The Utility Of A Maximum Entropy Species Distribution Model For Ixodes Scapularis In Predicting The Public Health Risk Of Lyme Disease In Ontario, Canada

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The Utility of a Maximum Entropy Species Distribution Model for *Ixodes scapularis* in Predicting the Public Health Risk of Lyme Disease in Ontario, Canada

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Degree Completed Spring 2021
Abstract

Introduction: Lyme disease is an emerging public health threat in Ontario, Canada due to the range expansion of the tick vector, *Ixodes scapularis*. Tick abundance and density are important predictors of human Lyme disease risk and are typically measured using active tick surveillance (dragging). New cost-effective tools are needed to augment current surveillance activities.

Objective: The objective of this study was to evaluate the ability of a Maximum entropy species distribution model to predict *I. scapularis* density and abundance in three regions of Ontario – Ottawa, Kingston, and southern Ontario – in order to determine its utility in predicting the public health risk of Lyme disease.

Methods: Ticks were collected via dragging at 60 sites across the three regions. Model-predicted habitat suitability was calculated as the mean predicted habitat suitability within a 1000m radius of the site. Spearman’s correlation coefficient was used to quantify the continuous relationship between model-predicted habitat suitability and tick density, and negative binomial regression was used to quantify the relationship between tick density and dichotomized model-predicted habitat suitability.

Results: The Spearman’s correlation coefficients for the full study area, Kingston region, and Ottawa region were 0.517, 0.707, and 0.537 respectively, indicating a moderate positive relationship and ability of the model to predict tick density. Negative binomial regression found an incidence rate ratio of 33.95 in sites with model-predicted ‘suitable’ habitat compared to those with ‘not suitable’ habitat, indicating that the total number of ticks per site was significantly higher at sites situated in areas with predicted suitable habitat.

Conclusions: These findings demonstrate that model-predicted habitat suitability is moderately associated with tick density, particularly in areas with known established tick populations, and
therefore reflective of the risk of acquiring a tick bite. The use of this Maxent model may be a cost-effective tool for identifying areas in Ontario posing the greatest public health risk of Lyme disease.
Acknowledgements

I would like to thank Dr. Manisha Kulkarni and Dr. Peter Krause for their support and guidance throughout this project. I would also like to thank Andreea Slatculescu for her guidance in interpreting Maxent model results, and the INSIGHT field team for collecting the active surveillance data.
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Introduction

Lyme Disease in Ontario

Lyme disease (LD), a tick-borne bacterial illness, is an emerging public health threat in Ontario, Canada. The causative agent there, as in the rest of North America, is *Borrelia burgdorferi* sensu stricto (s.s.), which is transmitted to humans by the eastern blacklegged tick, *Ixodes scapularis* [1, 2]. Northward expansion of the blacklegged tick has been observed in Ontario since the 1990s and is projected to continue, driven in part by climate and land-use changes [3-6]. In 2019, the provincial LD incidence rate in Ontario was 7.9 per 100,000 population; however, incidence rates vary substantially by region [7]. In 2019, the health units of Kingston-Frontenac and Lennox & Addington (KFL), Ottawa, and Wellington-Dufferin-Guelph (WDG) reported incidence rates of 138.6 per 100,000 population, 17.1 per 100,000, and 2.9 per 100,000, respectively [8].

The public health risk posed by LD depends on ecological factors, which influence the density of *B. burgdorferi*-infected ticks in the environment and climatic, and human behaviour, which influences individual exposure to tick bites [9-12]. While climate factors play an important role in determining the potential range of vectors on a larger geographic scale [4, 13-16], ecological factors such as understory density, presence of shrubs, dominant tree type, canopy cover, proportion of forested land, and forest fragmentation are known to play a role in *I. scapularis* distribution on a local level [17-20]. Traditionally, active and passive tick surveillance techniques have been used to estimate the public health risk of LD. In Ontario, drag sampling is used to map LD risk areas, defined as the 20km radius from the center of a location where blacklegged ticks were found through drag sampling [21]. These surveillance activities are time and resource intensive and alternative risk estimation strategies are needed to augment public
health decision-making [22]. The contribution of climatic and environmental factors to tick population establishment has been incorporated in the development of complex modeling strategies to predict blacklegged tick habitat suitability [4, 19, 23, 24].

**Modeling current and future Lyme disease locations**

Species distribution models (SDMs) are statistical models that relate species distribution data to environmental and/or spatial characteristics at particular sites [25]. Maximum entropy (Maxent) is an extensively used and high performing SDM that can be used with presence-only data, referring to a list of locations where the species in question is known to be present [25, 26]. In the case of ticks, this data may come from active field surveillance, where drag sampling is conducted at sites known or suspected to have ticks, or passive surveillance where ticks have been found by members of the public [27]. The model uses these data alongside randomly selected pseudo-absences, a random sample of pixels from the study area used as background points in place of absences, and spatially-explicit environmental covariates to generate a probability distribution across a landscape. This distribution is conceptualized as habitat suitability [28-30].

Slatculescu et al. used a Maxent model to estimate the potential distributions of the *B. burgdorferi* bacterium and of *I. scapularis* ticks in southeastern Ontario and to identify factors that contribute to pathogen and tick establishment [30]. To create the model for *I. scapularis*, the authors used presence-only data acquired through active field sampling of immature and adult *I. scapularis* ticks at 120 sites from 2015-2018 [30]. Presence points for *I. scapularis* were defined as unique georeferenced locations where ticks were found [30]. For environmental factors (the independent variables [or covariates]) of the model, the authors used satellite remote sensing data pertaining to climate, land cover / land use, and elevation [30]. The model was validated using
two independent datasets – one from active field surveillance (dragging) at 25 new field sites in 2019, and one from passive surveillance of ticks submitted to local public health departments by residents bitten by *I. scapularis* ticks between 2015 and 2017 [30]. Although the model was created and validated using presence-only data from specific sampling locations, the Maxent output is continuous across the user-defined landscape, allowing the predicted degree of habitat suitability to be modeled and interpolated on a fine scale [28].

This model has been shown to accurately predict tick occurrence, defined as the presence or absence of ticks at a given location by drag sampling; however, knowledge of occurrence is not optimally useful for public health purposes, which requires an additional understanding of human LD risk to prioritize areas for surveillance and public health messaging. In Ontario, tick abundance (the number of ticks at a given location), density (the number of ticks per unit of area), and establishment (whether all three life stages have been detected for two consecutive years) are important indicators of LD risk [22, 27, 31]. Researchers in the field of conservation biology are also interested in the relationship between the habitat suitability predicted by presence/absence models and population density, generally in the context of invasive species [22, 31]. Accordingly, several studies have sought to quantify the relationship between model predictions and species abundance or density using a variety of statistical methods such as linear regression, quantile regression, and Spearman’s correlation [32-37]. A small subset of these studies has demonstrated a positive relationship between modeled suitability and observed abundance for different taxa, such as plants, birds, and arthropods [33, 35-37]. For example, Jimenez-Valverde et al. compared the predicted suitability of an artificial neural network model with abundance measured using pitfall traps for 48 arthropod species in the Azores and found significant positive correlations for nine species [35]. In a study of vertebrates in Australia,
VanDerWal et al. found a positive relationship between Maxent model-predicted environmental suitability and abundance, measured using field surveys, for the majority of species (>84%) [36]. To our knowledge this association has never been tested for *I. scapularis* in Canada.

**Aims and hypotheses**

Our primary aim was to assess the potential utility of a maximum entropy (Maxent) species distribution model for *Ixodes scapularis* for public health decision-making regarding LD risk in Ontario. We assessed whether such a model is an effective means of predicting current and/or future trends in tick abundance and LD risk. We planned to do this by quantifying the relationship between model-predicted tick habitat suitability and observed tick density (rather than occurrence) in three regions with different levels of human LD incidence in Ontario – Kingston (higher LD incidence), Ottawa (medium LD incidence), and southern Ontario (lower LD incidence) – corresponding to different degrees of tick population establishment. We hypothesized a moderate and biologically significant correlation between model-predicted tick habitat suitability and observed tick density, with the strength of association increasing with degree of tick population establishment. The findings of this study should help determine the usefulness of this model in public health planning, decision-making, and messaging in regard to Lyme disease risk in Ontario [38, 39].

**Methods**

**Study location**

The three regions selected for this study represent different stages of blacklegged tick establishment in Ontario, where active tick surveillance activities were undertaken in 2019. In this study, the Kingston region is defined as all sites within a 130km radius of the City of
Kingston or located along the St. Lawrence River (Fig. 1). The KFL Health unit, which covers most of the region defined in this study, has a population of around 200,000 [40]. The Ottawa region is defined as all sites within a 60km radius of the City of Ottawa, which has a population of around one million people [41]. The Kingston region has recorded established tick populations for more than a decade whereas ticks have more recently been detected in the Ottawa region [10]. Both of these regions are located in eastern Ontario, which has a high amount of forested area. The southern Ontario region is defined as all sites west of the City of Belleville and is highly agricultural. It contains some locations with long-established tick populations along the Great Lakes shoreline, but few records of ticks from sites situated in the interior zone [6, 10, 12, 31, 42]. This is the largest of the three regions of study, encompassing several health units, with the majority of sites located in the WDG and Hamilton health units which have populations of 284,461 and 536,917, respectively [43, 44]. The region also includes the populous health units of Peel and Halton, which have a combined population of 1,930,174 [45, 46].

**Field Sampling and Tick Density**

Data was combined from three different tick surveillance initiatives that took place in 2019. Field data for the Ottawa and Kingston regions (28 and 15 sites, respectively) were collected by the Interdisciplinary Spatial Informatics for Global Health (INSIGHT) Lab at the University of Ottawa, while southern Ontario region data (10 sites) were collected by researchers at the University of Guelph as part of the Canadian Lyme Disease Research Network (CLyDRN) (Fig. 1). Ottawa region data were supplemented by other surveillance activities funded by the Public Health Agency of Canada [42]. Seven additional sites – five in in southern Ontario and two in Ottawa – were sampled by the INSIGHT Lab as part of a prior study [30]. Within each region, sites were chosen in consultation with local health unit partners and had to be publicly accessible
woodlands with the potential for tick occurrence. Land access permits for tick sampling were obtained from the National Capital Commission (Ottawa), the City of Ottawa, Ontario Parks, and individual conservation area authorities, where applicable.

Active surveillance was conducted at twenty-eight sites in the Ottawa region representing urban, suburban, and rural areas that included parks, recreational trails, and conservation areas [47]. Fifteen sites were sampled in the Kingston region, which is located southwest of Ottawa, where the St. Lawrence River meets Lake Ontario. Thirteen sites were sampled in the southern Ontario region near the western edge of Lake Ontario, which has historically experienced a low burden of LD relative to provincial levels [48]. Ottawa sites were visited in May to July, while Kingston and southern Ontario sites were visited in July.

Active surveillance was conducted at all sites using the drag sampling method described by Public Health Ontario [49]. Ticks were collected by dragging a 1m$^2$ cloth over the forest floor and vegetation for 2000 m$^2$. Approximately every 50 metres, the drag cloth was checked for ticks and geographic coordinates were logged using a handheld global positioning system (GPS) device (Garmin eTrex 20x). All adult and nymphal ticks were placed in plastic tubes and transported on ice to either the University of Ottawa or the National Microbiology Laboratory for species identification and testing. Adults and nymphs were examined by microscopy for species and sex identification using standard taxonomic keys [50-54]. *Ixodes scapularis* abundance was calculated as the sum of all adults and nymphs collected at a site, and density was calculated as this sum divided by the sampling area in square metres.

**Model-Predicted Habitat Suitability**

The output of the Slatculescu et al. Maxent model is a raster of predicted habitat suitability on a scale from 0-1 covering all of Ontario south of the Ottawa River. To extract the suitability values
for each site (n=60), the sites were first mapped as points in ArcGIS Pro using their geographic coordinates. Then, circular “buffers” with a 1000m radius were created around each point, and the zonal mean of the suitability within each buffer area was calculated. The 1000m radius was chosen to represent a biologically significant geographic area for ticks and their hosts while minimizing the inclusion of water at sites located near the Great Lakes. The zonal mean suitability was also calculated using 500m and 1500m-radius buffers to be used in a sensitivity analysis. Patterns in *I. scapularis* density were mapped along with the model-predicted habitat suitability raster using ArcGIS Pro v2.6.0 (ESRI, Redlands, USA). All map figures were created using publicly available spatial data for administrative boundaries and predefined ArcGIS basemap layers (ESRI, Redlands, USA).

*Spearman’s correlation coefficient*

A scatterplot of model-predicted habitat suitability vs tick density was used to visualize the relationship between the two variables and demonstrated a monotonic, non-linear relationship. Spearman’s correlation coefficient was therefore computed to quantify the relationship between continuous predicted tick habitat suitability and *I. scapularis* density across all three regions. The data were then stratified by region and Spearman’s correlation was computed for the Ottawa and Kingston region strata. The analysis could not be performed for the southern Ontario region due to the small sample size and high number of zero density sites. Statistical significance was tested at the $\alpha = 0.05$ level. As a sensitivity analysis, Spearman’s correlation was also computed using model-predicted habitat suitability extracted with 500m and 1500m-radius buffers.

*Negative binomial regression*

To assess the association between predicted habitat suitability and tick density, the predicted habitat suitability output from the Maxent model was first categorized into “suitable” or “not
suitable” by selecting a binary threshold. Three binary threshold values were chosen based on the Maxent model output, taking into account the fractional predicted area and omission rate for each threshold value. These thresholds corresponded to the “equal training sensitivity and specificity” threshold, “10 percentile training presence”, and “maximum training sensitivity plus specificity” (Table 1) [30]. The fractional predicted area refers to the proportion of pixels predicted as suitable – locations where a presence point would be found – while the omission rate refers to the fraction of presence points that fall into pixels not predicted as suitable.

Negative binomial regression was used to model the relationship between dichotomized predicted suitability and tick abundance for each threshold using the full dataset that included all 60 sites. Sampling area was adjusted for by including a log(area) term in the model. Statistical significance was again tested at the $\alpha = 0.05$ level. Negative binomial regression was chosen over Poisson regression based on the over-dispersion of the data and lower BIC scores. All analyses were conducted using RStudio 1.2.5001 [55]. The MASS package was used to perform negative binomial regression and the mfx package was used to calculate incidence rate ratios from the regression model [56, 57].

**Results**

**Tick density and Maxent model-predicted habitat suitability**

We assessed the utility of a Maxent model for predicting *I. scapularis* density in Ontario using active field surveillance data from 60 sites in three regions. The mean (sd) observed tick densities in the Ottawa, Kingston, and southern Ontario regions were 0.43 (0.71), 0.62 (1.33), and 0.01 (0.03) ticks per 100 metres squared, respectively. The mean model-predicted suitability
within a 1000m radius of a site was 0.82 (0.16) in the Ottawa region, 0.35 (0.33) in the Kingston region, and 0.30 (0.30) in the southern Ontario region.

**Relationship between observed tick density and predicted habitat suitability using Spearman’s correlation coefficient**

The relationship between observed tick density and model-predicted habitat suitability was wedge-shaped for the full study area, the Kingston region subset, and the Ottawa region subset, with Ottawa and the full study area in particular demonstrating a strong wedge-shaped pattern (Fig. 2). The upper limit of observed density increased with increasing predicted habitat suitability; however, this was not a linear relationship as low tick density was often observed at sites predicted as having a high proportion of suitable tick habitat within a 1000m radius.

Spearman’s correlation for the full study area (n = 60) revealed a moderate positive relationship between model-predicted habitat suitability and observed tick density (r = 0.517, p < 0.001) as did Spearman’s correlation for the Ottawa stratum (n = 28, r = 0.537, p = 0.002) (Table 2). In the Kingston stratum, Spearman’s correlation demonstrated a fairly strong positive correlation (n = 17, r = 0.707, p = 0.003). The correlation for the southern Ontario region could not be computed since there were no ticks at all but one site.

As a sensitivity analysis, Spearman’s correlation was computed for mean model-predicted habitat suitability using 500m and 1500m-radius buffers. For the full study area, the Spearman’s correlation coefficients were 0.455 (p = 0.002) using a 500m buffer and 0.542 (p < 0.001) using a 1500m buffer. For the Ottawa region, the Spearman’s correlation coefficients were 0.308 (p = 0.028) and 0.489 (p = 0.001) using 500m and 1500m buffers, respectively. For the Kingston region, Spearman’s correlation coefficients were 0.673 (p = 0.003) using a 500m buffer and 0.762 (p < 0.001) using a 1500m buffer.
**Relationship between observed tick density and predicted habitat suitability using negative binomial regression**

Negative binomial regressions assessing the association between predicted tick abundance and binary predicted tick habitat suitability (i.e., categorized as “suitable” or “not suitable”) revealed significant associations at all thresholds. The model using the largest threshold value, “equal training sensitivity and specificity”, had the lowest BIC score and was therefore deemed to have the best fit (Table 3). Using this threshold, the incidence rate ratio (IRR) was calculated to be 33.95 (p < 0.001). Using the lower thresholds, the IRR was 24.30 (p < 0.001) for both models.

**Discussion**

This study used active tick surveillance data to evaluate the ability of an existing Maxent model to predict tick abundance and density on a fine scale in Ontario, Canada. The findings shed light on the model’s potential utility for estimating the public health risk of LD and informing public health decision-making. There was a moderate and statistically significant positive correlation between predicted habitat suitability and observed tick density across the entire sample (r = 0.517), and in the Ottawa and Kingston region subsets (r = 0.537, r = 0.707). Negative binomial regression revealed that when habitat suitability was dichotomized into “suitable” and “not suitable”, the total number of ticks per sites was 33.95 (95% CI = 8.53, 220.59) times higher at sites situated in areas with predicted suitable tick habitat compared to those situated in areas predicted to be unsuitable. The binary threshold value was chosen based on the model fractional predicted area and training omission rate, as well as a comparison of BIC scores between three possible thresholds. The selection of the highest of these three thresholds represents a conservative estimate of habitat suitability since it results in a smaller predicted area of
suitability and increases the possibility of excluding some suitable locations. These results suggest the model has a moderate ability to predict blacklegged tick density across the study region, with good predictive ability in a region with long-established tick populations. Moreover, when predicted suitability is dichotomized, the model-predicted “suitable” habitat is strongly associated with higher tick density.

Some sites with high predicted tick habitat suitability were found to have low tick density, but no sites with low predicted tick habitat suitability were found to have high tick density, creating a funnel-shaped distribution. This finding mirrors those of similar studies of habitat suitability models for vertebrates and plants, which found that high suitability does not necessarily equate to a high species abundance, and that predicted habitat suitability typically indicates the upper limit of species abundance rather than mean abundance [33, 36]. Similarly, Pearce and Ferrier found that for locations where a species was found to be present, their models were not able to predict increasing abundance [33, 37]. The findings of these studies suggest that environmental factors that influence species’ distributions may not equally influence species abundance and therefore density [33].

In our study, sites with low observed tick density that were predicted to have highly suitable tick habitat tended to be located in similar areas, either along the Ottawa and Rideau Rivers on the eastern side of the City of Ottawa (for sites in the Ottawa region) or along Lake Ontario (for sites in the southern Ontario region). Sites predicted to have high tick habitat suitability and where high tick density was observed were mostly found in the region of eastern Ontario falling between the western side of the City of Ottawa and the northern portion of the Kingston region. Qualitatively, the high suitability/low density sites in the Ottawa region tended to be in areas comprised of built-up land use with minimal surrounding forest. Conversely, the
high suitability/high density sites were located in areas characterized by a high proportion of forest land cover. In a previous study, Burrows et al. used active surveillance data from 2017-2019 to assign “ecological classifications” to twenty eight sites in the Ottawa area with the goal of identifying sites that currently have established tick populations (established sites), sites that have little evidence of tick colonization (low-stable and non-zero sites), and sites that appear to have tick populations in the process of becoming established (emerging sites) [31]. Three of the Ottawa-area high suitability/low density sites in our study were also included in the Burrows et al. study. Of these three sites, two (sites 23 and 25) were determined to have emerging tick populations. This may indicate that the Slatculescu et al. model accurately classified these sites as highly suitable, and that we are likely to see tick abundance increase at these sites.

Spatiotemporal differences in the degree of tick colonization are expected due to the ongoing process of tick emergence in Ontario. This may explain some of the variability in observed tick density in areas of high predicted tick habitat suitability. Discrepancies between predicted tick habitat suitability and observed tick density may also be explained in part by the inherent limitations of the Maxent model. Since the model only includes land cover and climate variables, the differences in observed densities at highly suitable sites may be due to abiotic factors affecting the ability of ticks to colonize an area, e.g., geographic barriers to dispersal, or ecological factors not captured in the model. For example, the availability of hosts necessary for the tick’s lifecycle, such as white-footed mice and white-tailed deer, may be influenced by factors other than climate and landcover. One such factor is forest fragmentation, which has been found to influence tick abundance through the movement of deer and small mammals [58-60]. These mammals are often found near forest edges, for example those created by roads and freeways, and may facilitate the dispersal of blacklegged ticks [18, 20, 61]. The effect of host
species abundance and diversity on blacklegged tick populations is complex. Previous studies in Ontario have found that greater biodiversity can lead to lower nymph abundance, and it is speculated that this may be a result of poor-quality hosts removing and eating a large proportion of ticks through grooming; however, this effect depends on the structure and composition of the small mammal community [18, 62, 63]. In addition, sampling biases (including differences in operator experience, conditions during dragging, and protocol variations) may have occurred during the collection of the data used to train and validate the model, although we used a standardized protocol for tick sampling across all sites, which increased comparability [30].

This study has several limitations. Due the small sample size, conclusions from the regionally stratified correlations should be interpreted with caution. We were unable to test the correlation between predicted tick habitat suitability and tick density only using sites where ticks were present, since removing zero density sites resulted in insufficient sample size and power. The inclusion of such an analysis would have improved the robustness of our findings by demonstrating whether the model can predict increasing abundance in locations of known tick presence [33, 37]. Importantly, while the analysis demonstrates a relationship between the variables of interest, it is not able to fully explain the reasons for the variation that was observed between tick densities at sites predicted to have high tick habitat suitability. Future studies should seek to understand the ecological factors not included in this model that may result in low tick abundance in areas predicted to be highly suitable.

Conclusions

This study provides valuable insight into the utility of species distribution models for public health planning and decision-making. The passive and active tick surveillance strategies
traditionally used to estimate LD risk have inherent limitations. Passive surveillance, which refers to submissions of ticks from the public, has low specificity while active surveillance is time and resource intensive. As a result, innovate tools are needed to support LD risk estimation. In their original paper, Slatculescu et al. noted that their model results were consistent with human LD incidence rates in the province of Ontario, accurately predicting high suitability in eastern Ontario which has the highest LD incidence rates per 100,000 population [12, 30, 48]. Our study further confirms that model-predicted tick habitat suitability is reflective of public health risk by demonstrating a positive relationship between the model predictions and observed tick abundance and density. Abundance and density, particularly for nymphs, have been shown to be highly correlated with human LD incidence and therefore are important indicators of LD risk [64-66]. It is important to understand that the model predicts the upper limit of tick density because this suggests that areas predicted to have low suitability are unlikely to achieve high tick densities. Conversely, areas predicted to be highly suitable may experience increasing tick abundance in the future. This more robust understanding of the model output allows us to make informed decisions about how to interpret the results in the context of public health decision-making.

In sum, our findings suggest that a Maxent model for predicting tick habitat suitability and abundance can provide more nuanced information on human LD risk than the risk maps currently used by Public Health Ontario. The latter simply define a risk area as the 20km radius from the center of a location where blacklegged ticks were found through drag sampling [21]. This more nuanced picture provided by the Maxent model can allow for limited active surveillance resources to be targeted to areas most likely to experience increasing blacklegged
tick abundance and Lyme disease risk. Further research should seek to identify interventions suitable such a targeted approach.
References

13. Ogden NH, Bigras-Poulin M, O’Callaghan CJ, Barker IK, Lindsay LR, Maarouf A, et al. A dynamic population model to investigate effects of climate on geographic range and


**Tables**

**Table 1. Maxent model threshold values**

<table>
<thead>
<tr>
<th>Threshold Description</th>
<th>Threshold Value</th>
<th>Predicted Area</th>
<th>Training Omission Rate</th>
<th>Implications for Sensitivity &amp; Specificity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Equal training sensitivity and specificity</td>
<td>0.487</td>
<td>0.116</td>
<td>0.125</td>
<td>The highest threshold balances sensitivity and specificity; balances probability of false positives and false negatives</td>
</tr>
<tr>
<td>10 percentile training presence</td>
<td>0.375</td>
<td>0.163</td>
<td>0.083</td>
<td>Favours sensitivity over specificity; increased probability of false positives</td>
</tr>
<tr>
<td>Maximum training sensitivity plus specificity</td>
<td>0.351</td>
<td>0.174</td>
<td>0.042</td>
<td>The lowest threshold maximizes sensitivity; highest probability of false negatives</td>
</tr>
</tbody>
</table>

**Table 2. Spearman’s correlation coefficient**

<table>
<thead>
<tr>
<th>Model</th>
<th>500m buffer</th>
<th>100m buffer</th>
<th>1500m buffer</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>r</td>
<td>p-value</td>
<td>r</td>
</tr>
<tr>
<td>Full study area</td>
<td>0.455</td>
<td>0.002</td>
<td>0.517</td>
</tr>
<tr>
<td>Kingston region</td>
<td>0.673</td>
<td>0.003</td>
<td>0.707</td>
</tr>
<tr>
<td>Ottawa region</td>
<td>0.308</td>
<td>0.028</td>
<td>0.537</td>
</tr>
</tbody>
</table>

**Table 3. Negative binomial regression**

<table>
<thead>
<tr>
<th>Model</th>
<th>IRR</th>
<th>95% CI</th>
<th>p-value</th>
<th>BIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>High threshold</td>
<td>33.95</td>
<td>8.53, 220.59</td>
<td>&lt;0.001</td>
<td>316.15</td>
</tr>
<tr>
<td>Medium threshold</td>
<td>24.30</td>
<td>5.29, 160.29</td>
<td>&lt;0.001</td>
<td>333.63</td>
</tr>
<tr>
<td>Low threshold</td>
<td>24.30</td>
<td>5.29, 160.29</td>
<td>&lt;0.001</td>
<td>333.63</td>
</tr>
</tbody>
</table>
Figures

Figure 1. Model-predicted habitat suitability and observed *Ixodes scapularis* density. (A) Full study area. (B) Ottawa region. (C) Kingston region. (D) Southern Ontario region.
Figure 2. Scatterplots of model-predicted habitat suitability vs observed density for (A) the full study area, (B) the Kingston region, (C) the Ottawa region, and (D) the southern Ontario region.  
(A) The full study area shows a wedge-shaped relationship between model-predicted habitat suitability and observed tick density, with a moderate, positive Spearman’s correlation coefficient of 0.517 (p<0.001). (B) The Kingston region shows a stronger, positive Spearman’s correlation than the full study area (0.707, p=0.002). (C) The Ottawa region shows a relationship very similar to the full study area with a clear wedge-shaped pattern and a Spearman’s correlation of 0.537 (p=0.003). (D) The southern Ontario region contained primarily zero density sites.