

## Expanding geographical distribution of the mosquito, *Culex pipiens*, in Canada under climate change

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### A B S T R A C T

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*Culex pipiens*

Species distribution

Range expansion

Climate change

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An important first step in assessing the possible effects of climate change on the risk of mosquito-borne disease in Canada requires an understanding of the potential shifts in the geographic range of mosquito populations under projected future climate. Risk maps of potential habitat suitability of the mosquito *Culex pipiens*, an important vector of West Nile and other arboviruses, were created using logistic regression models under conditions of current and projected climate. Current predictions for *Culex pipiens* distribution are that suitable climatic conditions for the species can be found in southern Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island and southern parts of Newfoundland and Labrador. Projected ranges of the mosquito were obtained using output from models of the Coupled Global Climate Model of the Canadian Centre for Climate Modelling and Analysis and the National Center for Atmospheric Research Community Climate System Model. Using both models, predictions of *Culex pipiens* range expansion were found for areas further north of the current estimated distribution in Ontario, Quebec, New Brunswick and Newfoundland and Labrador as well as increasing potential habitat suitability in parts of the prairies (Manitoba, Saskatchewan and Alberta) from the 2020s through to 2080s. The degree of range expansion varied according to the greenhouse gas emissions scenario ('A2' - high emissions scenario and 'B1' - low emissions scenario) used in calibrating the climate models. These findings suggest that through its effects on *Culex pipiens* survival and geographic range, climate change may broaden the range of some mosquito-borne pathogens and as a result expose new human populations to these disease-causing agents.

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### Introduction

Large scale environmental perturbations such as climate change may drive vector-borne disease emergence and re-emergence by changing their geographical distribution and dynamics (Confalonieri et al., 2007). Current projections suggest that Canada will experience greater warming than other regions of the world owing primarily to its northern latitude and large landmass (Lemmen & Warren, 2004). Given this, increased risk of vector-borne disease transmission may become problematic in Canada. Studies examining future trends of mosquito-transmitted diseases such as malaria and dengue have predicted increased transmission intensity and extended spatial distributions of these diseases with

climate change (Hales, de Wet, Maindonald, & Woodward, 2002; Martens, Jetten, Rotmans, & Niessen, 1995; Ogden et al., 2008).

Evidence has been accumulating that the range distribution of a number of species has already started to shift as a result of changing climatic conditions and suggests that this pattern is likely to continue with further climate change (Ogden et al., 2008; Ogden et al., 2010; Parmesan & Yohe, 2003; Purse et al., 2005). Although mosquito abundance is strongly subject to biotic factors such as predation, competition and vector control activities at local scales (Brownstein, Holford, & Fish, 2005), at larger geographical scales, abiotic factors such as landscape and climate play more dominant roles. Ecological niche models (ENM) and bioclimatic envelope models have been increasingly used to model the potential impacts of climate change on species distributions (Gonzalez et al., 2010; Hales et al., 2002; Kuhn, Campbell-Lendrum, & Davies, 2002; McKenney, Pedlar, Lawrence, Campbell, & Hutchinson, 2007b; Pearson & Dawson, 2003).

Recent experience with West Nile virus (WNV) has shown that Canada is not immune to the threat of invasive vector-borne

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pathogens. Furthermore, mosquito surveillance has revealed the presence of new mosquito species that have recently invaded Canada (Thielman & Hunter, 2006). The potential for species invasion combined with rapid climatic change may further exacerbate the potential for pathogen emergence and transmission. Given that arthropod species such as mosquitoes are believed to be highly sensitive to changes in climate (Gage, Burkot, Eisen, & Hayes, 2008; Martens et al., 1995), it is likely that the distribution of a number of mosquito species may have already changed or will change under climate projections (Confalonieri et al., 2007). However, available data on national distributions of mosquito species in Canada are dated, of poor resolution, and in some cases unreliable (Berrang-Ford, McLean, Gyorkos, Ford, & Ogden, 2009). This highlights a need for up-to-date information on the distribution of vector species, including mosquitoes in and proximal to Canada. Maps of potential distributions of vectors and vector-borne diseases can serve as useful tools for public health policy development and planning for vector control activities to mitigate increasing vector-borne disease risks under projected future climate (Brownstein et al., 2005; N. Ogden et al., 2008).

Since the introduction of WNV into North America in 1999 (Lanciotti et al., 1999) and Canada in 2001 (Venter, 2001), mosquito surveillance has been undertaken in a number of provinces (Giberson, Dau-Schmidt, & Dobrin, 2007; Thielman & Hunter, 2006). The mosquito fauna of Canada include over eighty species (or subspecies) ranging in abundance and composition and occupying a wide range of temporary, permanent or semi-permanent habitats (Thielman & Hunter, 2006; Wood, Dang, & Ellis, 1979). Mosquito-borne arboviruses of human importance currently known to be endemic in, or occasionally introduced into, Canada include WNV, western equine encephalitis virus, St. Louis encephalitis virus (SLEV), eastern equine encephalitis virus, Jamestown Canyon virus, California Encephalitis virus and Snowshoe hare virus, the first three of which share common mosquito vectors primarily from the *Culex* species complex (*Culex tarsalis* and *Cx. pipiens* in particular) (Hongoh et al., 2009). *Cx. pipiens* has an historical record of association with diseases of human importance in Canada including SLEV and WNV. It is found primarily in the eastern provinces of Canada including: Ontario, Quebec, New Brunswick and Nova Scotia but also in the westernmost province of British Columbia. Larvae of this species develop in a wide variety of artificial containers (e.g., bird baths, used tires, catch basins) and other temporary standing water sites (e.g., roadside ditches); all of which usually have high organic content (Wood et al., 1979) and are most frequent in urban areas. Although *Cx. pipiens* has a reported preference for feeding on birds, some researchers suggest that it is precisely this which makes them ideal bridge (bird-to-human) vectors for humans as the species will switch to feeding on humans following avian host species dispersal (Kilpatrick, Kramer, Jones, Marra, & Daszak, 2006). Updated information on the current distribution of *Cx. pipiens*, and estimates of potential changes in the geographic distribution of this species with climate change are thus relevant to assessments of climate change impacts on emergent mosquito-borne disease risks in Canada.

Here we create a predictive model to examine the potential change in distribution of *Cx. pipiens* under climate change. To do this, we estimate the potential spatial distribution of *Cx. pipiens* at the national scale using a logistic regression model with data from Canadian provinces assembled in a geographical information system. We then examine how the distribution of this species is likely to expand under future climate scenarios using output from models of the Coupled Global Climate Model of the Canadian Centre for Climate Modelling and Analysis and the National Center for Atmospheric Research Community Climate System Model. Based on our model, we predict that climate change is likely to contribute to the expansion of *Cx. pipiens* distribution in Canada.

## Material and methods

### Mosquito data

*Cx. pipiens* presence and absence data were derived from mosquito surveillance carried out by provincial agencies or contractors across the country (Table 1). These data were primarily collected in the context of WNV surveillance, biological surveys or research studies carried out between the years 2000 and 2007.

Mosquito data included the collection date, location and mosquito species (where available). Adult mosquitoes were caught using CO<sub>2</sub>-baited CDC light traps, gravid traps or New Jersey light traps. Trap locations were classified as either present or absent for *Cx. pipiens* based on recorded observations and used as the response variable in subsequently constructed logistic regression models. An absence location was one in which mosquito sampling took place but no *Cx. pipiens* was found. Data on the abundance of *Cx. pipiens* was available for most localities; however, because of inter-provincial variability in sampling methods and collection intensities, these data were not considered sufficiently comparable to include in the analysis.

### Environmental data

Climate data were obtained from Natural Resources Canada (NRCAN) in the form of spatially continuous grids generated as individual Canada-wide climate years for the period ranging from 2000 to 2007 and matched with the mosquito surveillance data. These grids were created using data recorded from climate stations across Canada and modelled using the ANUSPLIN suite of programs developed by Hutchinson in 2004 which makes use of thin-plate smoothing splines to estimate climate variables as a function of latitude, longitude and elevation (McKenney, Pedlar, Lawrence, Campbell, and Hutchinson (2007a)). Climate predictors tested for inclusion in the current study consisted of measurements of annual mean, minimum and maximum temperature, annual mean precipitation, the annual temperature range, monthly minimum and maximum temperatures, monthly mean precipitation, the maximum temperature of the warmest period, the minimum temperature of the coldest period, mean temperature of the wettest, driest, warmest as well as coldest quarter, precipitation of the wettest, driest, warmest as well as coldest quarter as well as the Julian day number of the start and end of the growing season and the number of resulting growing degree days. The growing season refers to the period of the year when temperatures exceed 5 °C for at least 5 consecutive days as of March 1st and ends when temperatures are less than −2 °C as of August 1st (NRCAN 2010). Vegetation and land cover data (advanced very high resolution radiometer (AVHRR) Land Cover Data, Canada) were obtained from the Government of Canada, Natural Resources Canada, Earth Science Sector at a 1 km × 1 km resolution and categorized into 12 land cover classes as described by Palko and colleagues (Palko, St-Laurent, Huffman, & Unrau, 1996). All environmental data layers

**Table 1**  
Sources of mosquito data and years of surveillance.

Source	Years
Alberta Environment	2003–2007
Manitoba Public Health Division	2005–2007
New Brunswick Museum	2003–2004
Nova Scotia Department of Natural Resources	2000–2004
Ontario Ministry of Health and Long Term Care	2002–2007
Prince Edward Island Dept. Of Health and Social Services	2000–2001
Ministère de la Santé et des Services Sociaux (Québec)	2003–2006
Saskatchewan Ministry of Health	2003–2007

were converted to IDRISI Imagine image format in ArcGIS (version 9.2, ESRI Inc., Redlands, CA) with a pixel resolution of 0.0833 arc degrees. A 2 km buffer was drawn around each mosquito trap location to determine the dominant landcover class surrounding the traps. The 2 km buffer was chosen as this is within the typical flight range of *Cx. pipiens* (Diuk-Wasser, Brown, Andreadis, & Fish, 2006). Climate and landcover layers were sampled using ArcGIS to obtain data values for corresponding trap locations. Environmental data and presence/absence values for *Cx. pipiens* were stored and matched in a PostgreSQL database (PostgreSQL Global Development Group version 8.2) and exported into STATA (StataCorp version 11.0) for statistical analysis.

### Model building

Models were constructed to predict the probability of occurrence of *Cx. pipiens* as a function of direct effects of temperature and precipitation on *Cx. pipiens* distribution assuming no future changes in landcover and evaluated based on receiver operating characteristic (ROC) curve and kappa values. The ROC curve provides a model independent method for graphically comparing the true positive results (sensitivity) versus the false positive results (1-specificity) between differing models (Bewick, Cheek, & Ball, 2004). The kappa statistic provides a measurement of the agreement (predictive accuracy) between observed and predicted values beyond that which might be predicted by chance alone (Fielding & Bell, 1997; Landis & Koch, 1977). Two primary models were constructed using multivariable logistic regression in STATA. Where used, late fall climate predictors were lagged by one year behind the response variable to control for possible reverse causality (Berrang-Ford, Lundine, & Breau, in press). A random 10% subset of both presence and absence locations were set aside during model construction and reserved as a test dataset. All models were subject to tests for model fit and predictive success using the reserved test dataset.

In the first approach (Model A), a backward stepwise procedure was employed to find a best-fit model. Univariable models were constructed and only those variables with likelihood ratio *p*-values less than 0.25 were retained for further analysis (Klute, Lovallo, & Tzilkowski, 2002). Pairs of variables that were strongly correlated with each other (Spearman rank correlation;  $p > 0.8$ ) were considered for elimination where the more significant variable (lowest log likelihood) was retained. A backward stepwise procedure with an alpha of 0.05 was used to retain variables for inclusion in the model. Following this, a principal components analysis was performed using STATA on the remaining variables to identify signals that were strongly correlated with the sampled distribution (Agresti & Finlay, 1997).

A second model (Model B) was constructed using multivariable logistic regression and based on findings in the literature regarding *Cx. pipiens* biology. Female adult *Cx. pipiens* emerge in the spring as a result of warming air and ground temperatures. Suitable standing water sites for larval development are usually created by precipitation and/or snow melt (Wood et al., 1979). Reproduction is maintained throughout the summer and is shut down in the fall following reduced daylight hours and cooling temperatures (Wood et al., 1979). For this reason, measurements of spring warming and precipitation as well as cooling fall temperatures were posited to be key limiters of *Cx. pipiens* occurrence. Climate measurements corresponding to both the sampled year and the year prior to sampling were tested for inclusion in the analysis as these were postulated to affect the survival and distribution of *Cx. pipiens* in the sampled year. Once variables were identified, an examination of density histograms plotted in the software package, R (R Foundation for Statistical Computing version 2.9.2 <http://www.R-project.org>),

were used to indicate possible thresholds or transformation values in the predictors which could be used to increase model predictive ability.

### Current and future range projections

Following the construction of mosquito distribution models informed by climate data matched to year of mosquito sampling (years 2000 through to 2007), maps of the “current distribution” of *Cx. pipiens* were created from the models described above using the most recently available and complete climate data (year 2007). The predicted distributions from models A and B were compared and combined by means of the map algebra function in ArcGIS Spatial Analyst to calculate the inverse logistic transformation of the resultant map layer. The inverse logistic transformation calculates the probability of occurrence given the logit (Y): Presence probability =  $\exp(Y)/(1 + \exp(Y))$ .

Mosquito distribution models A and B were combined to examine the potential range shifts of *Cx. pipiens* under future climate emissions scenarios. Model predictions have been combined in previous studies in an attempt to compensate for potential omissions or over-predictions by one model over the other (Foley, Rueda, Peterson, & Wilkerson, 2008). Two different global circulation models were used to examine future range projections: downscaled output from the third version of the Coupled Global Climate Model (CGCM3) of the Canadian Centre for Climate Modelling and Analysis as well as the National Center for Atmospheric Research Community Climate System Model version 3.0 (CCSM3.0). The projection data provided by the CGCM3 and CCSM3.0 are based on the IPCC 4th Assessment report conducted in 2007.

‘A2’ and ‘B1’ emissions scenarios were used to examine the projected range of *Cx. pipiens* under future climate forcings. The ‘A2’ emissions scenario is described by the Intergovernmental Panel on Climate Change (IPCC) as a future in which the world is heterogeneous and self-reliant, with continuously increasing global populations and economic development that is primarily regionally focused and technological development that is somewhat reduced compared with other scenarios (Intergovernmental Panel on Climate Change (IPCC), 2000). The ‘A2’ emissions scenario predicts between a 2.0–5.4 °C increase in global average temperatures by 2090–2099 with the best estimate at 3.4 °C change in the same time frame (Intergovernmental Panel on Climate Change (IPCC), 2000). In contrast to the ‘A2’ scenario, the ‘B1’ emissions scenario is described by the IPCC as a future in which the world quickly transitions to cleaner and more energy efficient technologies with supportive economic structures focused on service and information and where global population peaks mid-century and declines thereafter. (Intergovernmental Panel on Climate Change (IPCC), 2000). Temperature increases under the ‘B1’ emissions scenario are the lowest among all the emissions scenarios and range from 1.0 to 2.2 °C change at 2090–2099 with the best estimate at 1.75 °C change in the same time frame (Intergovernmental Panel on Climate Change (IPCC), 2000).

Three time periods were examined in the current analysis: the 2020s (2011–2040), the 2050s (2041–2070) and the 2080s (2071–2100). Projected climate habitat suitability maps were created under the ‘A2’ and ‘B1’ scenarios for each of the three models at all time periods. The predicted output from the models was combined to create *Cx. pipiens* distribution estimates for each of the previously mentioned time periods, scenarios and models and classified as having either a high suitability or low suitability of *Cx. pipiens* survival based on a 0.5 cutoff threshold as used in the logistic regression models. The number of pixels with suitable habitat were counted and used to compare the changes in range size of *Cx. pipiens* with climate warming over time.

## Results

*Cx. pipiens* was observed in Ontario, Quebec, Nova Scotia and New Brunswick. Recorded observations varied by province with Ontario having the highest and New Brunswick the lowest number of observations. A map of the mosquito trap locations (Fig. 1) shows that *Cx. pipiens* presence was recorded from Ontario eastward and absence locations occur from Alberta eastward. Mosquito surveillance data have been collected both in British Columbia and Newfoundland; however, these data were not available for the current study. In all, 2779 distinct observation locations were used, including 1133 presence points and 1646 absence points.

A summary of the model fit results for current range predictions using both the training and testing dataset is shown in Table 2. Models had prediction concordance values ranging from 80.9% to 82.8%, sensitivity values (proportion of true presence points correctly predicted) ranging from 80.3% to 82.4% and specificity values (proportion of true absence points correctly predicted) ranging from 81.4% to 83.1%. The models correctly predicted *Cx. pipiens* presence in 81.2%–81.8% of locations contained in the reserved test dataset. Models were assessed for goodness-of-fit using the Hosmer–Lemeshow (Hosmer & Lemeshow, 2000) test and found to have acceptable fit ( $p > 0.05$ ). All models were checked for the presence of spatial autocorrelation using a global Moran's I and a cutoff threshold of 2 km; this distance was used to account for the estimated typical flight of *Cx. pipiens* and therein potential dispersal effects from common breeding sites. There was no evidence of significant spatial autocorrelation in the models.

Twenty-four climate and two landcover variables (within 2 km of cropland and within 2 km build-up land) (Table 3) were retained in Model A. A comparison model was built without landcover

**Table 2**

Comparison of fit between models.

Model	log(L) <sup>a</sup>	AIC <sup>b</sup>	K <sup>c</sup>	CCR TR <sup>d</sup>	Sens <sup>e</sup>	Spec <sup>f</sup>	CCR test <sup>g</sup>	H–L <sup>h</sup>	p <sup>i</sup>
A	–1107.08	0.818	0.648	82.8	82.4	83.1	81.8	10.2	0.249
B	–1214.90	0.881	0.610	80.9	80.3	81.4	81.2	11.8	0.162

<sup>a</sup> log(L) – Log likelihood.

<sup>b</sup> AIC – Akaike's information criterion.

<sup>c</sup> K – Kappa score.  $K < 0.4$ : poor;  $0.4 < K < 0.75$ : good;  $K > 0.75$ : excellent (Landis & Koch, 1977).

<sup>d</sup> CCR – Correctly Classified predictions (TR: training dataset).

<sup>e</sup> Sens – Sensitivity.

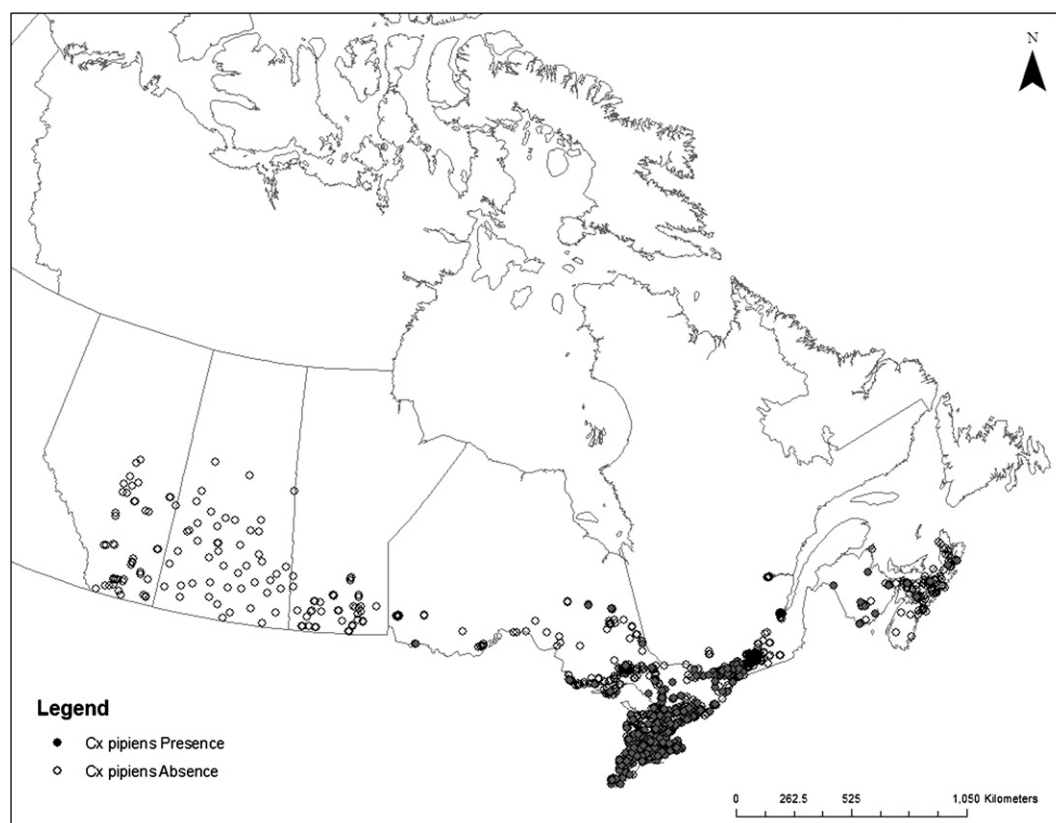
<sup>f</sup> Spec – Specificity.

<sup>g</sup> CCR – Correctly Classified predictions (Test: Test dataset).

<sup>h</sup> H–L – Hosmer–Lemeshow.

<sup>i</sup> p – Hosmer–Lemeshow p-value where  $p > 0.05$  considered significant.

variables and produced very similar prediction distributions to Model A suggesting that landcover variables included in the model contributed little to the predicted distributions. Although Model A had good overall fit, its interpretability is limited due to the high number of predictor variables used, as well as the absence of biological or causal input in model development. As stepwise methods attempt to fit the least correlated terms within a model, these methods are susceptible to the correlation inherent in the predictor dataset and are at risk of fitting the model to noise in the data (Rogers, 2006). In order to get a better sense of the signals in the data, a principal component analysis (PCA) was used as an interpretive tool. The PCA was run on the resultant terms from the stepwise selection procedure, not with the purpose of further reducing the terms in the model, but rather to see if coherent patterns might be present in the variable set. The results of the principal component analysis suggest that the first component (P1)



**Fig. 1.** Distribution of localities in Canada where *Cx. pipiens* has been collected or not observed. The localities where *Cx. pipiens* was present (filled circles) or absent (empty circles) were used in the training dataset. Although surveillance data exist and this species has been recorded in the provinces of British Columbia and Newfoundland and Labrador, these data were not available for inclusion in the analysis. © V. Hongoh. All rights reserved.



was most closely related to measures of annual mean temperature and cold period temperatures in particular, the second component (P2) was most closely related to aspects of warm period temperature and the third component (P3) appeared more closely related to measures of precipitation. Subsequent factors encompassed other measurements of spring temperature, winter temperature, fall temperature and precipitation to varying degrees of importance which were not easily distinguishable between factors. In all, the first 7 principal components captured 86.69% of the variation in the environmental data layers.

Model B was constructed based on the literature of the ecology of *Cx. pipiens* and was found to have good overall fit. Eight predictors were retained in Model B capturing two of the main climate signals thought to be important in the ecology of *Cx. pipiens* (Table 4). Measurements of warming spring temperature and precipitation were captured in the mean temperature for March and the mean precipitation for April whereas cooling fall temperatures were captured in the mean temperatures for September and November.

#### Comparison of model with current distribution

The combined mean distribution predictions from the models showed strong consensus among the models for eastern Canada, whereas distribution predictions in the west and the province of British Columbia in particular, showed lesser agreement between the models likely due to a lack of training data in this region of the model. Model A gave the most generous estimate of *Cx. pipiens* presence probability overall capturing all test data points and predicting a range distribution 151% larger than model B. In particular, Model A predicted a higher presence probability of *Cx. pipiens* in the prairies, whereas Model B predicted very little presence probability in the west. Probability predictions in the east were more similar between the two models; however, Model A predicted greater presence probability in New Brunswick, Nova Scotia and Newfoundland and Labrador. Model B gave a more conservative estimate of the current presence of *Cx. pipiens* with predicted range distributions very similar to Model A in southern

Ontario and Quebec. Model A may be over-predicting the presence of *Cx. pipiens* in Alberta and parts of British Columbia, although data were not available to verify presence in the latter region. As a result of poor reliability of model predictions in western Canada, distribution predictions under future climate scenarios were only examined for central and eastern Canada.

#### Risk maps under current and predicted climate

The habitat suitability surfaces resulting from each of the models (A and B) were produced and their combined means are shown for each of the three time periods (2020s, 2050s and 2080s), both emissions scenarios (A2 and B1) as well as both global climate models (CGCM3 and CCSM3.0) (Figs. 2 and 3). Habitat suitability range expansion predictions show strong similarity between both the Canadian (CGCM3) and U.S. global climate model (CCSM3.0). Models showed a trend of a northward expansion of the suitable habitat range of *Cx. pipiens* in Canada although expansion under the 'B1' scenario was generally more conservative than under the 'A2' scenario and observable with both global climate models. The models also suggested a possible western expansion of suitable climate conditions for *Cx. pipiens*. The amount of suitable habitat varied between the models at all time periods (2020, 2050 and 2080), as well as scenarios ('A2' and 'B1') and global climate models (CGCM3 and CCSM3.0) (Table 5). Under scenario 'A2', the increase of suitable habitat range for *Cx. pipiens* in the 2020s is initially concentrated primarily in southern Ontario, parts of southern Quebec and parts of the Maritimes provinces (New Brunswick, Nova Scotia and Prince Edward Island) as well as Newfoundland and Labrador. Suitable habitat range expansion continues northward and westward further into central Ontario, southern Quebec and a larger region of New Brunswick and Newfoundland by the 2050s. By the 2080s, increasing parts of central Ontario, most of southern Quebec and nearly 100% of the Maritimes with the exception of Labrador are predicted to be habitable to *Cx. pipiens*. The 2020s show an increase of 145% with the CGCM3 and 127% with CCSM3.0 over currently predicted distributions, whereas the 2050s and 2080s show an increase of 255% and 518% respectively over current distribution predictions using the CGCM3 and 181% and 211% using the CCSM3.0. Under scenario 'B1', in the 2020s, projected range expansion was primarily concentrated in the Maritime provinces and Newfoundland and Labrador as well as southern parts of Alberta. This trend continues for the 2050s and 2080s but at a much slower rate than that predicted by the 'A2' scenario.

#### Discussion

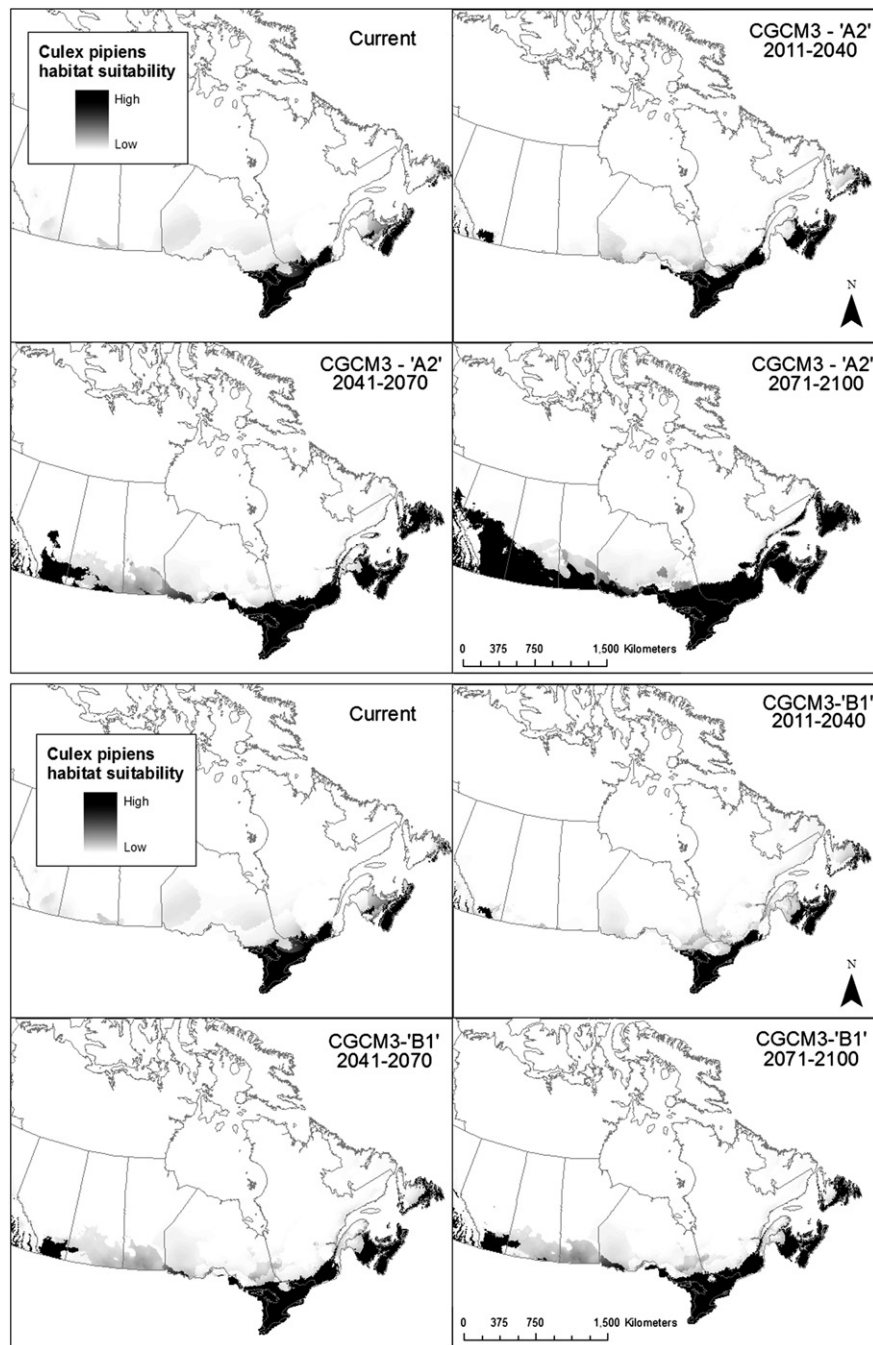
The modelled results provide the first quantitative estimate of the potential direct effects of climate change on the geographic range of *Cx. pipiens* in central and eastern Canada assuming no

**Table 3**  
Parameter estimates for multivariable logistic regression Model A.

Description	Coef.	Std. Err.	Z	p-value
Annual mean temperature	4.959	0.887	5.59	<0.001
Annual mean precipitation	−0.026	0.005	−5.29	<0.001
Max temperature of the warmest period	−1.106	0.236	−4.70	<0.001
January mean minimum temperature	−0.379	0.115	−3.31	0.001
May mean minimum temperature	−0.606	0.195	−3.11	0.002
June mean minimum temperature	0.338	0.139	2.43	0.015
September mean minimum temperature	−0.897	0.196	−4.57	<0.001
October mean minimum temperature	−0.864	0.229	−3.78	<0.001
January mean maximum temperature	−0.381	0.150	−2.55	0.011
April mean maximum temperature	−0.498	0.147	−3.40	0.001
September mean maximum temperature	0.670	0.197	3.39	0.001
November mean maximum temperature	−0.458	0.187	−2.46	0.014
December mean maximum temperature	−0.416	0.135	−3.09	0.002
January mean precipitation	0.026	0.007	3.64	<0.001
February mean precipitation	0.051	0.009	5.82	<0.001
March mean precipitation	0.028	0.010	2.85	0.004
April mean precipitation	0.056	0.007	7.79	<0.001
May mean precipitation	0.044	0.006	7.38	<0.001
June mean precipitation	0.022	0.006	3.57	<0.001
July mean precipitation	0.027	0.006	4.42	<0.001
August mean precipitation	0.036	0.007	5.32	<0.001
September mean precipitation	0.031	0.007	4.62	<0.001
October mean precipitation	0.026	0.006	4.41	<0.001
November mean precipitation	0.026	0.008	3.23	0.001
Within 2 kms of Cropland	0.053	0.160	3.30	0.001
Within 2 kms of Built-up land	0.441	0.167	2.64	0.008
Intercept	−15.085	4.320	−3.49	<0.001

**Table 4**  
Parameter estimates for multivariable logistic regression Model B.

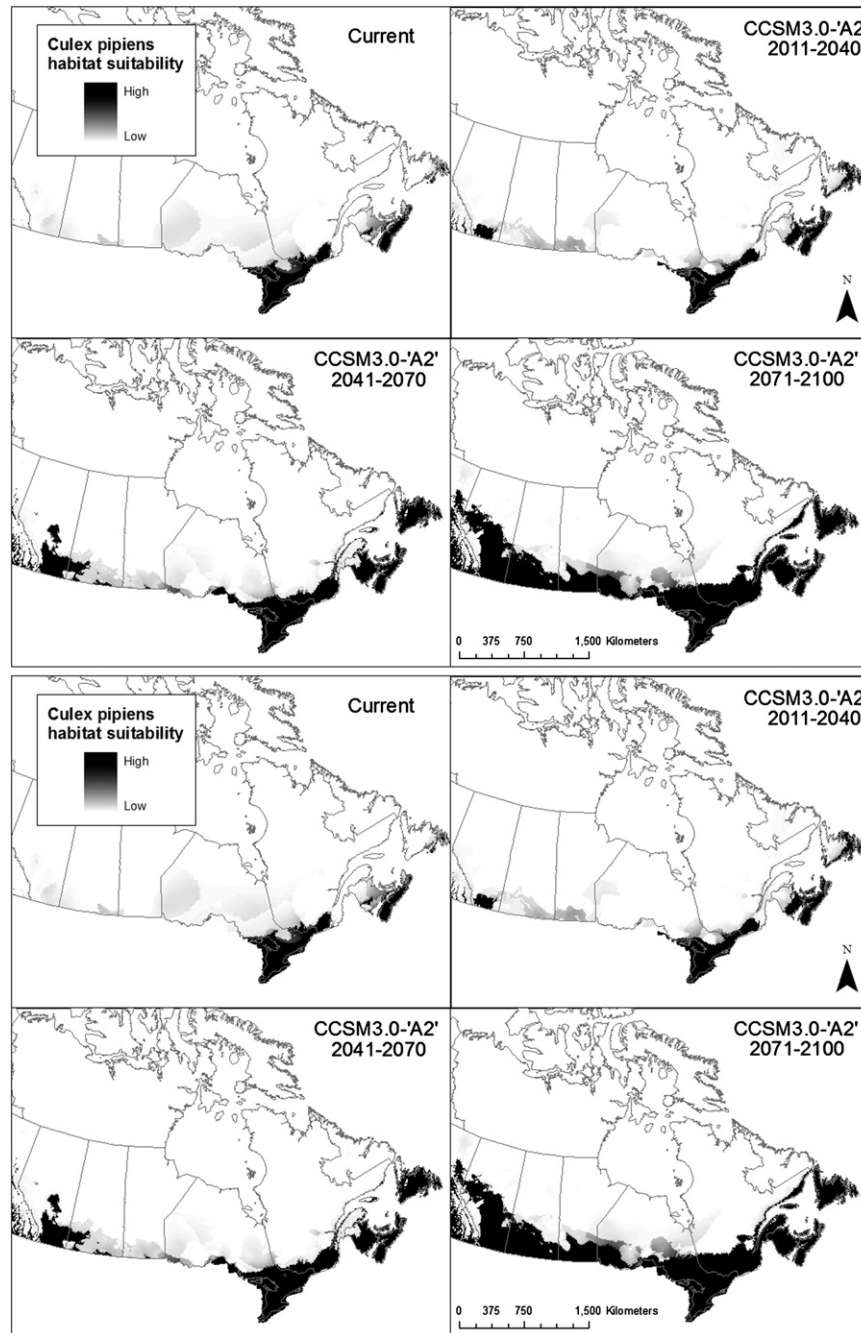
Description	Coef.	Std. Err.	Z	p-value
Annual mean temperature above 2 °C	−0.067	0.059	−1.14	0.256
Annual precipitation between 600 and 1000 mm	0.001	0.001	7.40	<0.001
Mean March minimum temperature	0.148	0.025	5.90	<0.001
April mean precipitation below 130 mm	0.025	0.002	11.49	<0.001
Mean September maximum temperature above 21 °C	0.081	0.013	6.24	<0.001
Mean November minimum temperature of previous year above −4 °C	0.241	0.064	3.79	<0.001
Mean minimum temperature for July above 13 °C	0.067	0.016	4.18	<0.001
Mean precipitation for August below 125 mm	0.010	0.002	4.21	<0.001
Intercept	−5.158	0.356	−14.49	<0.001



**Fig. 2.** *Cx. pipiens* habitat suitability under CGCM3 emissions scenario 'A2' and 'B1'. The combined model projections of *Cx. pipiens* habitat suitability under future climate forcings for the 2020s, 2050s and 2080s using CGCM3 emissions scenario 'A2' (top four maps) and 'B1' (bottom four maps). © V. Hongoh. All rights reserved.

changes in landcover. Predictions for *Cx. pipiens* distribution showed that suitable climatic conditions for the species can be currently found in southern Ontario, Quebec, New Brunswick, Nova Scotia, Prince Edward Island and southern parts of Newfoundland and Labrador. The results of this study contribute further evidence to the body of literature that predicts northward expansion of species' distributions with ongoing climate change (Brownstein, Holford, & Fish, 2003; Ogden et al., 2008; Parmesan & Yohe, 2003). The combined map of the models is in agreement with previous maps made by Darsie and Ward (2005) (Fig. 4) which indicated that *Cx. pipiens*' range included part of southern Ontario and Quebec as well as Nova Scotia, New Brunswick and British Columbia. Darsie and Ward's distribution maps (2005) are based on

Wood et al.'s (1979) records of *Cx. pipiens*' occurrence available at the time. The models constructed in the current study were generally found to have a good agreement with known occurrences of *Cx. pipiens* and suggest that climate is likely a key contributor to *Cx. pipiens* distribution. Mosquito surveillance efforts between provinces were not consistent and potential bias may have been introduced as a result. More precise estimates of the species' current occurrence in the province of British Columbia will require additional training data from this region which were not available for the present study; maps for this part of the country were not included. The combined distribution map produced in the current study also includes some probability of occurrence of the species in southern parts of the prairies as well as Newfoundland and



**Fig. 3.** *Cx. pipiens* habitat suitability under CCSM3.0 emissions scenario 'A2' and 'B1'. The combined model projections of *Cx. pipiens* habitat suitability under future climate forcings for the 2020s, 2050s and 2080s using CCSM3.0 emissions scenario 'A2' (top four maps) and 'B1' (bottom four maps). © V. Hongoh. All rights reserved.

**Table 5**

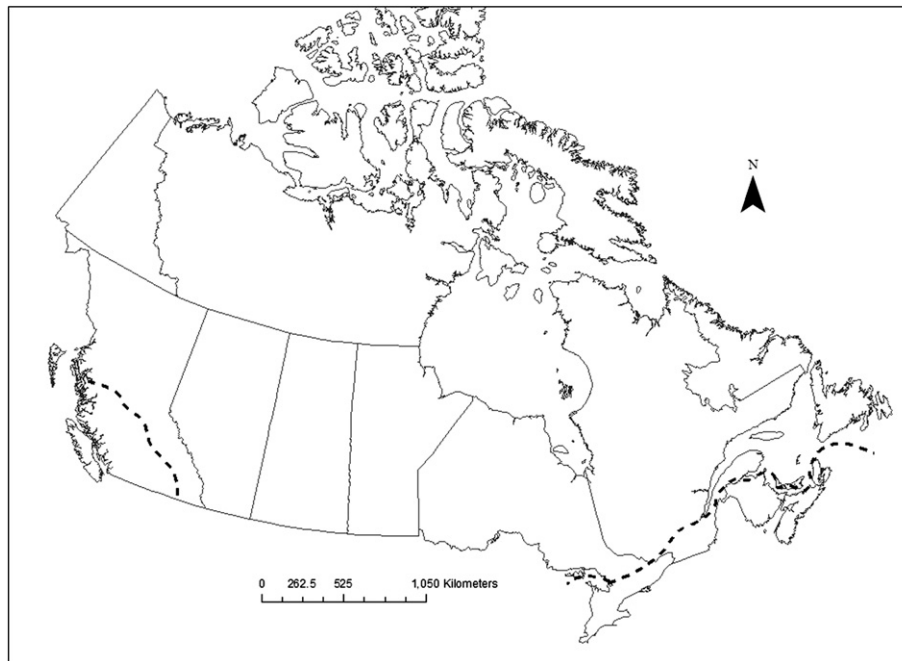
Predicted habitat suitability comparison under the 'A2' and 'B1' emissions scenarios using CGCM3 and CCSM3.0.

	CGCM3		CCSM3.0	
	A2	B1	A2	B1
2020s	145%	127%	151%	164%
2050s	255%	181%	279%	199%
2080s	518%	211%	555%	235%

Table 5 lists the differences in percent change predicted by the combined models for *Cx. pipiens* habitat suitability for the 2020s, 2050s and 2080s over and above current predicted distribution of the species under both the 'A2' and 'B1' emissions scenarios and using both the Canadian Global Climate model (CGCM3) and U.S. Global Climate model (CCSM3.0).

Labrador. The current training dataset included numerous recorded absences for the Prairie Provinces; however, since the majority of traps from the Prairie Provinces were located in urban areas, the current sampled observations give little information about the nature of the mosquito fauna outside urban areas in this region. Model predictions for Newfoundland are supported by a recent survey of mosquito fauna which reported the occurrence of *Cx. pipiens* in this province (Hustins, 2006).

The results obtained using Model A (using pattern matching) and Model B (using selected biologically plausible variables) were consistent. In particular, climate signals during the spring and fall identified in Model B appeared as the most important factors in determining *Cx. pipiens* distribution. The importance of temperature



**Fig. 4.** *Cx. pipiens* distribution as mapped by Darsie and Ward (2005). The distribution of *Cx. pipiens* in Canada based on records from Wood et al. (1979) and Darsie and Ward (2005). © V. Hongoh. All rights reserved.

and precipitation for *Cx. pipiens* distributions is likely linked directly to reproduction because *Cx. pipiens*' eggs are laid in water and require standing water of sufficiently warm temperature in order to hatch (Wood et al., 1979). The identification of spring and fall terms as important for *Cx. pipiens* distribution in Canada is consistent with the biology of the species as spring warming permits female emergence from hibernation and spring precipitation provides potential oviposition sites for the species (Wood et al., 1979). Conversely, cool fall temperatures leads to cessation of host-seeking activity in the species (Wood et al., 1979). In models which included previous year terms, measures of winter precipitation were found to be important negative predictors of the species, suggesting that the relative severity of the winter season may play a role in the survival success of the species. Although biologically plausible cues were identified as important for predicting occurrence of *Cx. pipiens* in Canada, it should be emphasized that direct causal mechanisms cannot be made in the context of the present study as it was designed to identify correlatively important signals for predicting species occurrence. Nevertheless, repeated year observations afforded by the multiple years of sampling collected strengthen the predictive ability of the models.

Using projected climate data obtained from both the CGCM3 and CCSM3.0 global climate models, range expansion of *Cx. pipiens* was predicted into Ontario, Quebec, New Brunswick and Newfoundland and Labrador as well as increasing potential climate suitability in parts of the prairie provinces (Manitoba, Saskatchewan and Alberta). Northern range expansion under projected climate is consistent with results from other studies on species range distribution changes (Brownstein et al., 2005; Gonzalez et al., 2010; Hales et al., 2002; Harrison, Berry, Butt, & New, 2006; Martens et al., 1995; McKenney et al., 2007b; Ogden et al., 2008). Although predictions for the current study under the 'B1' emissions scenario are far more conservative over time than under the 'A2' emissions scenario, this variation reflects uncertainty in future human responses to climate predictions, not methodological precision. Potential range expansion was associated with warming minimum temperatures at higher latitudes, notably warmer spring and fall temperatures captured in the model which are thought to be important limiting factors of *Cx. pipiens* in its north easternmost range. Range expansion of *Cx. pipiens*

in the current study was more conservative than predictions for the range expansion of the tick vector of Lyme disease in Canada (N. Ogden et al., 2008) a factor which may be due to the dual importance of both temperature and precipitation for the ecology of mosquito vector reproduction while predictions for tick vector spread have been thought to be primarily temperature driven. In its southernmost range, *Cx. pipiens* is thought to extend to the 36th parallel in the United States (Darsie & Ward, 2005; Hongoh et al., 2009). Southern range contraction has been found in some species and may also occur with *Cx. pipiens* although this was not explored in the present model as the data for the southernmost range of the species (*Cx. pipiens* presence in the United States) were not included in the current model.

Changes in the spatial distribution of *Cx. pipiens* in its northernmost range are likely to include range expansion as well as an extension of the growing season. It is presumed that the onset of reproductive diapause would be similar in more northern and western localities where *Cx. pipiens* populations might establish and much of the enhanced growing season would thus occur during the spring months. Mosquito-borne pathogen transmission necessitates the co-occurrence of a suitable vector, reservoir host and infective pathogen. An increase in the suitable climatic conditions and duration of the spring growing season of *Cx. pipiens*, a known vector of a number of mosquito-borne arboviruses, could have an effect on the levels of circulating arboviruses in Canada with implications for future disease outbreaks. A longer growing season may allow for a greater number of generations of *Cx. pipiens* to be produced allowing increased enzootic virus amplification. If this increase occurs in highly populated urban areas within the distribution of *Cx. pipiens* this may have a much greater potential health impact than further northward expansion of the vector into more sparsely-populated regions of the country in the north. On the other hand, the range expansion of the vector, *Cx. pipiens*, is the required first step for potential range expansion of mosquito-borne diseases. Public health impacts could be further influenced by low herd immunity and insufficient adaptive capacity to control emerging outbreaks. It is important to note that the results in the current study do not model circulating viruses; however, they highlight that early detection of "emerging mosquito-borne diseases" will require ongoing surveillance to record changes or



shifts in the distribution and abundance of vectors as well as potential pathogens. How and where changes to the distribution of important disease vectors occurs will need to be carefully monitored in order to allow the rapid deployment of targeted public health interventions, if and when they are necessary.

Species distribution modelling is based on the ecological theory that species occupy habitats in which environmental conditions are most suitable for their reproduction and survival. Ecological niche modelling builds upon this theory by intersecting the data layers representing the environmental conditions where the species of interest are most frequently found. The ecological niche modelling concept allows for a mapping of the environmental space with conditions most similar to those in which the species is known to survive. However, implicit in this modelling approach is that the species under observation is at equilibrium with its environment and not currently undergoing major range distribution changes (Guisan, Edwards, & Hastie, 2002). Statistical model fitting of the climate space of a species is an appropriate first step in the assessment of the distribution of a species (Pearson & Dawson, 2003). With regards to model predictions under future emissions scenarios, there are a number of additional factors other than climate that can affect a species' distribution and which may in turn be affected by climate change and have a combined synergistic impact on the future range distribution of a species (Araujo, Pearson, Thuiller, & Erhard, 2005). These factors include interactions with other species, such as competition with other mosquito species, predation by other species or different adaptive capacities of supporting flora, habitat changes as a result of human activities or other natural events, the potential adaptive capacity of the species itself as well as the species' dispersal ability (Araujo et al., 2005; Pearson & Dawson, 2003). At a continent-wide scale, however, climate variables may be one of the strongest observable signals for determining habitat suitability and can thus inform national and regional evaluation of potential range distribution change under projected climate change scenarios.

The current and potential future distributions of *Cx. pipiens* modelled in the present study describe the potential presence and absence of this mosquito vector at spatial locations across Canada. We caution that the results modelled here are not meant as an absolute prediction of the future, but rather indicate a consistent pattern of species range expansion resulting from ongoing climate change. Field validation is a recommended next step in order to assess the reliability of the models. However, the taxonomic challenges when looking for *Cx. pipiens* in new localities must be considered. *Culex pipiens* adult females are not readily differentiated morphologically from *Cx. restuans* adult females (Crabtree, Savage, & Miller, 1995). The latter species occurs from Atlantic Canada to Alberta and it is highly probable that anything but pristine specimens of *Cx. pipiens* (and the quality of specimens in routine surveillance is often poor) would be mistakenly identified as *Cx. restuans*. *Cx. restuans* is reported to feed preferentially on birds (Apperson et al., 2004). Misidentification of *Cx. restuans* as *Cx. pipiens* may lead to over-estimation of the human risk of potential disease; however, *Cx. restuans* may play an important role as an enzootic (bird-to-bird) vector of human disease by maintaining viruses in circulation in reservoir hosts. Thus routine surveillance needs to be supplemented with, at least periodic, molecular differentiation of *Culex* species to maximize the likelihood of early detection of founding populations of *Cx. pipiens* in much of its predicted range in Canada. Additionally, an assessment of the intra-year variability or presence of the mosquito vector would provide additional information as to the potential interactions between vector populations and potentially circulating arboviruses. One of the underlying questions requiring investigation is what effect might changes in climate, such as the timing and degree of warming during the transmission season, have on the transmission dynamics of mosquito-borne viruses. Climatic factors which promote vector

reproduction may shift the timing of vector pathogen peaks earlier in the transmission season thereby increasing the risk of spill-over into human populations. Process-based models have been used to incorporate the relationships between climate variables on biological parameters such as vector reproduction, survival, biting rates and extrinsic incubation periods and provide a useful tool for examining potential interactions under projected climate; these could be used to address the temporal aspects of infection risk of mosquito-borne arboviruses under geographically variable climatic conditions (Hales et al., 2002; N. H. Ogden et al., 2005).

## Conclusions

This study provides updated maps of the potential distribution of *Cx. pipiens* under current and predicted climate change models. The risk maps suggest a possible northward expansion of *Cx. pipiens* in Canada as well as some potential westward expansion of the species over the next several decades. *Cx. pipiens* has been implicated in the transmission of a number of mosquito-borne pathogens including WNV and SLEV and changes in the distribution of this mosquito vector are likely to in turn, influence the range and possibly the transmission dynamics of some of the pathogens borne by this species. Limiting vector-borne disease risk rests in part on the ability of public health agencies to assess human risk of exposure to vector-borne pathogens and their ability to effectively implement vector control programs and other disease prevention strategies. The risk maps presented here indicate potential range expansion of *Cx. pipiens* under projected climate change and highlight a need for continued surveillance and monitoring for potential changes in vector distribution in order to adapt to the changing disease risks which are likely to occur under projected climate change.

## Competing interests

The authors declare that they have no competing interests.

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