Predicting the speed of tick invasion: an empirical model of range expansion for the Lyme disease vector *Ixodes scapularis* in Canada

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Summary

1. Over the past two decades, *Ixodes scapularis*, the primary tick vector of the Lyme disease pathogen *Borrelia burgdorferi* in North America has expanded its range northward from the USA to colonize new regions in southern Canada. We have previously projected range increases for *I. scapularis* based on temperature suitability, but to what extent this is matched by actual tick range expansion is unknown.

2. Since 1990, *I. scapularis* ticks have been collected across Canada offering a unique opportunity to track the range expansion of an arthropod vector. We used these data to model time-to-establishment for tick populations across Canada to identify factors influencing the rate of spread.

3. Our results point to both long-distance dispersal of ticks by migratory birds and local dispersal by resident hosts as important potential mechanisms underlying patterns of tick range expansion.

4. Temperature (accumulated degree days > 0 °C) was the most important determinant of environmental suitability for tick population establishment, suggesting that climate warming may facilitate range expansion.

5. Model projections suggest that *I. scapularis* range will expand *c.* 46 km year^{-1} in the coming decade, with climate warming expected to increase the rate of spread. This expansion is likely to result in a substantial increase in human Lyme disease risk, with the proportion of the human population of eastern Canada inhabiting areas with established tick populations increasing from 18% in 2010 to over 80% by 2020.

6. This first empirical model of *I. scapularis* invasion supports theoretical range projections based on climate suitability and provides a unique data-driven estimate of the speed of northward range expansion for *I. scapularis* at the continental scale.

7. *Synthesis and applications.* By tracking *I. scapularis* invasion in Canada over the past two decades, we show that *I. scapularis* is rapidly expanding its range and is likely to colonize the most densely populated areas of southern Canada in the coming decade. These projections suggest that prompt action is necessary to prepare the Canadian public for a likely epidemic of Lyme disease, with emphasis on focusing surveillance activities to confirm the locations of emerging Lyme disease risk.

Key-words: Acari: Ixodidae, bird migration, *Borrelia burgdorferi*, climate change, dispersal, emerging infectious disease, public health, species distribution, surveillance, survival time analysis

Introduction

Since its emergence in North America the 1970s, Lyme disease has become one of the most frequent vector-borne zoonoses in the temperate world with more than 30 000 cases reported annually in the United States alone (CDC 2011). This increase has been driven by the range expansion of *Ixodes scapularis* Say, the primary tick vector of Lyme disease in North America, out of two separate foci in the Northeast and Midwest of the United States (Hoen *et al.* 2009). Climate suitability

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studies suggest that *I. scapularis* will continue to expand its range northward in the coming decades, invading the most densely populated regions of southern Canada, and that this process may be accelerated by climate warming (Ogden *et al.* 2006a, 2008b). However, although increases in tick abundance in southern Canada have already been reported (Ogden *et al.* 2006b) and further range expansion appears highly likely (Ogden *et al.* 2009), the rate at which range expansion will occur is unknown. Furthermore, the relative importance of ecological mechanisms hypothesized to be drivers of the process of tick invasion, namely tick dispersal from endemic populations (Madhav *et al.* 2004; Ogden *et al.* 2008a) and tick population establishment (Ogden *et al.* 2006a; Diuk-Wasser *et al.* 2010), has yet to be evaluated empirically.

Climate suitability is thought to be important in limiting the spread of *I. scapularis*, although the geographical footprint of climate suitability probably extends beyond the current documented range of the tick (Ogden *et al.* 2006a). Temperature affects tick development rate and questing activity and is thought to be a key factor influencing the potential northern range limit for *I. scapularis* in North America (Ogden *et al.* 2005, 2006a). Other abiotic variables such as rainfall (Estrada-Pena 2002), elevation (Rand *et al.* 2003; Diuk-Wasser *et al.* 2010), soil composition (Kitron, Bouseman & Jones 1991; Guerra *et al.* 2002) and microhabitat characteristics such as vapour pressure (Bertrand & Wilson 1996; Lindsay *et al.* 1999; Diuk-Wasser *et al.* 2010) are also likely to be important determinants of tick survival. White-tailed deer *Odocoileus virginianus* Zimmermann are key hosts for adult *I. scapularis*, with low deer density (i.e. < 7 deer km^{-2}) thought to limit tick establishment (Rand *et al.* 2003); however, deer densities are high and unlikely to be limiting in most areas of current climate suitability for the tick. Ticks are consistently associated with deciduous woodland habitat (Ginsberg & Zhioua 1996; Guerra *et al.* 2002), although in Nova Scotia, *I. scapularis* populations have become established in coniferous forest (L. R. Lindsay, unpublished data).

Although the potential range for *I. scapularis* is likely to increase substantially in the coming decades because of climate warming (Ogden *et al.* 2006a), the spread of *I. scapularis* populations across this potential range relies on the ecological process of tick dispersal, which may occur on a different timescale and proceed non-homogeneously in time and space. An added complexity for multi-host parasites such as *I. scapularis* is that dispersal may occur via different host species and at multiple spatial scales. Long-distance dispersal of ticks (averaging 425 km for nymphal ticks) is thought to occur primarily via the transport of immature ticks by passerine birds during spring migration (Ogden *et al.* 2008b). In contrast, dispersal of ticks by mammalian hosts is thought to occur over relatively short distances (< 5 km); however, deer, in particular, are capable of transporting large numbers of adult ticks, including gravid females, and may play an important role in dispersing ticks to neighbouring habitats (Madhav *et al.* 2004). The relative importance of long-distance vs. local dispersal mechanisms is likely to have a strong influence on the speed and spatial pattern of tick range expansion, and may also influence long-term population dynamics and gene flow. Phylogeographic studies of *I. scapularis* and *Borrelia burgdorferi* Johnson, the agent of Lyme disease, support south–north dispersal and north–south population mixture (Qiu *et al.* 2002; Ogden *et al.* 2011). However, no study has sought or provided empirical support for the influence of either long- or short-distance dispersal mechanisms on the pattern of *I. scapularis* invasion.

Ongoing range expansion of *I. scapularis* makes Lyme disease an emerging threat to human and animal health in Canada (Ogden *et al.* 2009). Anticipating how long it will take for ticks to become established in different regions is critical for targeting public health interventions to the right communities at the right times. We combined national passive surveillance data on tick abundance across Canada (1990–2008) and parametric survival analysis to model the process of *I. scapularis* population establishment across the northern margin of its range in North America. Survival analysis is a promising approach for modelling biological invasions (Hastings *et al.* 2005), but has only rarely been applied in this context (e.g. Jules *et al.* 2002). It is particularly well-suited for predicting the timing of invasion, allowing us to evaluate the role of environmental factors, and both local and long-distance dispersal, on the speed of tick invasion. This first empirical model of *I. scapularis* range expansion, based on a 19-year continental-scale data set, provides unique timeline projections for the ongoing northward spread of *I. scapularis* in North America, and new insight into the relative importance of vector dispersal and climate change in shaping the pattern of emerging Lyme disease risk in Canada.

Materials and methods

TICK SURVEILLANCE

Since 1990, ticks have been collected across Canada and submitted by veterinarians, medical practitioners and the general public via provincial authorities to the National Microbiology Lab in Winnipeg, Manitoba, for species identification and testing for *B. burgdorferi* (Ogden *et al.* 2006b). The number of ticks submitted annually from each Canadian census subdivision (CSD; Statistics Canada 2003) provides an index of local tick abundance. The mean area of CSDs was 285 km^2 (SD = 5750 km^2), although this value was lower and less variable (mean 85 km^2, SD = 277 km^2) across the primary zone of tick invasion (south of latitude 46°N in southern Quebec, Ontario and the Maritime Provinces). Tick submissions are accompanied by information on travel by humans and companion animals outside of the CSD, and this was used to exclude ticks that probably originated from other areas (see Ogden *et al.* 2006b). To control for detection bias because of increased search effort in areas with greater human population density (Ogden *et al.* 2006b), we modelled the relationship between total annual tick submissions and population size for each CSD using a generalized additive model with a nonparametric smooth function to capture the nonlinear form of the relationship (Koffi *et al.* in press). The residuals from this fitted relationship were then used as an index of tick submissions (Tick Index, TI) corrected for search effort.

TIME-TO-ESTABLISHMENT

The detection of *I. scapularis* ticks in a particular location does not always indicate the presence of a reproducing population of ticks. Ticks are dispersed widely by hosts including migratory birds and such ticks can survive one moult, quest and attach to a host even though there is no locally reproducing population (Ogden *et al.* 2006b). We hypothesized that the probability of a CSD containing an established population of *I. scapularis* ticks increases with increasing values of TI. To identify the threshold value of TI that signals the presence of an established population, we contrasted annual values of TI with the presence or absence of established tick populations in 71 CSDs in Quebec that were sampled using active surveillance conducted in 2007–2008 using methods (collection of ticks from the environment and on sentinel hosts) that are the 'gold standard' for detecting reproducing tick populations (Ogden *et al.* 2010). Active surveillance sites with at least two adult ticks or one immature tick in 2007, collected from the environment by dragging or on small mammals, invariably yielded multiple instars of ticks in the following year, providing minimum criteria for the presence of an established tick population (see Koffi *et al.* in press). We used sensitivity-specificity plots to select a threshold of TI above which a CSD was likely to contain an established tick population, using the sensitivity–specificity equivalence point approach (Liu *et al.* 2005) to identify an optimal cut-off biased neither towards sensitivity nor specificity. Finally, we analyzed the full passive surveillance data set to identify years from 1990 to 2008 in which the tick submissions for each CSD exceeded the establishment threshold. A CSD was considered to contain an established tick population in the second consecutive year in which TI values exceeded the establishment threshold, because elevated numbers of ticks in two consecutive years provided stronger biological evidence of a locally reproducing population.

STATISTICAL ANALYSES

We used parametric survival regression to model the effect of environmental suitability and dispersal on time-to-establishment, that is the duration (years since the start of surveillance in 1990) that CSDs across Canada remained free of established *I. scapularis* populations. We chose to use parametric survival analysis, as opposed to semiparametric approaches such as Cox proportional hazards regression, because it allows straightforward projection of survival times beyond the time window of the data (Hosmer, Lemeshow & May 2008). Specifically, we used accelerated failure time models with a Weibull distribution and frailty terms to model random effects. Models were fitted using package 'survival' 2.36-1 in R 2.12.0 (R Development Core Team 2008).

Habitat suitability

We used annual accumulated degree days $> 0\ °C$ (DD $> 0\ °C$, where $0\ °C$ is the lower temperature limit for tick development) to model the effects of temperature on environmental suitability for ticks (Ogden *et al.* 2005). Mean monthly temperatures from 1990 to 2008 were obtained from Environment Canada for the *c.* 800 climate stations in the region (the number of reporting stations varied from year to year). Each day of the year was assigned the mean temperature for its month, and temperatures $> 0\ °C$ were summed for all days of the year to obtain annual accumulated degree days $> 0\ °C$ for each climate station. Annual DD $> 0\ °C$ was calculated for each CSD by interpolating values from all reporting climate stations to a 4×4 km grid in ArcGIS 9.3 (ESRI Inc., Redlands, CA, USA) and calculating

the average value for the grid cells falling within the CSD boundary. Total annual rainfall (mm) for each CSD was calculated in a similar way to temperature, by interpolating annual rainfall measures from all climate stations. Temperature and rainfall measures from 1990 to 2008 were averaged for each CSD to obtain a representative measure for the study period. We calculated the mean elevation (m) of each CSD by averaging values from a 1×1 km topographic grid. Finally, we used the GeoBase land cover classification (GeoBase 2009) to calculate the % area of each CSD made up of either deciduous forest ($> 75\%$ broadleaf trees) or mixed coniferous-deciduous forest (forest where neither broadleaf nor coniferous trees $> 75\%$).

Dispersal

To model the effects of long-distance dispersal, we used an index of tick immigration for bird-borne nymphal ticks derived by Ogden *et al.* (2008b): the total number of US counties endemic for *I. scapularis* within 425 km (the maximum estimated transport distance of nymphal ticks by migrating songbirds) of the focal CSD. We modelled the effects of local dispersal by interpolating the corrected index of tick submissions (TI) from neighbouring CSDs to obtain a distance-weighted index of local tick immigration for each focal CSD. Values for each year (1990–2008) were summed to obtain a cumulative measure of tick immigration from surrounding CSDs over the study period.

Region

Geographical region was included as a random effect to account for possible regional variation in ecology and sampling effort. We divided the area of tick emergence into four regions along provincial boundaries from west to east: Manitoba, Ontario, Quebec and the Atlantic Provinces (New Brunswick, Prince Edward Island, Nova Scotia, and Newfoundland and Labrador). Although *I. scapularis* ticks are occasionally submitted through passive surveillance from provinces west of Manitoba, submissions from CSDs in these areas have thus far remained well below the establishment threshold and we therefore did not include data from these areas when fitting survival models.

Model selection

We ranked models containing all subsets of predictors by Akaike's Information Criterion (AIC) and selected the model with the lowest AIC value for use in inference and prediction (Burnham & Anderson 2002). All continuous predictors were standardized (mean = 0, SD = 1) to allow meaningful comparison of coefficients (Quinn & Keough 2002). We used the final survival model to predict the year of *I. scapularis* establishment for each CSD.
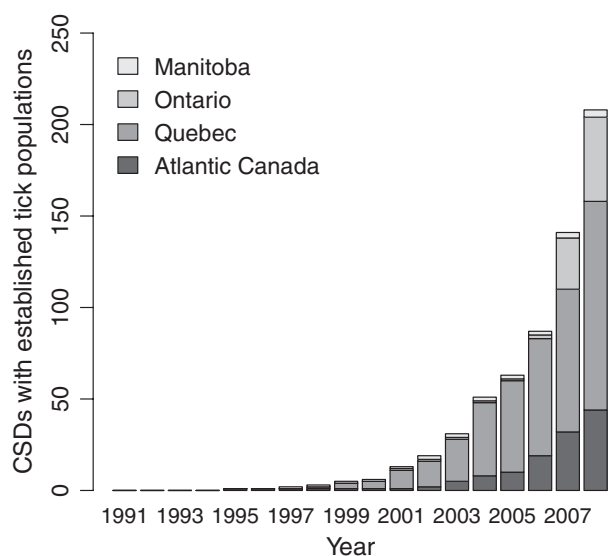
Model projections

Predicted establishment times were used to map the year of probable *I. scapularis* population establishment for CSDs across Canada and to estimate the rate of *I. scapularis* range expansion and the projected increase in the proportion of the human population (2001 census values) inhabiting areas with established tick populations. Where the square root of colonized area increases linearly over time, the slope of this relationship approximates to the velocity of the range expansion front (Hastings *et al.* 2005) and we estimated this value using linear regression. In addition, to assess the sensitivity of model projections for tick invasion rates to potential climate change, we used the fitted model to estimate survival times based on the maximum and

minimum temperatures (accumulated degree days) observed in each CSD from 1990 to 2008. The projected range expansion obtained from tick invasion rates under current climatic conditions was then compared with our previous estimates for the limit for tick establishment under current climate set by the geographical extent of threshold temperature conditions for *I. scapularis* population survival (Ogden *et al.* 2005).

Results

The number of Canadian CSDs with probable established populations of *I. scapularis* (TI exceeded the establishment threshold for two consecutive years) has increased exponentially since 1990 (Fig. 1). This increase occurred in all regions investigated; however, the majority of CSDs with newly estab-

lished tick populations are located in Quebec. Although values of TI generally increased from year to year in a given CSD, only 35% of CSDs that exceeded the establishment threshold for the first time in a given year remained above the threshold the following year. In contrast, 79% of CSDs that exceeded the establishment threshold for two consecutive years remained above the threshold the following year.

The survival model that best explained the emerging pattern of tick establishment included temperature, elevation, rainfall, and both local and long-distance dispersal (Table 1). Temperature was the strongest predictor of tick establishment, with a steep drop in predicted time-to-establishment with increasing annual DD > 0 °C (Table 2, Fig. 2a). Tick populations established more quickly in areas with greater annual rainfall and more slowly in high-elevation areas (Fig. 2b,c). CSDs with high tick submissions in neighbouring CSDs and those within 425 km of many tick-endemic US counties were colonized more rapidly (Fig. 2d,e), with local dispersal having a slightly greater influence than long-distance dispersal.

Model projections suggest that *I. scapularis* range expansion will proceed quickly in the coming decade (Fig. 3), with colonized area increasing 14-fold from 23 000 km^2 in 2010 to 317 000 km^2 in 2020. This expansion is predicted to occur mostly within the previously estimated geographical limits for the survival of *I. scapularis* populations, with suitable habitat for *I. scapularis* 'filling up' rapidly. The square root of colonized area is predicted to increase linearly over time from 2005 onward (Fig. 4a), with an estimated range front velocity of 46 km per year (slope ± SE = 45·69 ± 1·14, R^2 = 0·99, t_{24} = 39·98, P < 0·001). The speed of range expansion appears moderately sensitive to variation in temperature within the range of observed temperatures from 1990 to 2008, with a range front velocity of 35 km per year for temperature conditions equivalent to the coolest year on record for each CSD (slope ± SE = 35·40 ± 0·67, R^2 = 0·99, t_{20} = 53·18, P < 0·001) and 55 km per year for the hottest year or record (slope ± SE = 55·32 ± 1·19, R^2 = 0·99, t_{26} = 46·36, P < 0·001). Therefore, rate of expansion itself may be accelerated by a changing climate. However, although speed of colonization differed, the spatial pattern of range expansion was similar among temperature scenarios.

Fig. 1. Increase in the number of census subdivisions (CSDs) in Canada with probable established populations of *Ixodes scapularis* ticks from 1991 to 2008. A CSD that exceeded the threshold of passive surveillance tick submissions associated with the confirmed presence of an established populations in the field, and did so for two consecutive years, was considered to have a probable established population (see Materials and methods).

Table 1. Survival models of time-to-establishment for *Ixodes scapularis* ticks. Models shown are the best eight models of 63 models considered, making up the 95% confidence set of models selected by Akaike's Information Criterion (AIC) (Burnham & Anderson 2002). LogLik is the log likelihood of the model. The model Akaike weight, w_i, is the probability of being the best model in the set of all models considered. % Dev is the proportional reduction in deviance relative to the intercept-only model. AUC is the area under the curve of a receiver operating characteristic plot for the prediction of establishment status of each census subdivision (CSD) and year in the passive surveillance data set

Model terms	LogLik	AIC	ΔAIC	w_i	% Dev.	AUC
Temperature + long-distance + local + elevation + rainfall	−824·94	1665·94	0·00	0·28	0·226	0·897
Temperature + long-distance + local + elevation	−826·39	1666·81	0·88	0·18	0·226	0·898
Temperature + long-distance + local	−827·73	1667·48	1·55	0·13	0·224	0·898
Temperature + long-distance + local + rainfall	−826·89	1667·81	1·88	0·11	0·223	0·896
Temperature + long-distance + local + elevation + rainfall + forest	−824·93	1667·93	1·99	0·10	0·221	0·894
Temperature + long-distance + local + elevation + forest	−826·35	1668·76	2·82	0·07	0·221	0·894
Temperature + long-distance + local + rainfall + forest	−826·49	1669·03	3·09	0·06	0·219	0·896
Temperature + long-distance + local + forest	−827·53	1669·10	3·16	0·06	0·220	0·897

Table 2. Parameter estimates for the best survival model selected by Akaike's Information Criterion (AIC). All predictors are standardized (mean = 0, SD = 1). Log (scale) is the fitted scale parameter used in accelerated failure time models

Parameter	Estimate	SE	Z	P
Intercept	3·368	0·093	36·40	<0·001
Temperature (DD > 0 °C)	−0·206	0·029	−7·07	<0·001
Local Dispersal Index	−0·150	0·030	−4·92	<0·001
Long-Distance Dispersal Index	−0·070	0·017	−4·03	<0·001
Elevation (m)	0·059	0·032	1·83	0·068
Annual rainfall (mm)	−0·050	0·032	−1·57	0·117
Log (scale)	−2·039	0·068	−29·77	<0·001

Our model suggests a major shift in potential human exposure to *I. scapularis* ticks in the coming decade, with the proportion of the human population of eastern Canada inhabiting areas with established tick populations expected to increase from *c*. 18% in 2010 to 82% by 2020 (Fig. 4b). These estimates seem relatively sensitive to temperature variation, with an increase from <1% in 2010 to only 40% in 2020 under the minimum temperature scenario vs. an increase from 33% in 2010 to 93% in 2020 under the maximum temperature scenario. However, all scenarios suggest that the proportion of the human population inhabiting areas with established tick populations will exceed 75% by 2025.

Discussion

Our study provides new evidence that *I. scapularis* has expanded its range to include many new regions in southern Canada, and suggests that this range expansion will increase rapidly in the coming decades. This first empirical model of
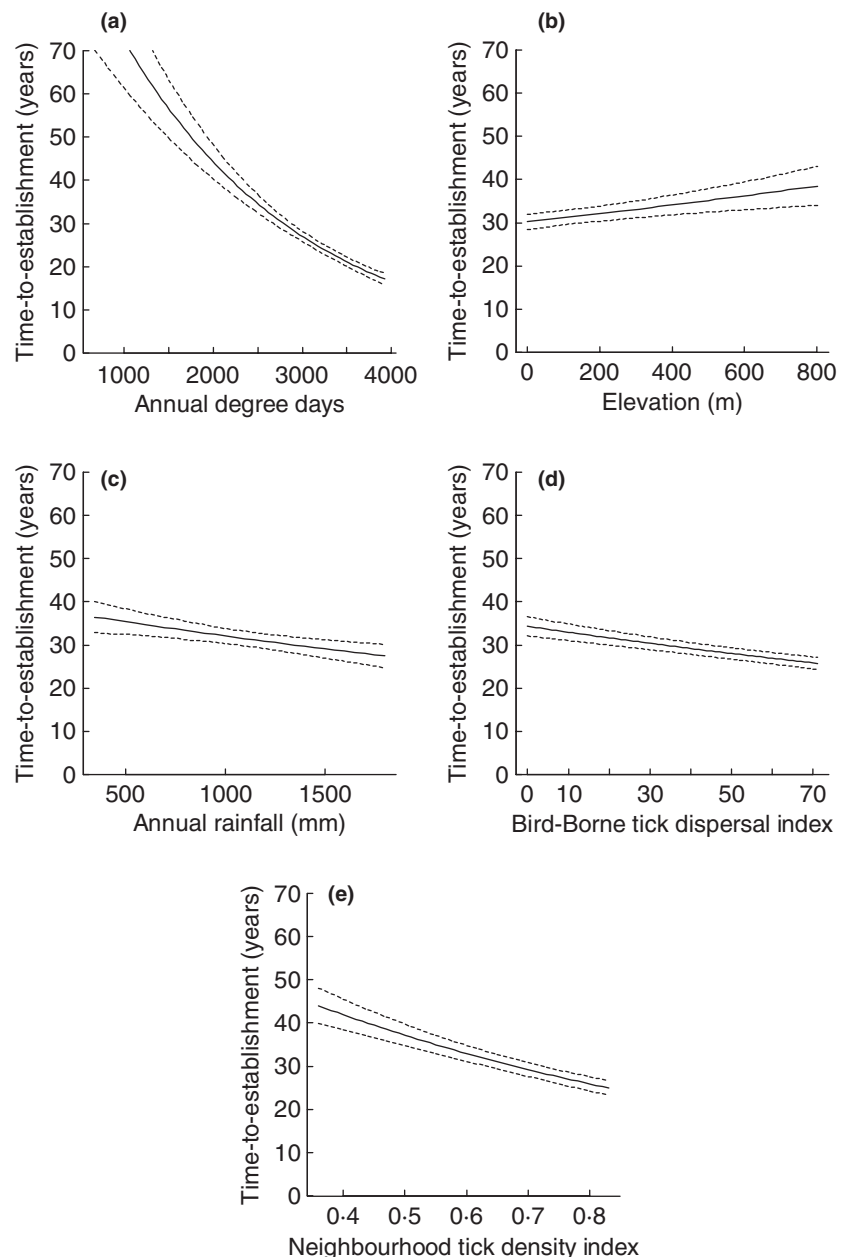
Fig. 2. Predictors of time-to-establishment for *Ixodes scapularis* populations in Canada retained in the best survival model selected by Akaike's Information Criterion (AIC): (a) Temperature (annual accumulated degree days > 0 °C), (b) elevation (m above sea level), (c) rainfall (mm year^{-1}), (d) long-distance tick dispersal by migratory birds and (e) local dispersal from neighbouring tick populations. Dashed lines are ±1 standard error.
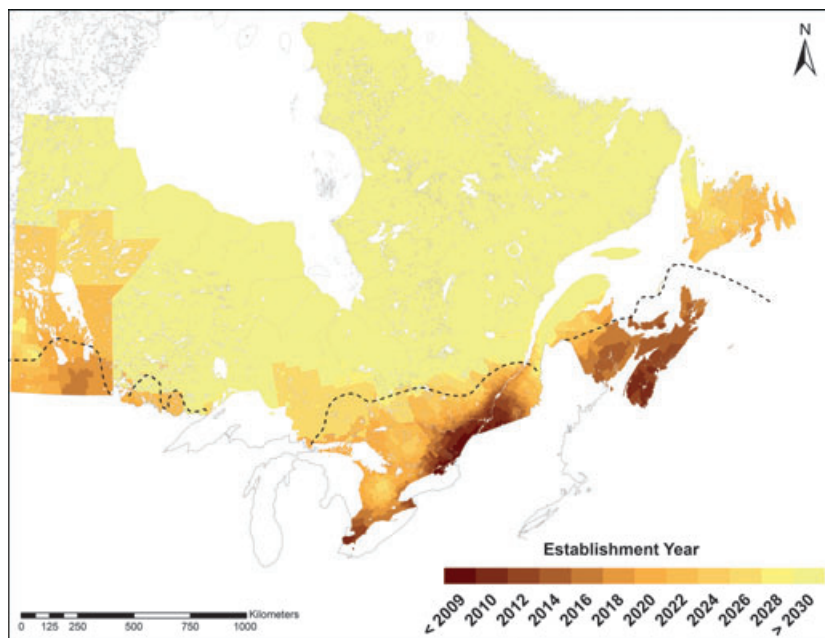
Fig. 3. Projected range expansion of *Ixodes scapularis* ticks in eastern Canada. The dashed line shows the estimated limit of current temperature suitability for *I. scapularis* ticks (Ogden *et al.* 2005).
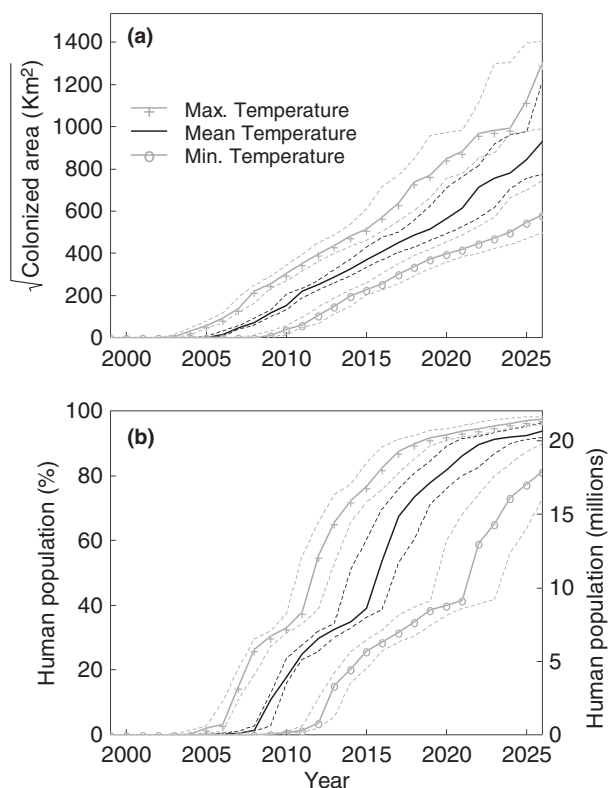
Fig. 4. Projected increase in (a) geographical area within Canada containing established populations of *Ixodes scapularis* ticks and (b) human population inhabiting areas with established tick populations. In (a), the slope of each line approximates the velocity of spread. Model projections based on the mean annual temperature (accumulated degree days > 0 °C) recorded for each census subdivision (CSD) between 1991 and 2008 are indicated in black. Grey lines are model projections based on the maximum (crosses) and minimum (circles) temperatures observed in each CSD between 1991 and 2008. Dashed lines are ± 1 standard error.

I. scapularis spread suggests that in much of eastern and central Canada, the rate of tick invasion is such that its projected range on the basis of temperature (Ogden *et al.* 2006a, 2008b) is becoming occupied in a time frame that supports our previous projections for the geographical extent of Lyme disease risk (Ogden *et al.* 2008b), and while the geographical extent of suitable tick habitat is expected to increase with climate warming, our study indicates that the rate of invasion is likely to increase with a warming climate too.

Previous models of potential range expansion for *I. scapularis* have focussed on temperature as a key determinant of habitat suitability, proposing a minimum of 2800–3100 cumulative annual DD > 0 °C as necessary conditions for tick population persistence (Ogden *et al.* 2005). Our model suggests that temperature not only affects where ticks can establish, but also the speed of range expansion, with warmer areas being colonized more rapidly, which is consistent with field studies (Ogden *et al.* 2010). Projected range expansion matches well with the locations of confirmed endemic populations of *I. scapularis*, identifying areas in south-east Manitoba, southern Ontario, south-west Quebec and Nova Scotia as foci of tick emergence in Canada. However, our model also suggests that variation in rainfall and elevation may accelerate or slow establishment within these regions. The fact that the relative abundance of deciduous forest habitat had a negligible effect on speed of establishment could appear surprising at first sight given that it is considered optimal habitat for ticks, but is consistent with previous work that also found no effect of forest abundance at the geographical scale of this study (Ogden *et al.* 2008b). Small patches of woodland that provide habitat islands for migrating songbirds (Keller & Yahner 2007) and are often characterized by high rodent abundance (Nupp & Swihart 1996), probably play an important role in facilitating tick establishment, and very small forest fragments would not

be detected at the scale of the land cover data base used in this study. Habitats such as coniferous forest or wetland edge may also play a more important role than previously thought. Data on geographical variation in host abundance and diversity were not available at the scale of this study, but would be interesting to explore at finer spatial scales because both overall host density (Madhav *et al*. 2004; Ogden *et al*. 2005) and host community composition (Keesing *et al*. 2009) could potentially alter invasion success for ticks.

Cumulative tick abundance in neighbouring areas was a consistent predictor of establishment speed in all models in the confidence set selected by AIC, suggesting that local dispersal of ticks by resident hosts may be important for tick population establishment. This observation contrasts with the conventional notion that migratory birds provide the sole source of *I. scapularis* ticks arriving in new areas (Smith *et al*. 1996; Ogden *et al*. 2008a), but agrees with recent work showing spatial clustering of emerging tick populations in southern Quebec (Ogden *et al*. 2010). Proximity to US counties with established tick populations also increased the speed of establishment, and bird-borne ticks are likely to be playing an important role in seeding new populations. However, the relatively weak effect of proximity to endemic US counties may indicate that dispersal of bird-borne ticks is sufficiently widespread and uniform that it explains relatively little fine-scale geographical variation in establishment time, as suggested by previous studies (Ogden *et al*. 2006b, 2008a). In contrast, dispersal of ticks by mammalian hosts probably has a strong influence on tick dispersal at the landscape scale, but further investigation is needed to determine the range over which such dispersal occurs, the relative importance of different host species, and factors such as landscape composition that may impede or facilitate tick movement.

Data collected through passive surveillance have the advantage of providing a unique portrait of *I. scapularis* establishment across Canada and through time. However, the degree to which voluntary tick submissions reflect true population levels is sensitive to factors that affect search effort. We accounted for the primary association between human population density and search effort, but other factors may have influenced local tick submissions. In particular, where differences in search effort exist among study regions these may influence predicted speed of establishment. For instance, evidence of widespread tick occurrence in the Atlantic Provinces may be explained by intensive passive surveillance in Nova Scotia and New Brunswick in recent years. The number of CSDs predicted to currently contain tick populations is much higher than the small number known to exist in this region as a consequence of active field surveillance. Likewise, a gradual increase in public vigilance for ticks may have increased the sensitivity of passive surveillance for detecting established populations over time; however, if this were a strong effect, we might expect active field surveillance carried out in southern Ontario, Manitoba and Nova Scotia early in the study period to have detected tick populations that were 'missed' by passive surveillance, and this was not the case. Although including region as a random effect in our model accounted

for some of these differences, more sophisticated corrections for search effort and other biases inherent in large-scale surveillance data sets might be achieved in the future by modelling the process of data generation using a state-space approach (e.g. Beyer *et al*. 2011).

By explicitly modelling time-to-establishment, we provide the first fine-scale estimate of the speed of *I. scapularis* range expansion, suggesting that the northern range front is progressing rapidly (*c*. 46 km per year) within the existing region of climate suitability for ticks. Establishment and growth of tick populations across southern Canada, where human populations are concentrated, is likely to result in a steep increase in human contact with ticks carrying Lyme disease and other tick-borne diseases. Previous work suggests that, in Canada, Lyme disease risk emerges some time after tick population establishment (Ogden *et al*. 2010), and *I. scapularis* establishment therefore does not immediately equate with Lyme disease risk. Thus, while our study suggests emergence of some tick populations in Canada prior to 2004, it is unlikely that these populations posed significant Lyme disease risk. However, as *B. burgdorferi* does eventually emerge in established tick populations, tracking *I. scapularis* establishment in Canada can provide an early signal of emerging Lyme disease risk. Consequently, predictions of where and when tick populations will establish could be usefully applied to guide future active surveillance to confirm suspected emerging locations of Lyme disease risk and provide a quantitative basis for weighing the costs and impacts of different public health strategies.

Our model provides a useful first approximation of the timeline for *I. scapularis* range expansion, identifying important mechanisms and making broad-scale projections of invasion patterns. Although we focused on northward range expansion, similar mechanisms are likely to be important for spread in the other parts of *I. scapularis'* range in North America, albeit with possibly different effects (e.g. high temperatures and desiccation may limit expansion in the south); thus, while our models are unlikely to be directly applicable for predicting southern or western range expansion, time-to-establishment models parameterized with data from these regions would provide useful estimates of region-specific expansion speeds and further insight into the generality of dispersal mechanisms identified in this study.

Acknowledgements

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