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Landscape factors influencing roost site selection by monarch butterflies *Danaus plexippus* during fall migration in Ontario, Canada

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ABSTRACT: Worldwide, insect populations are declining, and the eastern migratory group of the monarch butterfly *Danaus plexippus* in North America has not escaped this fate. The conservation of this iconic species is an international priority but requires knowledge of how monarchs interact with the landscape during different stages of the annual cycle. To better understand habitat needs of monarchs departing their core breeding range in southern Ontario, Canada, we examined how various landscape features influenced roost site selection during fall migration — an instrumental resource link between the breeding and wintering grounds. Using dedicated fall migration surveys along the Great Lakes coastlines and a citizen science dataset collected across all of Ontario, we evaluated the relationship between roost site occupancy and 18 landscape variables using a boosted regression tree (BRT) modelling approach. Results suggest that a closer distance to the Great Lakes, increased goldenrod *Solidago* spp. cover, moderate forest cover, rural road cover, and urban land cover are all important to roosting site selection. Our research provides important insights into the habitat characteristics of stopover sites, which will help guide future investigations and conservation actions to preserve monarch butterflies and their migratory phenomenon.

KEY WORDS: *Danaus plexippus* · Fall roost · Habitat selection · Declining populations · Migration · Boosted regression tree

1. INTRODUCTION

The plight of terrestrial insects has become apparent in recent years with drastic declines reported in populations worldwide. Specifically, a meta-analysis of 166 studies from across all continents, except Antarctica, found that the abundance of terrestrial insects is declining at a rate of 9% per decade (van Klink et al. 2020). Certain insect populations are declining at even more alarming rates. For example, in Germany, flying insects have declined 75% over less than 3 decades (Hallmann et al. 2017). The factors implicated for these declines are consistently documented and are shared across many other groups of declining terrestrial fauna. Specifically, habitat loss and degradation and pesticide use are the most ubiquitous drivers for the decline of insects, while natural pests, pathogens, and climate change also play a role (Sánchez-Bayo & Wyckhuys 2019).

Monarch butterflies *Danaus plexippus* (hereafter ‘monarchs’), specifically the migratory groups, are among the declining species of insects. Monarchs are

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divided into 2 subgroups in North America: the western and eastern migratory groups, which are divided by the Rocky Mountains. The eastern migratory group, which breeds across central and eastern United States and southern Canada and overwinters in central Mexico, has shown an unstable and declining population over the past 2 decades (Thogmartin et al. 2017). The US Fish and Wildlife Service (2020) estimates, under current conditions, monarchs face a 48–69% chance of reaching a population level at which extinction is unavoidable by the year 2080. Similar to other insects, the decline in monarchs has been largely attributed to changes in climate, deforestation in the overwintering range, exposure to insecticides and herbicides, loss of breeding habitat, and natural threats such as predation and parasitism (reviewed by Wilcox et al. 2019). The loss of breeding habitat is largely driven by a decline in availability of its host plant *Asclepias* spp., likely driven by agricultural herbicide use for weed control (Hartzler 2010, Pleasants & Oberhauser 2013, Wilcox et al. 2019).

Monarchs are currently listed as 'special concern' in Canada under the federal Species at Risk Act (SARA). However, the Committee on the Status of Endangered Wildlife in Canada upgraded its listing to Endangered, since recent population declines meet the designation threshold (COSEWIC 2016), and the IUCN recently listed migratory monarchs as Endangered on its Red List of Threatened species (IUCN 2022). If monarchs are up-listed by the federal government, a 'Recovery Strategy' must be published by Environment and Climate Change Canada within 1 yr of listing, which usually requires a local understanding of monarch population dynamics, environmental and human-induced stressors, and habitat needs during breeding and migration to guide evidence-based recovery planning.

Each fall, thousands of monarchs depart southern Ontario, one of the Canadian core breeding areas (Flockhart et al. 2019), and migrate along the north shores of the Great Lakes. During their migration, monarchs form overnight roosts on trees and shrubs before continuing their southbound flight. Classifying roosting habitat preferences during fall migration in this region is therefore important to aid in the identification of critical habitat (i.e. habitat that is defined by Canada's Species at Risk Act as necessary for the survival or recovery of a species), and thus to the Recovery Strategy planning process. Observational data has provided some insight into where roosts form in Ontario; however, little is known about how landscape characteristics influence roosting site selection in Ontario or elsewhere in their range. This knowledge can inform where to best invest conservation resources for both preservation and restoration of habitats that suit migratory monarchs.

The primary objective of this research is to describe the landscape characteristics that influence monarch roost site selection during fall migration in Ontario, Canada. To achieve this, we used data collected from a dedicated field study investigating monarch roosts, conducted by Environment and Climate Change Canada (ECCC), and roost observations from Journey North, a citizen science (aka community science) database (Sheehan & Weber-Grullon 2021). The 2 roost datasets were assessed separately, which allowed for the comparison between the results from 2 independently derived datasets. Boosted regression tree (BRT) modelling was used to assess factors influencing roost site selection across the study area. We chose BRT modelling because of its high performance in species distribution modelling using presence-only data by employing pseudo-absences (Elith et al. 2006). The use of BRT models allowed us to examine how each landscape variable affected roost distribution by means of partial dependence plots and will facilitate the future creation of distribution mapping with current and hypothetical landscape data. Additionally, the scale of maximum effect, the spatial scale at which each independent variable most highly correlated with the dependent variable, was calculated to determine at which spatial scale to tabulate land cover variables. While our analysis was largely exploratory, we anticipated that monarch roosts would be found near nectaring resources, which are important for refueling during migration (Svancara et al. 2019). Further, we anticipated roosts would be closer to large migratory diversion lines, such as the Great Lakes, as these can create barriers to movement and concentrate migrants along their borders (Goodrich & Smith 2008).

2. MATERIALS AND METHODS

2.1. Study area

The extent of the study area for the roost distribution model using ECCC survey data was scoped to 2710 km^2 of land along a 2 km shoreline buffer of Lake Ontario, Lake Erie, and Lake Huron (Fig. 1A), because sampling for this component of the study focused on near coastline roosts. The analysis of monarch roost distribution using Journey North data was conducted in a 96 680 km^2 portion of southern Ontario, Canada (Fig. 1B). Both study areas were

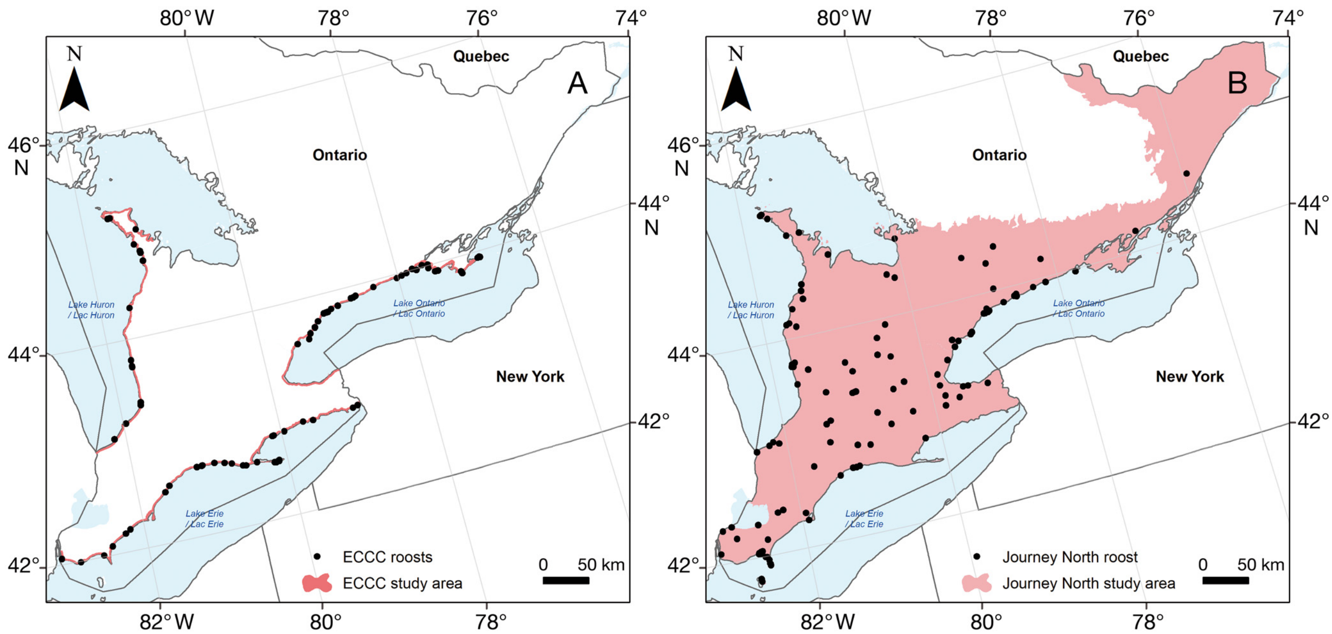

Fig. 1. Locations of monarch butterfly *Danaus plexippus* roost sites in southern Ontario, Canada, collected by (A) Environment and Climate Change Canada (ECCC; 72 roosts) and (B) Journey North (109 roosts)

within the Mixedwood Plains Ecozone, characterized by a mild and moist climate, with mean annual temperatures ranging from 2.8–9.4°C and receiving 759–1087 mm precipitation per year (Mackey et al. 1996). There is a general gradient in climate conditions (primarily decreasing temperatures and growing days) from southwest to northeast. The natural vegetation is mixed deciduous–coniferous forests and tolerant hardwood forests, including Carolinian forests in the south. However, 57–78% of the land has been converted to agriculture since European arrival, and 7% is urban (Crins et al. 2009).

2.2. Landscape variables

To evaluate monarch habitat selection during fall migration, we evaluated the relationship between occupancy and 18 landscape variables: slope, aspect, 2 distance to water variables, and 14 land cover variables (Table 1). Slope and aspect, which affect solar radiation and have been shown to affect overwintering site selection by monarchs (Leong et al. 1991), were derived from the 30 m resolution ASTER digital elevation model (Abrams et al. 2020). The distance to water variables, distance to Great Lakes and distance to internal water (i.e. non-Great Lakes water), were calculated as the Euclidean distance from each cell of a 30 m resolution raster to the nearest water. Internal open waters included lakes, ponds, rivers, and streams in the 2016 Census Boundary Files (Statistics Canada 2016a,b). Finally, land cover was adapted from the 15 m resolution Southern Ontario Land Information System version 3 (MNRF 2019), the 30 m resolution Annual Crop Inventory (AAFC 2020), and 5 m resolution goldenrod-dominated *Solidago* spp. land cover (Lindsay 2022). The land cover datasets were reclassified (Table S1 in the Supplement at www.int-res.com/articles/suppl/n050p267_supp.pdf) to 14 classes: (1) open water, (2) wetland, (3) forest, (4) sparse forest, (5) shrubland, (6) grassland, pasture, and forage, (7) row crops, (8) natural barren, (9) parkland (i.e. mown recreation areas), (10) rural roads, (11) urban roads, (12) anthropogenic, (13) goldenrod, and (14) unclassified. Unclassified land cover originated from the Southern Ontario Land Information System v3 dataset and primarily consisted of untilled farmland, urban brown fields, and rights-of-way corridors (MNRF 2019). Land cover classes were included in the analysis for 3 main purposes: (1) because of their known influence on monarch habitat selection (e.g. goldenrod, which is a nectaring resource for pollinators), (2) to account for suspected biases in the datasets (e.g. urban areas, which is a known source of bias in citizen science datasets), and (3) for exploratory purposes (e.g. wetlands). Although goldenrod was not the only floral resource in the study area, it was the only appropriate floral resource dataset available and is known as an important nectaring resource for migratory monarchs (Rudolph et al. 2006). Rural roads

Table 1. The 18 explanatory variables used in the boosted regression tree models used to predict monarch butterfly *Danaus plexippus* fall roost distribution in Ontario, Canada

Variable	Original resolution (m)	Source
Open water cover	15	MNRF (2019)
Wetland cover	15	MNRF (2019)
Forest cover	15	MNRF (2019)
Sparse forest cover	15	MNRF (2019)
Shrubland cover	15	MNRF (2019)
Pasture/forage/grassland cover	30	AAFC (2020)
Goldenrod dominant cover	5	Lindsay (2022)
Agriculture cover	30	AAFC (2020)
Natural barren cover	15	MNRF (2019)
Parkland cover	15	MNRF (2019)
Rural road cover	15	MNRF (2019)
Urban road cover	15	MNRF (2019)
Urban land cover	15	MNRF (2019)
Unclassified	15	MNRF (2019)
Distance to Great Lakes water	Derived from vector	Statistics Canada (2016a)
Distance to internal water	Derived from vector	Statistics Canada (2016b)
Slope	30	Abrams et al. (2020)
Aspect	30	Abrams et al. (2020)

were classified separately from urban roads because rural roads typically have verges which can support pollinators (Phillips et al. 2019), whereas urban roads often do not. All landscape variables were resampled to a resolution of 30 m to match the grain of the coarsest dataset.

2.3. Monarch roost data

We used 2 data sources for monarch roosts: a dataset provided by ECCC and the citizen science Journey North data (Sheehan & Weber-Grullon 2021). The ECCC dataset comprised of roosts observed during targeted field work along the north shores of Lake Ontario and Lake Erie and the east shore of Lake Huron during the years 2019, 2020, and 2021. All ECCC surveys took place during the first 2 wk of September, to match peak migration timing as identified using the Monarch Watch migration timing table (available at https://monarchwatch.org/tagging/#peak). Roost surveys were generally carried out in the late afternoon to evening, with a target time of 4 p.m. (16:00 h) to dusk. Before surveys commenced, previous roost sites were identified within National Wildlife Areas (NWAs) and along the shores of Lakes Ontario, Erie, and Huron, primarily using Journey North and Natural Heritage Information Center (NHIC) data. In addition, locations that appeared to have potential nectar sources (e.g. old fields, grasslands) were identified using aerial photos. Four NWAs were targeted for surveys: Long Point, Big Creek, Prince Edward Point, and St. Clair. Surveys in NWAs took place primarily on foot, whereas those outside were primarily driving surveys. Walking transect surveys in NWAs were done in suitable habitats. On-road survey routes included stops at identified roost sites and nectar resources as well as at regularly spaced random locations every 5 km along the driving route. Surveyors were also encouraged to stop and investigate any suitable nectar or roost habitat along the driving route. A roost was considered any location where ≥1 monarch was seen exhibiting resting or roosting behaviour on a tree or shrub, particularly in the later evening. Sub-roosts (i.e. those within 50 m of each other) were merged so that a single point represented a single roost.

The Journey North data, a citizen science dataset that collects geographic and temporal information on roost sites of monarchs, was filtered to include fall observations (August 15 through to the end of October) from 2016 to 2021, since prior to 2016 the accuracy of the recorded roost locations was not precise enough for this analysis. To better ensure sites were spatially independent, the datasets were randomly sampled to include only roosts that were at least 1000 m apart.

In addition to monarch presence locations from the ECCC and Journey North datasets, we also generated pseudo-absence locations to use in the models (Davis et al. 2012). The pseudo-absences were randomly generated locations within the study area and were restricted from being placed on open water land cover, and each were placed a minimum of 1000 m from another pseudo-absence location or a presence location. The number of generated pseudo-absence locations was equal to the number of presence locations because the predictive accuracy of BRT models is highest when the number of pseudo-absences matches the number of presences (Barbet-Massin et al. 2012).

2.4. Modelling

We used BRT, a machine learning method (Elith et al. 2008), to model monarch presence/absence in relation to the select landscape covariates across our study area. BRT model predictions are insensitive to collinearity (Elith et al. 2008). However, partial dependence plots and variable relative importance are affected, so we calculated collinearity amongst predictor variables to better interpret model results. Barbet-Massin et al. (2012) suggest running a BRT model a minimum of 10 times if the number of pseudo-absences is fewer than 1000. For each of the 2 data sources, the number of pseudo-absences was fewer than 1000, so we built 20 replicate models, each using a different random pseudo-absence selection. The results from the BRT models, namely the deviance explained, the area under the receiver operating characteristic curve (AUC), the partial dependence plots, and the relative influence, were averaged across the 20 models built for each data source. The models were built using a tree complexity of 5, a learning rate of 0.001, and a bag fraction of 0.5.

Aspect, slope, distance to Great Lakes, and distance to internal water were sampled at the roost and pseudo-absence locations, while the land cover variables were tabulated as the proportion of each land cover class within a buffer surrounding each roost and pseudo-absence location. Because we can't know *a priori* at which scale a land cover class will have an effect on monarch roost distribution, we calculated the buffer sizes used to tabulate the land cover classes as the scale of maximum effect for each of the land cover classes (Fyson & Blouin-Demers 2021). The scale of maximum effect was the scale at which a land cover class most highly correlated with roost presence/pseudo-absence. Monarchs have been found to have a perceptual range of at least 400 m (Grant et al. 2018) and have been tracked travelling more than 500 m on a forage outing (Fisher & Bradbury 2022), so we tabulated the land cover classes around roost locations in buffers ranging from 100 to 500 m in 100 m increments. Because the raster land cover data cannot be sampled in a perfect representation of the circular buffers, at the smallest buffer size, the tabulated area may differ by as much as 8.3% from the buffer area. Point biserial correlation values were calculated for each land cover class at each buffer size, and the buffer size with the highest absolute value was retained. The scale of maximum effect was re-calculated for each of the 20 models built for each dataset.

3. RESULTS

3.1. Roost data

A total of 193 roost locations from the ECCC dataset and 364 roost locations from the Journey North dataset were initially included in the analysis. The number of monarchs in each roost ranged from 1 to 408 (mean of 17.0) for the ECCC dataset and 1 to 10 000 (mean of 497.5) for the Journey North dataset. After randomly selecting roost locations at least 1000 m apart, we retained 72 roost locations from the ECCC dataset and 109 roost locations from the Journey North dataset for the analysis.

3.2. Roost distribution

3.2.1. ECCC data

The final BRT model built using the ECCC data explained approximately one-half (mean: 50.8%; SE: 1.3%) of the deviance in monarch roost distribution. The models were built with an average of 3710 trees (SE: 215) and an average cross-validation AUC of 0.924 (SE: 0.005) (Table S2). The scale of maximum effect of the landscape variables on roost occurrence varied by land cover class but was fairly consistent across model iterations. The average scale of maximum effect was 500 m (SE: 0) for open water, 210 m (SE: 32) for wetland, 450 m (SE: 12) for forest, 315 m (SE: 33) for sparse forest, 225 m (SE: 33) for shrubland, 220 m (SE: 29) for grassland, pasture, and forage, 140 m (SE: 28) for row crops, 240 m (SE: 22) for natural barren, 185 m (SE: 29) for parkland, 105 m (SE: 5) for rural roads, 225 m (SE: 28) for urban roads, 295 m (SE: 15) for anthropogenic, 140 m (SE: 11) for goldenrod, and 170 (SE: 11) for unclassified (Table S3). Correlation amongst predictor variables was low, with only 2 pairs having a correlation above 0.5 (parkland land cover and distance to the Great Lakes: −0.87; urban land cover and urban road cover: 0.53) (Table S4).

The most important variables in predicting roost occurrence based on the ECCC model were distance to the Great Lakes (mean relative influence [RI]: 55.1%; SE: 1.4%), rural road cover (mean RI: 10.0%; SE: 0.9%), goldenrod cover (mean RI: 6.4%; SE: 0.6%), slope (mean RI: 6.4%; SE: 0.6%), and unclassified land cover (mean RI: 6.3%; SE: 0.5%) (Table 2). Partial dependence plots of the top-ranking variables showed that the probability of roost occurrence was highest within 500 m of the Great Lakes and lowest

Table 2. Relative influence (RI) of the top 10 most important explanatory variables in the boosted regression tree models used to predict monarch butterfly *Danaus plexippus* fall roost distribution in Ontario, Canada. ECCC: Environment and Climate Change Canada

ECCC		Journey North	
Variable	RI (SE)	Variable	RI (SE)
Distance to Great Lakes	55.1 (1.4)	Distance to Great Lakes	35.0 (0.7)
Rural road cover	10.0 (0.9)	Urban land cover	16.5 (0.5)
Goldenrod cover	6.4 (0.6)	Forest cover	8.2 (0.5)
Slope	6.4 (0.6)	Slope	7.2 (0.2)
Unclassified	6.3 (0.5)	Distance to water (non-Great Lakes)	6.7 (0.3)
Distance to water (non-Great Lakes)	3.6 (0.3)	Aspect	6.3 (0.3)
Aspect	3.4 (0.2)	Grassland, pasture, forage	4.6 (0.2)
Forest cover	2.8 (0.3)	Goldenrod cover	4.6 (0.4)
Urban land cover	1.7 (0.4)	Rural road cover	4.2 (0.3)
Grassland, pasture, and forage cover	1.6 (0.2)	Agriculture	3.4 (0.2)

at distances greater than 750 m from the Great Lakes (Fig. 2). Rural road cover, goldenrod cover, and unclassified land cover positively influenced the probability of roost occurrence, while the probability of roost occurrence was highest on slopes between approximately 2 and 7 degrees from flat.

3.2.2. Journey North data

The final BRT model built using the Journey North data explained approximately one-third (mean: 33.3%; SE: 0.7%) of the deviance in monarch roost distribution. The final model was built with an average of 3008 trees (SE: 112) and an average cross-validation AUC of 0.867 (SE: 0.003) (Table S2). Similar to the ECCC model, the scale of maximum effect varied by land cover class but was fairly consistent across model iterations. The average scale of maximum effect was 500 m (SE: 0) for open water, 335 m (SE: 31) for wetland, 485 m (SE: 11) for forest, 120 m (SE: 20) for sparse forest, 490 m (SE: 10) for shrubland, 485 m (SE: 15) for grassland, pasture, and forage, 320 m (SE: 36) for row crops, 415 m (SE: 28) for natural barren, 430 m (SE: 21) for parkland, 105 m (SE: 5) for rural roads, 325 m (SE: 23) for urban roads, 270 m (SE: 22) for anthropogenic, 235 m (SE: 33) for goldenrod, and 215 m (SE: 35) for unclassified (Table S3). Also similar to the ECCC model, correlation amongst predictor variables was low, with the same 2 pairs having a correlation above 0.5 (parkland land cover and distance to the Great Lakes: −0.87; urban land cover and urban road cover: 0.68) (Table S4).

The most important variables in predicting roost occurrence based on the Journey North model were distance to the Great Lakes (mean RI: 35.0%; SE: 0.7%), urban land cover (mean RI: 16.05%; SE: 0.7%), forest cover (mean RI: 8.2%; SE: 0.5%), slope (mean RI: 7.2%; SE: 0.2%), and distance to water (mean RI: 6.7%; SE: 0.3%) (Table 2). Despite the differences in relative importance between the Journey North and ECCC models, the partial dependence plots from the Journey North model were generally very similar to the corresponding partial dependence plots from the ECCC model (Figs. 2 & 3, S1 & S2). The probability of roost occurrence was highest within 500 m of the Great Lakes and lowest at distances greater than 1200 m from the Great Lakes, was positively influenced by urban land cover and slope, was negatively influenced by forest cover, and was highest at distances of less than approximately 1000 m and greater than 7000 m from water (excluding the Great Lakes) (Fig. 3).

4. DISCUSSION

The BRT models used to predict roost site selection of monarch butterflies during fall migration generally performed very well, explaining 50.8 and 33.3% of the deviance and having a cross-validation AUC of 0.924 and 0.867 using the ECCC and Journey North data, respectively. These results suggest that monarch roost distribution was influenced by the landscape attributes selected. The 2 data sources produced similar results but with some exceptions that can largely be explained by difference in data collection methods. It should be noted that, although we present the model AUC values as a method to estimate model performance, AUC values may be of limited value in interpreting species distribution models and can be inflated by spatial autocorrelation

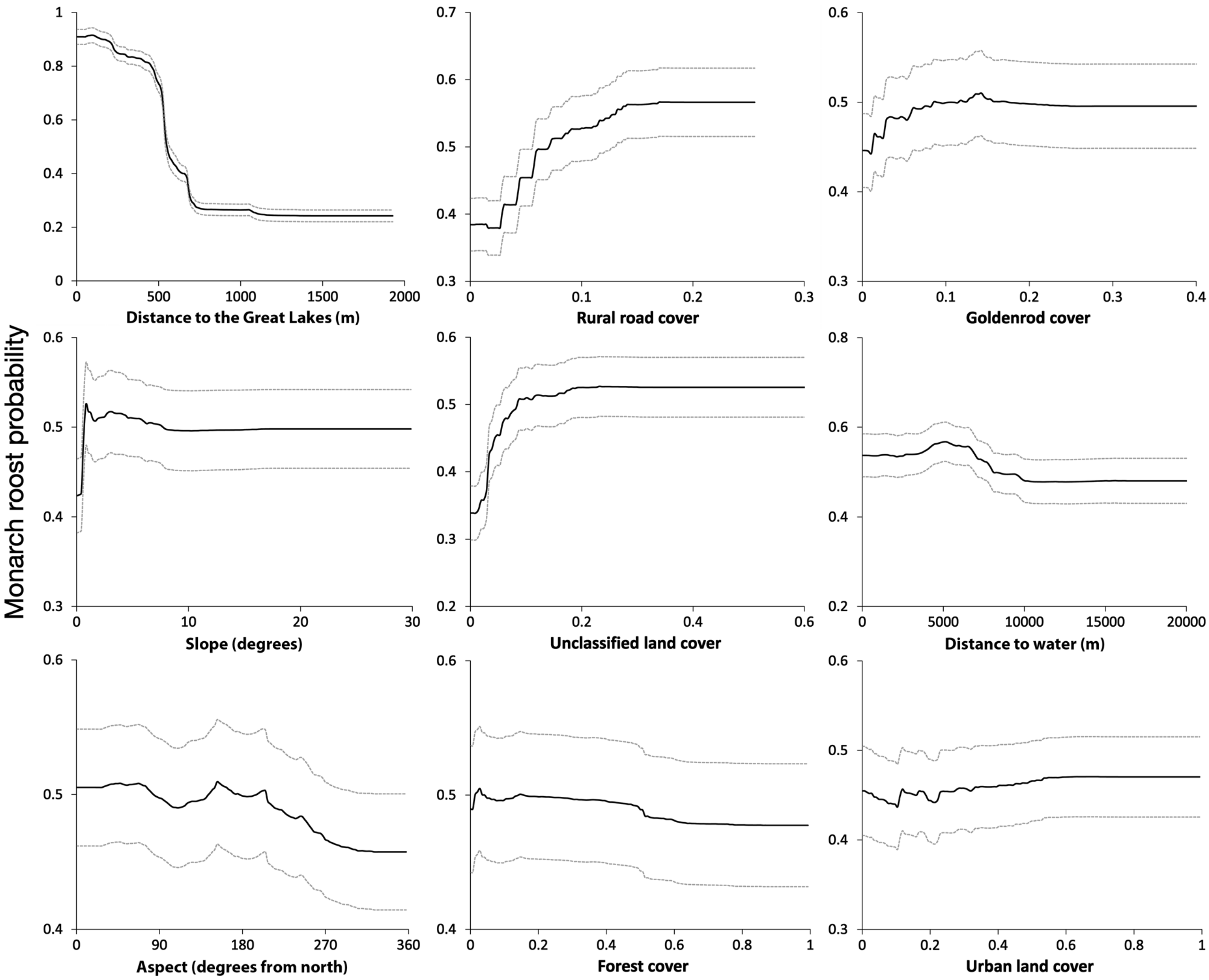

Fig. 2. Partial dependence plots of the top 9 overall most important explanatory variables in the Environment and Climate Change Canada boosted regression tree model used to predict monarch butterfly *Danaus plexippus* roost distribution in Ontario, Canada

(Jiménez & Soberón 2020, Westwood et al. 2020). Collinearity amongst predictor variables was overall very low (Table S4). While the final model predictions are not susceptible to collinearity, the partial dependence plots and relative influence can be (Elith et al. 2008). Partial dependence plots and relative influence of highly correlated variables should therefore be interpreted with caution.

4.1. Response to landscape variables

The partial dependence plots showed the change in the probability of monarch roost occurrence in response to a selected variable when the values of all other variables were held at their mean value. Each model produced 18 partial dependence plots (Figs. 2 & 3, S1 & S2). Here we discuss the plots of the top 3 variables for each model based on their relative influence: namely distance to the Great Lakes, rural road cover, urban land cover, goldenrod cover, and forest cover (Table 2). The shapes of the partial dependence plots for these 5 variables, when comparing between the ECCC model and the Journey North model, were very similar, so it's likely the plots are representative of true ecological phenomena given that the models were built from unrelated data sources and covered different geographic extents.

Partial dependence plots for distance to the Great Lakes, the most important variable in predicting monarch roost distribution (ECCC: 55.1 % RI; Journey North: 35.0 % RI), showed that the roosts are less likely to occur as distance to the Great Lakes in-

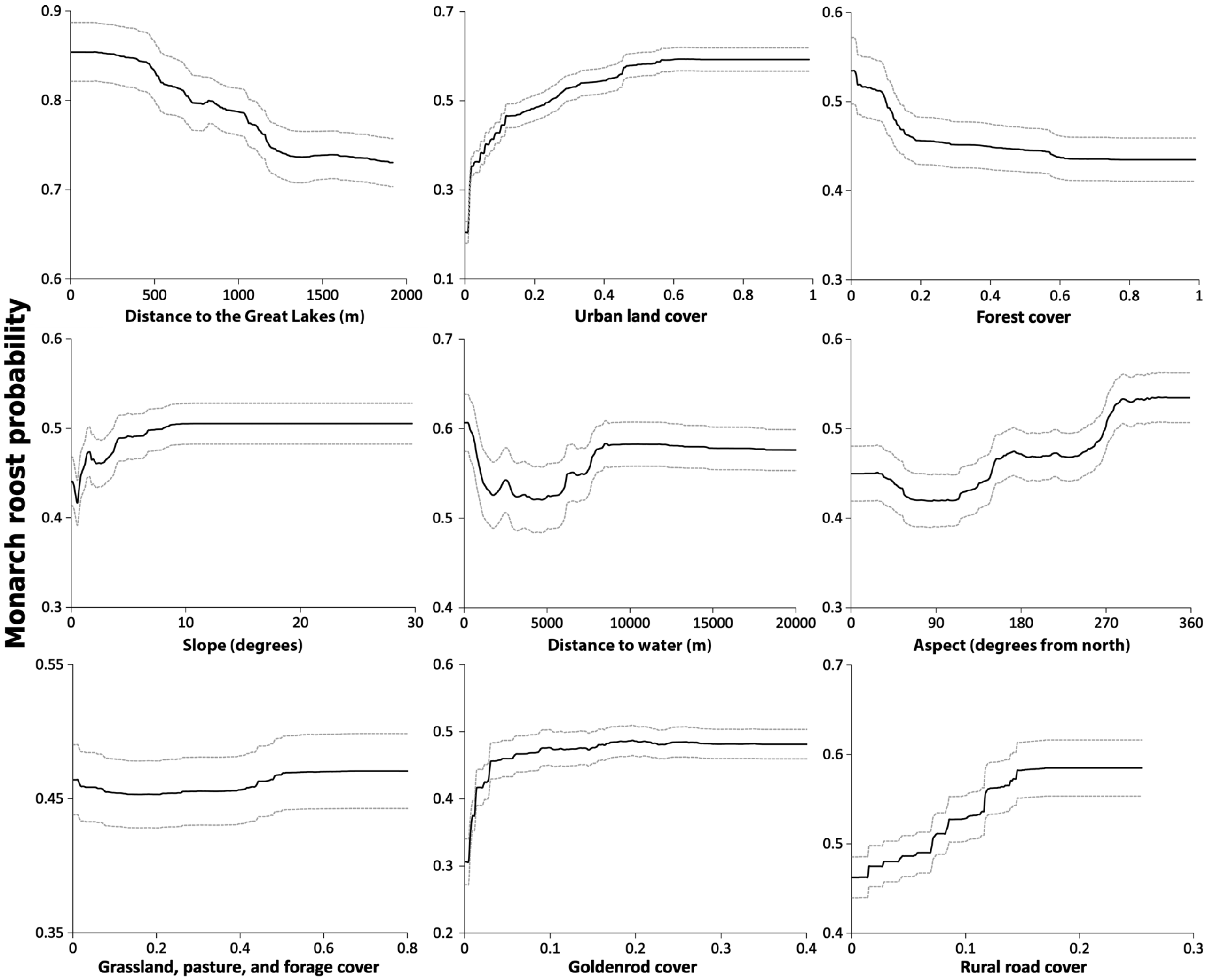

Fig. 3. Partial dependence plots of the top 9 overall most important explanatory variables in the Journey North boosted regression tree model used to predict monarch *Danaus plexippus* roost distribution in Ontario, Canada

creases. More specifically, roost distribution peaked with distance to the Great Lakes values of less than 500 m. This result supports our hypothesis that the Great Lakes coastlines are acting as diversion lines for outbound migratory monarchs. Diversion lines are landscape features, such as lakes, rivers, and habitat boundaries, that group migrants (Goodrich & Smith 2008). Specifically, monarchs may group along the Great Lakes coastlines to either avoid crossing the large bodies of open water and migrate around, or to wait for optimal conditions to cross, which has been observed at Long Point on Lake Erie (Crewe & McCracken 2015). This effect has also been observed for migratory monarchs crossing the Delaware Bay from Cape May, New Jersey, USA, where monarchs may accumulate until favourable winds allow crossing (Davis & Garland 2002), and for raptors during fall migration, where migrants are monitored at fixed HawkWatch sites known to concentrate individuals along the Great Lakes coasts (Goodrich & Smith 2008). Given other bodies of water, such as smaller lakes and rivers, did not influence monarch roost site selection to the same extent as the Great Lakes, this further supports the diversion line hypothesis. While it is possible that this finding is influenced by survey bias, particularly for the ECCC roost surveys conducted in proximity to the Great Lakes, this bias was mitigated by restricting the study area for the ECCC model to within 2 km of the Great Lakes. Additionally, the Journey North model, with no apparent distance to Great Lakes survey bias, returned very similar results.

Rural road cover was the second most important variable in predicting monarch roost distribution in the ECCC model and the ninth most important variable in the Journey North model (ECCC: 9.9% RI; Journey North: 4.1% RI). Both models showed that increased rural road cover increased the probability of monarch roost occurrence. In landscapes where floral resources are limited during the end of summer and fall, for example in areas with intensive agriculture, rural road verges can provide important nectaring opportunities for pollinators (Phillips et al. 2019). In such a landscape, which is common in southern Ontario, monarchs may preferentially select roosting sites in proximity to rural roads or where there is a high density of rural roads because of the nectaring habitat they provide. However, it is also possible that sampling bias has influenced this relationship. Specifically, the ECCC surveys were primarily conducted from rural roadsides, and the Journey North dataset was likely to have a similar sampling bias. The Journey North model showed urban road cover to have a nearly identical partial dependence plot as rural road cover but with a 3-fold lower RI, so a combination of survey bias and nectaring resources seems likely.

Urban land cover was the second highest ranking variable in predicting monarch roost occurrence for the Journey North model and the ninth highest for the ECCC model (ECCC: 1.7% RI; Journey North: 16.5% RI). Specifically, the probability of roost occurrence increased as urban land cover increased. It is possible monarchs are selecting roosting sites with higher surrounding urban land cover because they provide a thermal advantage (i.e. urban heat island effect; Diamond et al. 2014) or protection from strong winds which can disrupt roosting behaviour (Leong 2016). However, this result could also be an artifact of survey bias. The higher relative importance of urban land cover in the Journey North model (collected by members of the public) compared to the ECCC model (collected during a dedicated research program) suggests the former may suffer from this bias.

Goldenrod cover was the third highest ranking variable in predicting monarch roost occurrence for the ECCC model and the eighth highest for the Journey North model (ECCC: 6.4% RI; Journey North: 4.6% RI). The results from both models showed that an increase in goldenrod cover results in an increased probability of monarch roost occurrence. The results are not surprising given that goldenrod species (*Solidago* spp.) are important nectaring species for migratory monarchs (Rudolph et al. 2006) and represent an abundant floral resource in Ontario during the fall migration. Unclassified land cover, which primarily consisted of untilled farmland, urban brown fields, and rights-of-way corridors had a similar partial dependence plot and relative influence as goldenrod in the ECCC model. The similar response of roost occupancy to unclassified land cover was likely because unclassified lands were typically habitats that could host abundant fall floral resources.

Forest cover was the third highest ranking variable in predicting monarch roost occurrence for the Journey North model and the eighth highest for the ECCC model (ECCC: 2.8% RI; Journey North: 8.2% RI). Both models showed the probability of monarch roost occurrence to generally decrease with increased forest cover, but the Journey North model showed the highest probability of roost occurrence is below approximately 10% forest cover while the ECCC model showed the highest probability of roost occurrence is below approximately 40% forest cover. Monarch roosts are typically situated on trees, so some degree of tree cover is necessary to host roosts. However, landscapes dominated by forest habitats may have a limited availability of nectaring resources at the end of summer and fall because many forest dwelling forbs are spring ephemerals in southern Ontario. As a result of the timing of floral resources in forest habitat, increased forest cover may limit nectaring opportunities for migratory monarchs. A balance between available nectaring resources and forest cover that provides roosting opportunities is likely necessary to adequately support migratory monarchs.

4.2. Implications for conservation

Monarch stopover sites are an instrumental resource link between the breeding and wintering grounds. Describing the characteristics of these sites is therefore important to preserve this migratory phenomenon. Using dedicated fall migration surveys collected along the Great Lakes coastlines and a citizen science dataset collected across all of Ontario, this study provides some important insights into the habitat characteristics of stopover sites, which will help guide future investigations and conservation actions.

Physical landscape characteristics and habitat types are important factors in fall roosting site selection by monarchs, the specifics of which can help direct conservation actions. As observational data already suggested, our research formally demonstrates that the Great Lakes coastlines create diversion lines for migrating monarchs and that conservation activities should focus on preserving or restoring roosting habitat, such as forest, hedgerows, and shrubland, in proximity to the Great Lakes coasts. Additionally, we showed that a higher availability of nectaring habitat, such as rural road verges and goldenrod fields, increased the probability of monarch roosts. Therefore, any conservation actions to preserve or restore roosting habitat should be accompanied by the restoration or preservation of nectaring habitat in the surrounding landscape.

Given the ephemeral nature of monarch roosts, they are difficult to study using conventional field methods. Site occupancy and abundance on a particular day will be dependent on a host of environmental factors operating at different spatial and temporal scales. While our analyses use the best available data to assess fall roost site selection, future studies that count monarchs daily from fixed locations may be better suited to examine what environmental factors, such as temperature and wind patterns, are associated with greater migration activity and for assessing true use and non-use site occupancy. It will also be important to determine if higher abundance is indicative of higher quality roost sites, to better inform land management planning for monarch butterflies.

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