2). Distance between nearest grassland/wetland had a negative relationship with predicted Poweshiek skipperling presence (Fig. 2). Natural land cover was only a retained variable in the 2000 and 2005 models and displayed a positive relationship with predicted Poweshiek skipperling presence. Open water land cover was a model covariate in the 1985, 1990 and 1995 models and showed a positive relationship with predicted Poweshiek skipperling presence until about 20% of the land cover was open water, after which a negative relationship is displayed (Fig. 2). LDDs were the only climate variable retained in more than one model and did not display a consistent response curve across model time frames (Fig. 3).

#### Variable contribution: East extent

In the east extent, only land use variables were retained in the best models (Table 3). Top models had Akaike weights varying from 0.47 to 0.73, but the top three competing models for all time periods consisted only of land use variables (Table S3). The top models for all east extent in models were single-variable models. Open water within 10 km was included in the 1985 model. Natural land cover was the single variable retained in the other four models. The response curves of proportion of natural land cover were consistent across all time frames and showed a positive relationship to predicted probability of Poweshiek skipperling presence (Fig. S4).

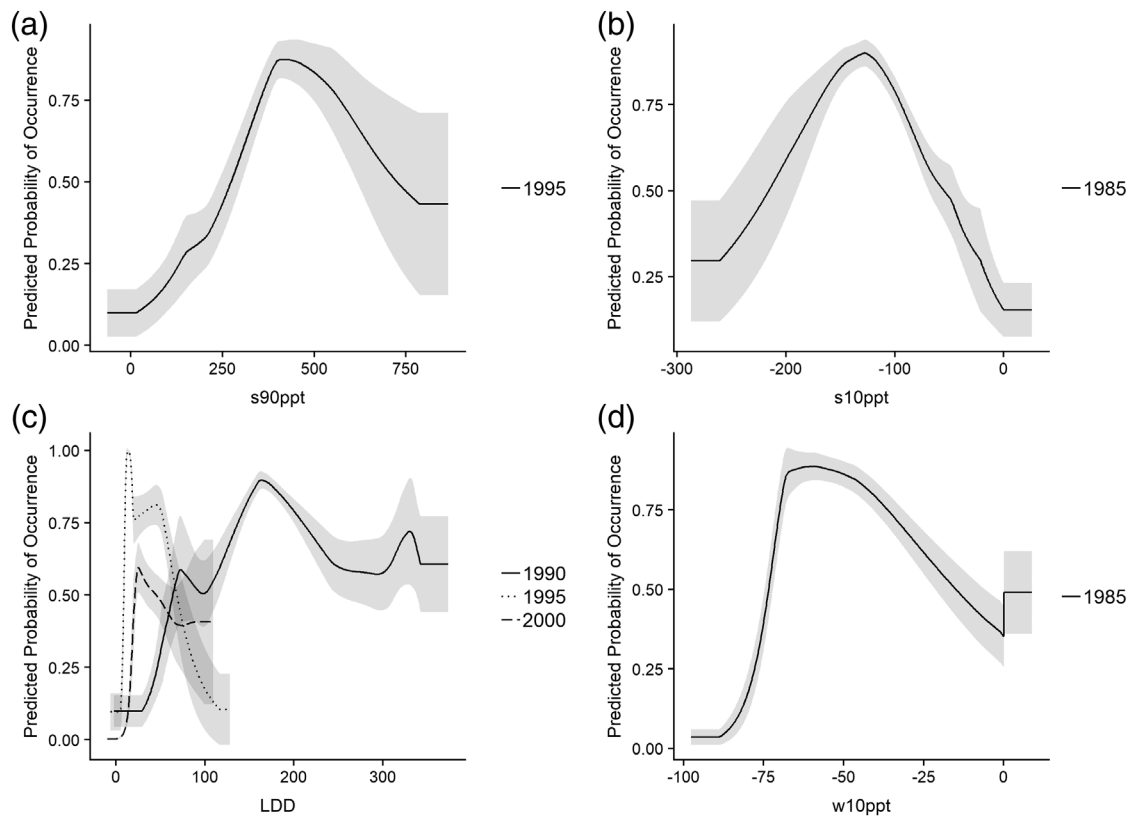
#### Variable contribution: West extent

In the west extent, a climate variable had the greatest permutation importance to the models in the 1985, 1990 and 1995 time frames but natural land cover and distance between grassland/wetlands had the greatest permutation importance in the 2000

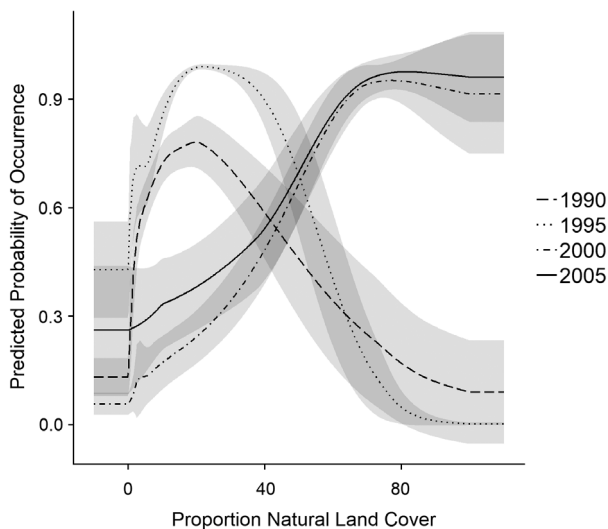


**Fig. 2.** Response curves of land use variables retained in ENMs for the total extent. Response curves illustrate how the predicted probability of presence changes as land use variables are varied. The mean response of the 100 replicate Maxent runs and the standard deviation is represented. Retained variables include (a) proportion of natural land cover, (b) proportion open water land cover, and (c) distance to nearest grassland/wetland (m).





**Fig. 3.** Response curves of climate variables retained in ENMs for the total extent. Response curves illustrate how the predicted probability of presence changes as climate variables are varied. The mean response of the 100 replicate Maxent runs and the standard deviation is represented. Retained variables include (a) summer high precipitation (mm), (b) summer low precipitation (mm), (c) LDDs (°C), and (d) winter low precipitation (mm).



**Fig. 4.** Response curves for the west extent models that retained proportion of natural land cover. Response curves illustrate how the predicted probability of presence changes as proportion of natural land cover is varied. The mean response of the 100 replicate Maxent runs and the standard deviation is represented.

and 2005 models, respectively (Table 3). All top models for the west extent had an Akaike weight of one (Table S3). The response curves of winter low precipitation did not display consistency across time frames, with the 1985 model showing predicted probability of Poweshiek skipperling occurrence increasing with less winter precipitation than historic precipitation until around 50 cm less precipitation and then predicted presence of Poweshiek skipperling decreases. This response was not observed in the 1990 model, with greater suitability predicted at the areas with the least and greatest winter low precipitation (Fig. S5). LDDs did not display consistent response curves, and the other three climate variables retained in a top model (change in diapause temp, low summer precipitation and high summer precipitation) were each only retained in a single time frame (Fig. S5). Proportion of natural land cover demonstrated a switch in response curves across time periods, with the log-normal bell curve response of the 1990 and 1995 models switching to a positive response curve in 2000 and 2005 models (Fig. 4).

## Discussion

The number of Poweshiek skipperling sites occupied throughout its historic range has declined precipitously since 1985, with the

historic core range of eastern Minnesota and western South Dakota being extirpated by the year 2010. By compiling a comprehensive data set of Poweshiek skipperling occurrences, we were able to provide support that the steepest declines of Poweshiek skipperling started in 2000–2005, with the declines beginning in the western sites. Prior to the most dramatic declines of Poweshiek skipperling, the presence of the species was being driven by climatic variables, which commonly drives the fundamental niche of insect species (Hellmann *et al.*, 2016). During and after the years of widespread declines, the presence of Poweshiek skipperling was driven by proportion of natural land cover and distance to nearest grassland/wetland. These results suggest that land use variables are currently the most important landscape-level variables to consider when developing risk assessments of extant and possible reintroduction sites.

Our models suggest that prairie sites with high proportions of natural land cover near other prairie habitats are most suitable in supporting extant Poweshiek skipperling populations. Sites with high prairie connectivity and natural land cover represent the areas across our study extent that have undergone the least amount of land use change due to agricultural intensification and urbanization. In our west models, the relationship between natural land cover and probability of occurrence changed over time. In models before the precipitous declines (1990 and 1995 models), probability of Poweshiek skipperling occurrence increased with increasing natural land cover until a threshold was reached, after which a negative correlation was observed. Nevertheless, in the models during and after the biggest declines in occupied Poweshiek skipperling sites, there was a positive relationship between natural land cover and probability of occurrence at all proportions. Across our study extent, there were almost no 100-km<sup>2</sup> patches that consisted entirely of grassland. Therefore, cells with 100% natural land cover existed in areas primarily surrounded by forest. Prior to the range-wide decline, dense surrounding forest did not increase suitability of this prairie obligate species. During the most dramatic loss of populations (2000–2010), our models suggest surrounding forest, although not itself a suitable habitat, increased the probability of Poweshiek skipperling occurring at a site. Forests could be buffering sites against anthropogenic stressors such as eutrophication and changes in hydrology. Eutrophication is suggested as a contributor to widespread decline in Dutch butterfly populations by decreasing nectar availability (WallisDeVries *et al.*, 2012). Forests may also provide a buffer from chemical drift, as the effects of pesticides on wild bees can be buffered by increasing proportion of natural habitat in the landscape (Park *et al.*, 2015). Although neither neonicotinoid use nor soybean aphid chemical use were retained in any top ENM, the spatio-temporal overlap between Poweshiek skipperling decline and the introduction and use trends of these pesticides warrants further examination. The county-level spatial resolution of our pesticide layers may have been too coarse of scale to examine the pesticide use heterogeneity in a way that is biologically relevant to Poweshiek skipperling.

The predicted probability of Poweshiek skipperling occurrence had an inverse relationship to distance to the nearest grassland/wetland, indicating the negative impact of fragmentation on occurrence. Saarinen *et al.* (2016) used conservation genetics

techniques to suggest that at the scale of hundreds of kilometres, gene flow was historically high between Poweshiek skipperling, demonstrating the importance that grassland fragmentation could have on population persistence. Habitat connectivity is critical for populations of butterfly species with limited dispersal capabilities to remain viable (Thomas *et al.*, 2009). Poweshiek skipperling has been proposed as an intermediary on the generalist–specialist spectrum due to their once common occurrence in tallgrass prairies and prairie fens, their observed oviposition on multiple grass genera, and their limited dispersal ability (Saarinen *et al.*, 2016). Whereas, generalist species often have high genetic diversity and are affected less by land use change, and specialist species are adapted to low genetic diversity and can be supported by specific conservation measures, species with intermediate habitat demands and originally high genetic diversity might be particularly susceptible to fragmentation due to inbreeding depressions (Habel & Schmitt, 2012). Historically, Poweshiek skipperling populations occurred in large prairie networks, and the disruption of gene flow due to the widespread destruction of prairie could be causing time-delayed extinctions due to an extinction debt (Tilman *et al.*, 1994; Krauss *et al.*, 2010).

Our models suggest that increased temperatures in the Midwest may be negatively affecting Poweshiek skipperling. Both LDDs, which focuses on temperature during the adult butterfly stage, and change in diapause temperature which focuses on temperature during diapause, displayed a negative correlation between predicted probability of Poweshiek skipperling occurrence and excessive temperatures. We note that the LDDs response curves in the 1990 models were overfitted and did not show the negative correlation described above. Overfitted models correspond too closely to the training set and may fail to predict future observations reliably (Burnham & Anderson, 2002). Warming may reduce butterfly fitness through direct effects of thermal stress, but also through secondary effects on adult immune function (Karl *et al.*, 2011). Warmer temperatures in winter may reduce snowpack, which is demonstrated to mitigate the negative impacts of extreme temperature events in overwintering butterflies by providing insulation at times of extreme cold and heat (Roland & Matter, 2016). Experimentally induced winter heatwaves were found to have more negative effects on survival of an imperilled wetland butterfly than summer heatwaves (Abarca *et al.*, 2019). When combined with habitat deterioration and fragmentation, climate change and land use change interactions can lead to collapses in butterfly populations (Oliver *et al.*, 2015).

The extreme precipitation variables retained in our models produced a bell-shaped response curve where intermediate climate values predicted the highest probability of occurrences. These response curves are similar to bioclimatic envelopes, where a species' climate tolerance determined to predict future range suitability under climate change scenarios (Pearson & Dawson, 2003). These intermediate response curves do not suggest that precipitation variables are a leading factor that contributed to the decline of Poweshiek skipperling but could be used to examine precipitation thresholds that if exceeded could negatively influence populations.

The climate factors used in our models were not the most predictive variables of Poweshiek skipperling site occupancy in the

years during or after the wide-spread decline of this species, but extreme weather events have vast potential to contribute to the extinction of this species. Extreme weather events can reduce moth populations by up to 90%, but many populations are dynamic entities that are able to cope with extreme weather events (Greco *et al.*, 2018). As of summer 2017, the remaining number of Poweshiek skipperlings across the four occupied Michigan sites was estimated to be around 231 individuals (Belitz *et al.*, 2019). With populations this small, a stochastic weather event could cause local extinctions.

Declines in the number of known occurrence records over time are typical for endangered species, thus causing challenges for creating accurate ENMs. Previous assessments of modelling methods have revealed that Maxent was capable of producing useful results with sample sizes as small as 5–10 occurrences (Hernandez *et al.*, 2006). The minimum number of occurrences required to obtain good model performance is lower for species with small geographic ranges (Hernandez *et al.*, 2006; Van Proosdij *et al.*, 2015). The entire range of Poweshiek skipperling is restricted to prairies in the upper Midwest, and the models with the smallest sample sizes were restricted to only the small area included in our east extent. Still, the number of occurrence sites used for each succeeding model time frame decreased, potentially leading to model uncertainty (Wisz *et al.*, 2008). However, the general agreement between our total extent and west extent models implies model stability. Our results are further strengthened because our best models for the total and west extents were strongly supported as the only competing model by their Akaike weight.

Declines in Poweshiek skipperling populations have left three extant populations in the United States and one in Canada. Successful conservation of endangered butterflies relies heavily on understanding the biology of the focal species, and then managing their habitats appropriately (Thomas *et al.*, 2009). Our models imply that the surrounding landscape is important to conserving Poweshiek skipperling populations. This is consistent with studies that call for insect conservation to address landscape-scale stressors (Bergman *et al.*, 2004; Cozzi *et al.*, 2008; Ekroos *et al.*, 2016). A multi-agency partnership working to conserve this species was created in 2015 and the conservation strategy focuses on captive rearing, augmentation of existing populations and reintroduction (Marquardt *et al.*, 2018). To best ensure the survival of this species, it is important to buffer populations at remaining sites against stochastic events. At a landscape level, our study suggests that preventing future habitat destruction in areas surrounding the extant sites is important to maintaining habitat suitability. If the ex situ captive breeding program (Delphey *et al.*, 2016) is successful at rearing enough Poweshiek skipperling for reintroduction, potential reintroduction sites must be evaluated not simply on resource availability within the prairie habitat, but landscape-level risk assessments must be considered as well. Maintaining viable populations of this endangered butterfly will rely on a multi-scale conservation approach that examines habitat suitability at both a microscale and a macroscale.

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## Supporting information

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

**Table S1.** Conversion of Enhanced historical land use and land cover and national land cover database into 5 land use categories used in the different spatiotemporal models. Numbers represent original classification categories

**Table S2.** List of environmental variables developed for possible use as a predictor variable in ecological niche models. Variables used as predictor variables in ecological niche models were selected after analyzing for correlation among these variables (see Table 1)

**Table S3.** Top three competing ecological niche models for each year and study extent. Potential models were determined using a backward selection technique where we started with a global model and removed the variable that contributed the least to the testing area under the curve (AUC) until there was only a single variable. We ranked models on difference from the top model using Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ) and Akaike weight ( $w_i$ )

**Figure S1.** Response curves of land use variables retained in ecological niche models for the east extent. Response curves illustrate how the predicted probability of presence changes as land use variables are varied. The mean response of the 100 replicate Maxent runs and the standard deviation is represented. Retained variables include (a) proportion natural and (b) proportion open water

**Figure S2.** Response curves of climate variables retained in ecological niche models for the west extent. Response curves illustrate how the predicted probability of presence changes as climate variables are varied. The mean response of the 100 replicate Maxent runs and the standard deviation is represented. Retained variables include (a) summer high precipitation (mm), (b) summer low precipitation (mm), (c) lethal degree days ( $^{\circ}\text{C}$ ), (d) winter low precipitation (mm), and (e) change in diapause temperature ( $^{\circ}\text{C}$ )

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