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Authors: Alkishe, Abdelghafar, and Peterson, A. Townsend

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Potential geographic distribution of *Ixodes cookei*, the vector of Powassan virus

Abdelghafar Alkishe[1,2]✉ and A. Townsend Peterson[1]

[1]*Biodiversity Institute, University of Kansas, Lawrence, Kansas, U.S.A. abduelkeesh8614@gmail.com*
[2]*Zoology Department, Faculty of Science, University of Tripoli, Tripoli, Libya*

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ABSTRACT: *Ixodes cookei* Packard, the groundhog tick or woodchuck tick, is the main known vector of Powassan virus (POWV) disease in North America and an ectoparasite that infests diverse small- and mid-size mammals for blood meals to complete its life stages. Since *I. cookei* spends much of its life cycle off the host and needs hosts for a blood meal in order to pass to the next life stage, it is susceptible to changes in environmental conditions. We used a maximum-entropy approach to ecological niche modeling that incorporates detailed model-selection routes to link occurrence data to climatic variables to assess the potential geographic distribution of *I. cookei* under current and likely future climate conditions. Our models identified suitable areas in the eastern United States, from Tennessee and North Carolina north to southern Canada, including Nova Scotia, New Brunswick, eastern Newfoundland and Labrador, southern Quebec, and Ontario; suitable areas were also in western states, including Washington and Oregon and restricted areas of northern Idaho, northwestern Montana, and adjacent British Columbia, in Canada. This study produces the first maps of the potential geographic distribution of *I. cookei*. Documented POWV cases overlapped with suitable areas in the northeastern states; however, the presence of this disease in areas classified by our models as not suitable by our models but with POWV cases (Minnesota and North Dakota) requires more study. ***Journal of Vector Ecology* 46 (2): 155-162. 2021.**

Keyword Index: Ecological niche modeling, *Ixodes cookei*, future climate scenarios, potential distribution, Powassan virus, North America.

INTRODUCTION

Ixodes cookei Packard, the groundhog tick or woodchuck tick, is a hard tick (Acari: Ixodidae) that infests a wide variety of small- and mid-size animals, including woodchucks, racoons, mink, foxes, weasels, and squirrels (Durden and Keirans 1996). *Ixodes cookei* is the main known vector of one of the Powassan virus (POWV) (genus *Flavivirus*) genotypes known as lineage 1, the infectious agent of Powassan encephalitis (Ebel 2010), but is not a highly efficient vector of the pathogen causing Lyme disease (Barker et al. 1993); another POWVr genotype is called deer tick virus which is transmitted by *I. scapularis* (Ebel 2010). POWV was first discovered in 1958 in Ontario after a human died of encephalitis (McLean and Donohue 1959). Since that time, POWV cases have been documented more, including in eastern Canada and northeastern United States (Gholam et al. 1999). In the United States, although Powassan encephalitis cases are rare, numbers of human cases have increased in recent years, from 8-12 cases in 2010-2011 to 21-37 cases in 2018-2019 (CDC 2020).

Environmental conditions are crucial for shaping the geographic distributions of tick species, as temperature increases are known to have caused range expansions of tick species (Gasmi et al. 2018, Molaei 2020). Previous studies have reported that *I. cookei* is distributed in the central and eastern United States, mostly in the northeastern States (Connecticut, Massachusetts, New Hampshire, Rhode Island, Vermont, and particularly in Maine) (Rand et al. 2007). They are also distributed in southeastern Canada, especially Québec, where they are the most common tick species (Gasmi et al. 2018, Scott et al. 2018). However, the full geographic distribution of *I. cookei* remains poorly studied. In Canada, for example, a recent study documented a range expansion from eastern Canada into southwestern British Columbia (Scott et al. 2018).

Ecological niche modeling (ENM) comprises methods and tools that allow researchers to estimate the set of conditions suitable for a species to maintain populations, by means of integrating known occurrence points with gridded data summarizing environmental conditions (Peterson et al. 2011). ENM is considered as a powerful tool and has been used widely in spatial epidemiology to understand geographic distributions of disease vectors, pathogens, human cases, and disease hosts (Escobar 2020). ENM comes with some caveats and challenges, such as species not having the ability to occupy the full set of suitable areas owing to limited dispersal ability or biotic interactions, and biases in sampling among regions. When taken carefully into account, these challenges can be minimized in terms of their effects on model outcomes (Peterson 2014).

Given the relative paucity of knowledge of the range of *I. cookei* and increasing Powassan encephalitis disease concerns (CDC 2020), we here present a first study using ecological niche modeling. Our aim is to identify suitable areas for *I. cookei* under current conditions, as well as highlighting the potential distribution of the species under future climate conditions (for the year 2050). This paper adds more detail of the likely geographic distribution of *I. cookei* and may benefit public health by identifying new or unrecognized areas of potential POWV transmission.

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MATERIALS AND METHODS

Occurrence records

A total of 402 occurrence points of *I. cookei* was obtained from various sources (Table 1). We cleaned and reduced the raw data records by removing records not clearly corresponding to the species of interest, points not confirmed in the literature, records missing coordinates or records with (0, 0) as coordinates, and duplicate records (supplementary materials; S1 file). We thinned the remaining records, using a spatial distance filter of 50 km, to avoid model bias and model overfitting resulting from spatial autocorrelation (Anderson et al. 2003), using the spTthin R package (Aiello-Lammens et al. 2015). After these steps, we had 52 occurrence points as final data inputs for our model (Figure 1). We divided the data randomly into two sets: 50% for model calibration and evaluation, and used the full set of data for creating final models following Cobos et al. (2019). We also did another model excluding occurrence points that are in western Canada (Figure 1) to test the ability of our models based on eastern points to anticipate those western distributional areas. We did not use a block-based sub-setting strategy (Muscarella et al. 2014) out of concern that such an approach may lead to problems in model transfer springing from poorer representation of environmental conditions in the calibration dataset (Owens et al. 2013).

Calibration area (M) and environmental data

The accessible area (termed **M**) for the species, which defines the area to be used in model calibration, was delimited based on a 500 km buffer around the available occurrence points (Barve et al. 2011), assuming that highly mobile vertebrates play a role in carrying ticks into areas some distance away from established populations, which avoids bias in model outcomes (Anderson and Raza 2010). We used 19 environmental predictors, based on average monthly temperature and rainfall data derived from weather stations during 1950-2000, from WorldClim version 1.4, at 10' (~17 km) spatial resolution (Hijmans et al. 2005); (available at http://www.worldclim.org). We removed variables 8, 9, 18, and 19 (combinations of temperature and precipitation) because of their known spatial artifacts that they are known to hold (Broennimann et al. 2012, Bede-Fazekas and Somodi 2020).

The remaining 15 variables were masked to the calibration areas (**M**); we then used principal component analysis (PCA) to reduce dimensionality among 15 variables that characterize variation in climate across the training and testing areas and to create sets of orthogonal predictors. In the end, we used 11 sets of variables, which represent all possible combinations of the first four PCs (supplementary materials; S2), which together explained 94% of overall variation. For transfers to future climate conditions, we used five general circulation models (GCMs) for two representative concentration pathway (RCP) emission scenarios (RCP4.5 and RCP8.5) for a twenty-year period centered on 2050 (years 2041-2060) from Climate Change, Agriculture and Food Security (CCAF), at 10' (~17 km) spatial resolution (available at http://www.ccafs-climate.org/data_spatial_downscaling). Those GCMs were from the Canadian Center for Climate Modeling and Analysis (CCCMA-CANESM2); National Science Foundation Department of Energy, National Center for Atmospheric Research (CESM1-BGC); NASA Goddard Institute for Space Studies (NASA GISS) (GISS – E2 - R); Institute Pierre-Simon Laplace (IPSL-CM5A-MR); and National Center for Atmospheric Research (NCAR) (CCSM 4). These emission scenarios represent low and high greenhouse gas concentrations, and thus may bracket likely future climate conditions.

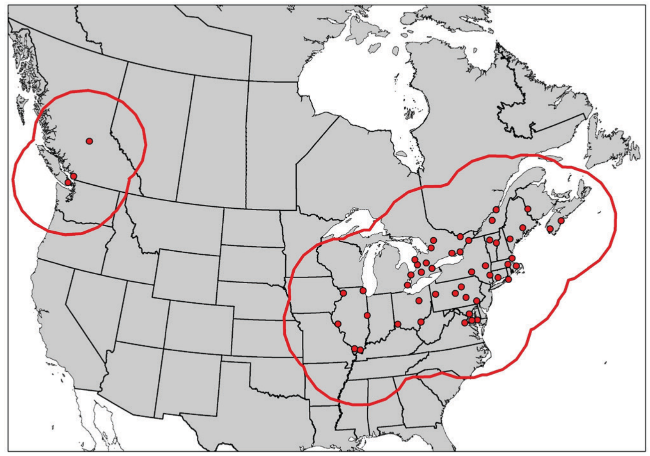

Figure 1. Occurrence points (red dots) and calibration areas (red buffer) for *Ixodes cookei*.

Ecological niche modeling

For model calibration, using the kuenm R package (Cobos et al. 2019) which uses a maximum-entropy algorithm implemented in Maxent (Phillips and Dudík 2008, Phillips et al. 2017). We tested all combinations of four feature classes (15 combinations: l, q, p, h, lq, lp, lh, qp, qh, ph, lqp, lqh, lph, qph, lqph) where linear = l, product = p, quadratic = q, hinge = h

Table 1. Sources of occurrence data of *Ixodes cookei.*

Source	Number of records	Reference
Global Biodiversity Information Facility	200	GBIF.org (09 April 2020) GBIF occurrence download. https://doi.org/10.15468/dl.4x3wrb.
VectorMap	14	http://vectormap.si.edu/Tick_Metadata.htm#vec148
BISON	173	https://bison.usgs.gov/#home
Literature	15	(Scott et al. 2018)

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and 17 regularization multiplier values (0.1 to 1 at intervals of 0.1, 2 to 10 at intervals of 1), as well as the 11 environmental datasets described above. In all, 2805 candidate models were tested and evaluated based on statistical significance of partial receiver operating characteristic (ROC) ($P \leq 0.05$) (Peterson et al. 2008) and omission rate ($E \leq 5\%$) (Anderson et al. 2003). Finally, among significant, low-omission models, we applied the Akaike Information Criterion corrected for small sampling sizes (AICc) (Warren and Seifert 2011) and delta AICc, which is the difference between AICc values and the minimum AICc among significant, low-omission models, for choosing the best candidate models to run finals models (criterion AICc < 2). This three-part model-selection procedure assures predictive models with relatively few parameters.

Final models

We used the complete set of occurrences and the parameterizations selected during model calibration. We used a 50% bootstrap with ten replicates to permit consideration of uncertainty deriving from availability of occurrence data, and transferred the models to all of North America in current and future climate scenarios. We summarized model results by calculating medians of final results obtained for each parameter value set. We used a fixed allowable omission error rate at 5% (Anderson et al. 2003) to binarize final models, in effect assuming that ≤5% of occurrence data have errors that might misrepresent environments used by the species. We summarized the results from current and future scenarios by calculating the differences in suitability (taking the median across GCMs) for each RCP from the present (Campbell et al. 2015). We represented agreement of changes of suitable areas across the five GCMs into predictions of range stability, gain, or loss. The kuenm R package (available at https://github.com/marlonecobos/kuenm) was used for all modelling analyses.

Uncertainty in model projections

We used mobility-oriented parity metric (MOP) following Owens et al. (2013) to assess the strict extrapolation risk considering the nearest 5% of the reference cloud. We also assessed model variability from replicates, parameters settings, GCMs, and RCPs in the model projections following Cobos et al. (2019), by inspecting variation on a pixel-by-pixel basis. These calculations were developed in the kuenm R package.

RESULTS

Present suitable areas

We had 2,624 statistically significant models ($P \leq 0.05$) from an initial total of 2,805 candidate models; 1,449 of significant models also met the omission rate criteria (OR ≤ 0.05), and just five models were identified as best models based on AICc. All best models were based on the predictor variables in Set 2 (PC1, PC2, and PC3; Table 2).

Results from initial models in which we did not include the occurrence points from western Canada successfully anticipated the distributional areas in the Pacific Northwest, particularly in British Columbia (Figure 2). This initial modeling pass thus successfully anticipated highly suitable areas in British Columbia, lending confidence in these models to anticipate other distributional areas.

In the United States, *I. cookei* showed high suitability across most eastern states, including Maine, New Hampshire, Vermont, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Pennsylvania, Delaware, Maryland, Washington D.C., West Virginia, Ohio, Indiana, Illinois, Michigan, and Kentucky, and in restricted areas of northern and western Virginia, western North Carolina, and eastern Missouri. Suitable areas were also identified in western states, including Washington, Oregon, and restricted parts of northern Idaho and northwestern Montana. Low suitability was observed in southern Minnesota, Iowa, eastern Kansas, northern Arkansas, and Tennessee, as well as in eastern California, southern Montana, northern Wyoming, northern Utah, and Colorado (Figure 3).

For Canada, high suitability was anticipated in southeastern Canada, including Nova Scotia, New Brunswick, eastern Newfoundland Labrador, southern Quebec, and Ontario. Suitable areas also were identified in western Canada, particularly in eastern and coastal British Columbia (Figure 3).

Future suitable areas

Model transfers to future conditions showed stability in suitability of areas across most of the northeastern United States and eastern and southern Canada (Figure 4). Reduction (loss) of suitable areas (with some differences between RCP 4.5 and RCP 8.5) was anticipated in Missouri, Tennessee, North Carolina, Virginia, West Virginia, Kentucky, Ohio, Indiana, Illinois, Michigan, and some areas in Pennsylvania

Table 2. Best models selected based on parameter settings in the process of model calibration, to produce final models for *Ixodes cookei*. Reg. = regularization; AUC = area under the curve; ROC = receiver operating characteristic; AICc = Akaike information criterion corrected for small sample size.

Feature class	Reg. multiplier	Variable set	Mean AUC ratio	Partial ROC	Omission rate at 5%	AICc	AICc	Parameters
L, Q, P	0.4	Set 2	1.397	0.00	0.038	955.596	0.000	8
L, Q, P	0.5	Set 2	1.385	0.00	0.038	955.945	0.349	8
L, Q, P	0.6	Set 2	1.404	0.00	0.038	956.355	0.759	8
L, Q, P	0.7	Set 2	1.390	0.00	0.038	956.821	1.224	8
L, Q, P	0.8	Set 2	1.387	0.00	0.038	957.337	1.741	8

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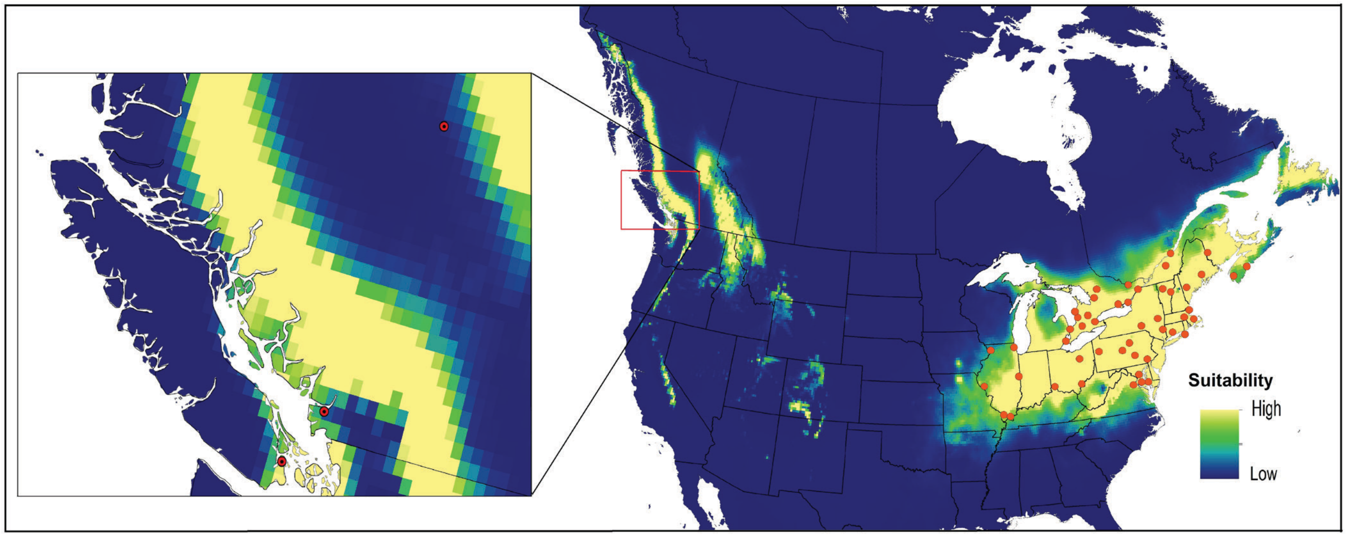

Figure 2. Initial model shows potential suitability areas without occurrence points in western Canada; yellow is high suitability and blue is low suitability. Red points indicate the occurrence points in British Columbia. The inset at left shows the western occurrence points overlaid on the prediction based on the eastern points, indicating that the eastern-points-model was able to predict the western distributional area.

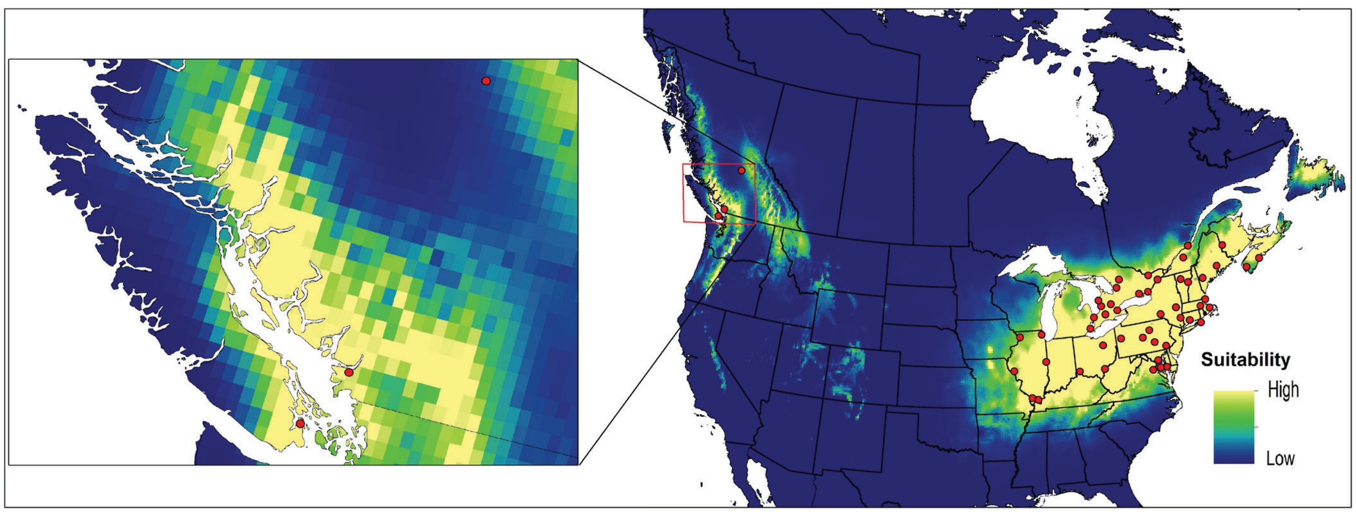

Figure 3. Potential suitability areas of *Ixodes cookei* based on all available occurrence data; shown are medians of final results; yellow is high suitability and blue is low suitability.

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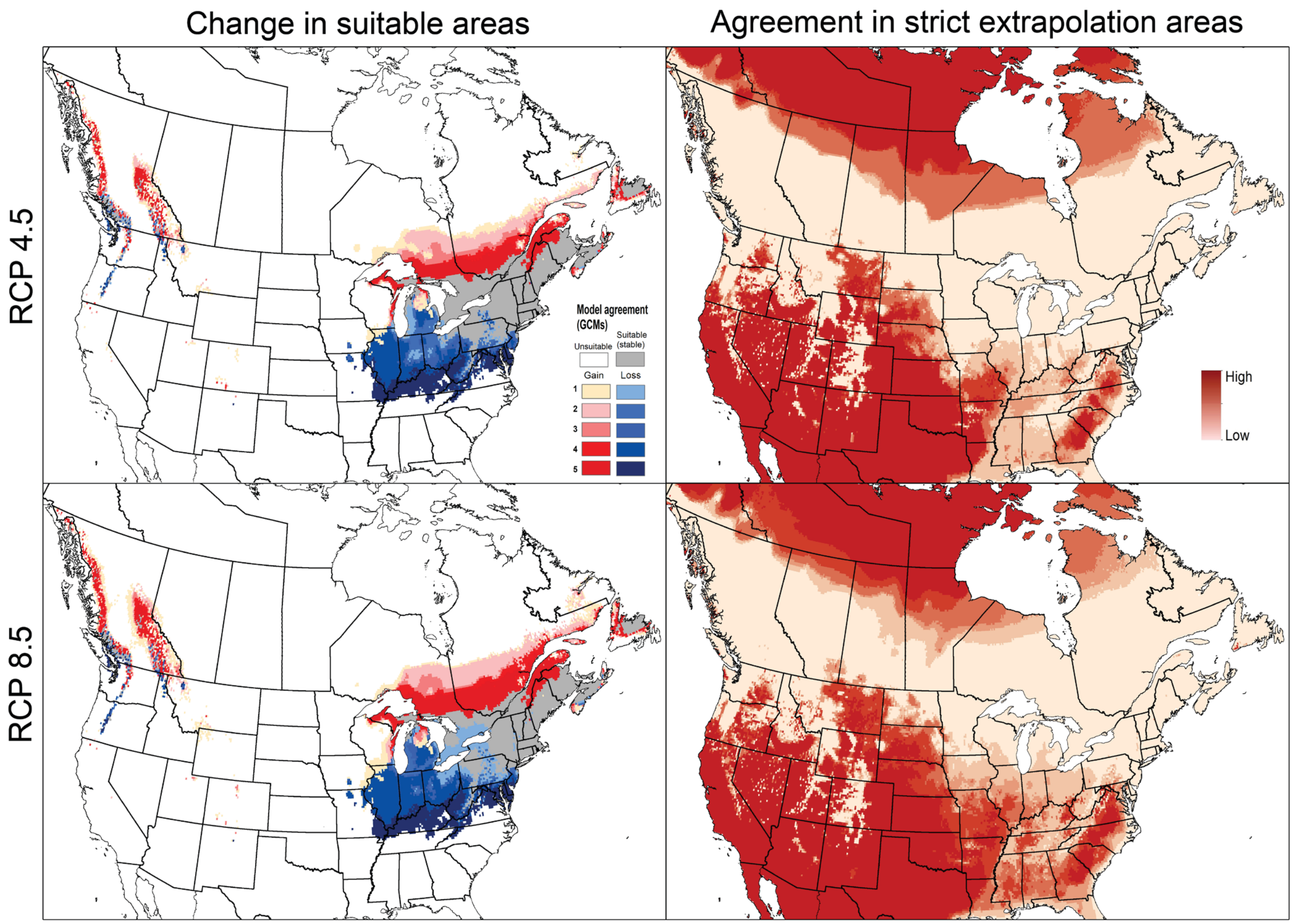

Figure 4. Left panels, potential suitable areas of *Ixodes cookei* based on binarizing (5% threshold), current conditions (in blue and gray) and future (blue = no longer suitable, red = newly suitable) conditions. Right panel, agreement in strict extrapolation areas among GCMs.

(Figure 4, RCP 4.5); RCP 8.5 included reduction in areas in southern Canada (Figure 3, RCP 8.5). Expansions (gains) in suitable areas were observed mostly in northwestern Canada (British Columbia) (Figure 4). In general, more dramatic reductions and expansions were observed under RCP 8.5 than under RCP 4.5.

MOP analysis results were slightly different between RCP 4.5 and RCP 8.5, but with high agreement in strict-extrapolation areas being concentrated in areas clearly not suitable for *I. cookei* (Figure 4). Variation among models suggested high uncertainty coming from GCMs in Missouri, Illinois, Ohio, Pennsylvania, Michigan, southern Ontario, and Quebec (Figure 5). Low uncertainty was observed from RCPs and replicates, with almost no variation from parameters (Figure 5).

DISCUSSION

Climate change has influenced distributions, activity, and biting rates of arthropod vectors in different regions around the world (Campbell-Lendrum et al. 2015). In the United States, for example, the number of tick-borne diseases has increased recently (CDC 2019b), especially with the warmest recorded winter in 2017. Some tick species have also established populations in new areas not known to be within the species' range in the past (Molaei 2020).

During recent decades, many crucial advances have been made in applications of disease ecology and biogeography to the challenge of mapping pathogen transmission risk (Peterson 2014). Crucial concepts, such as fundamental niche, realized niche, accessible areas (Peterson et al. 2011), and various analytic tools mentioned above have improved ENM workflow markedly. Here, we applied the most up-to-date methods in ecological niche modeling following Cobos et al. (2019) using kuenm R package, to estimate for the first time the potential distribution of *I. cookei*. We also included further analysis to assess model uncertainty from model projections to the future and new areas beyond the calibration area (**M**). Including analyses such as MOP (to identify strict-extrapolation areas) and model variability (to detect areas with high variability in model predictions) in model results help to identify areas with low confidence regarding the species' potential geographic distribution (Figures 4 and 5) (Owens et al. 2013, Alkishe et al. 2020).

Our models showed that suitable areas are concentrated across the eastern United States and southeastern Canada (Figures 3 and 4). Moreover, our study reflected the recent discovery of *I. cookei* in British Columbia (Scott et al. 2018),

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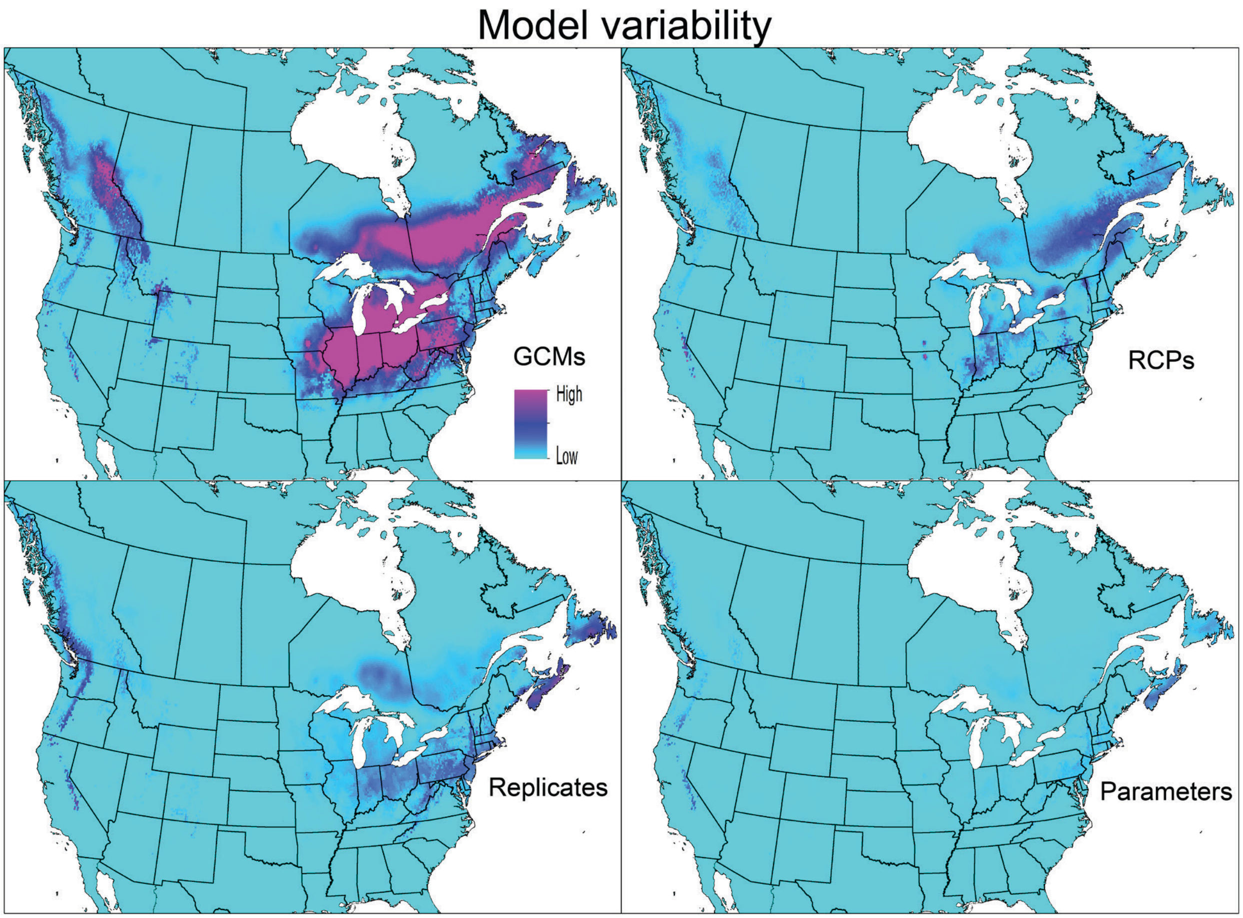

Figure 5. Median of variance coming from replicates, parameters settings, GCMs, and RCPs in future projections.

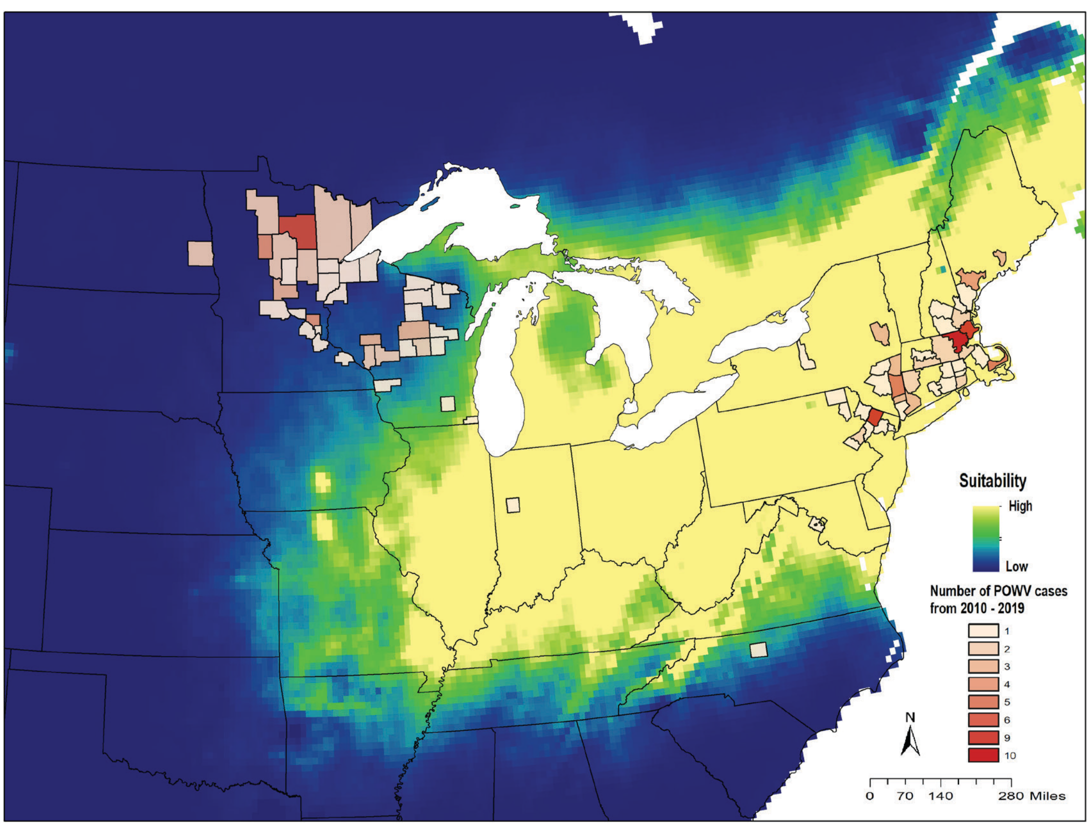

Figure 6. Potential geographic distribution of *Ixodes cookei* and Powassan encephalitis virus case incidences in the United States during 2010–2019.

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where our models identified areas as suitable for this species (Figure 3), even when the western occurrence records were omitted from the model development (Figure 2). Low stability in suitable areas and predicted potential expansions in ranges under future conditions was noted in the southern United States and northern Canada, respectively, which indicated that this species may lose large areas and shift its range northward, particularly into Canada (Figure 4). Climate change has already impacted the geographic distribution of many species (Parmesan and Yohe 2003, Peterson and Shaw 2003). Tick species are also susceptible to climate changes, as increasing temperatures can rearrange the geography of suitable areas for ticks (Gasmi et al. 2018).

Interestingly, potential suitable areas for *I. cookei* overlap broadly with the geographic distribution of documented POWV cases (CDC 2020) across the eastern United States, where most of the human cases have been documented (Figure 6). However, some areas that were not detected as suitable areas in our models, such as Minnesota and North Dakota, are known to yield POWV cases (CDC 2020). This finding may lead to the insight that this disease might be transmitted by other tick vectors such as *I. scapularis* and *I. marxi* (CDC 2019a), or alternatively, that our models are failing to anticipate that northwestern portion of the eastern range area of the species. More studies are needed to investigate the vector of POWV in those areas.

The biology of this species remains poorly studied, although one study has investigated the developmental period of each stage (larvae, nymph, and adult) under lab conditions (Farkas and Surgeoner 1991). We used climate variables (temperature and precipitation) to estimate the species' ecological niche based on their overall importance to shape the geographic range of the species. We excluded biotic factors such as host abundances from our analysis owing to the complexity of an enormous range of hosts, for which high-quality data are not available. An increasing number of POWV cases in the United States and Canada indicates a need for more active surveillance of the distribution ecology of *I. cookei*.

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