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Evaluation of the association between climate warming and the spread and proliferation of *Ixodes scapularis* in northern states in the Eastern United States

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Abstract

Ixodes scapularis (the blacklegged tick) is widely distributed in forested areas across the eastern United States. The public health impact of *I. scapularis* is greatest in the north, where nymphal stage ticks commonly bite humans and serve as primary vectors for multiple human pathogens. There were dramatic increases in the tick's distribution and abundance over the last half-century in the northern part of the eastern US, and climate warming is commonly mentioned as a primary driver for these changes. In this review, we summarize the evidence for the observed spread and proliferation of *I. scapularis* being driven by climate warming. Although laboratory and small-scale field studies have provided insights into how temperature and humidity impact survival and reproduction of *I. scapularis*, using these associations to predict broad-scale distribution and abundance patterns is more challenging. Numerous efforts have been undertaken to model the distribution and abundance of *I. scapularis* at state, regional, and global scales based on climate and landscape variables, but outcomes have been ambiguous. Across the models, the functional relationships between seasonal or annual measures of heat, cold, precipitation, or humidity and tick presence or abundance were inconsistent. The contribution of climate relative to landscape variables was poorly defined. Over the last half-century, climate warming occurred in parallel with spread and population increase of the white-tailed deer, the most important reproductive host for *I. scapularis* adults, in the northern part of the eastern US. There is strong evidence for white-tailed deer playing a key role to facilitate spread and proliferation of *I. scapularis* in the US over the last century. However, due to a lack of spatially and temporally congruent data, climate, landscape, and host variables are rarely included in the same models, thus limiting the ability to evaluate their relative contributions or interactions in defining the geographic range and abundance patterns of ticks. We conclude that the role of climate change as a key driver for geographic expansion and

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population increase of *I. scapularis* in the northern part of the eastern US over the last half-century remains uncertain.

Keywords

Ixodes scapularis; Climate warming; Geographic distribution; United States

1. Background

Ixodes scapularis (the blacklegged tick) is widely distributed in forested areas across the eastern United States (Eisen et al., 2016a; CDC, 2023). The public health impact of *I. scapularis* is greatest in the north (the Northeast, Upper Midwest, and Ohio Valley regions; see NOAA, 2023a), where nymphal stage ticks commonly bite humans and serve as primary vectors for multiple human pathogens, including Lyme disease spirochetes (Eisen and Eisen, 2018; Eisen, 2022). Notably, this part of the US also has seen the greatest increases in the geographic distribution and abundance of the tick over the last half-century (Eisen and Eisen, 2023). Climate warming is commonly attributed to having been a primary driver for the recent range expansions of *I. scapularis* in North America and the closely related *Ixodes ricinus* (the castor bean tick) in Europe (Gray et al., 2009; Medlock et al., 2013; Sonenshine, 2018; Gilbert, 2021; Ogden et al., 2021; Nuttall, 2022). However, spread and proliferation of the tick depends not only on climate conditions, but also on the presence of forested habitat and hosts for all life stages allowing the tick to complete its life cycle (Ogden et al., 2013, 2014a, 2021; Eisen et al., 2016b; Diuk-Wasser et al., 2021; Tsao et al., 2021).

In Europe, long-term data sets have linked climate warming to spread of *I. ricinus* and its associated human pathogens upward in elevation in mountainous areas in central Europe (Materna et al., 2008; Daniel et al., 2009; Danielova et al., 2010; Martello et al., 2014) as well as northward to higher latitudes in Scandinavia (Lindgren et al., 2000; Jaenson et al., 2009, 2012; Jaenson and Lindgren, 2011; Jore et al., 2014; Hvidsten et al., 2020). Expansion to higher latitudes also has been documented for *I. scapularis* in eastern Canada, with unidirectional spread of the tick from south to north over the last three decades (Ogden et al., 2006, 2008a, 2014b, 2021; Leighton et al., 2012; Clow et al., 2017; Ripoché et al., 2022). The scenarios from Scandinavia and Canada, with unidirectional northward range expansion, are consistent with climate warming-driven expansion of ticks into areas previously unsuitable for establishment due to being too cold for the ticks or a key host species. Notably, historical records of established tick populations were lacking for these regions.

By contrast, it appears that *I. scapularis* was once widely distributed across the eastern US. Rapid deforestation and near extinction of the primary reproductive host for *I. scapularis* adults, the white-tailed deer (*Odocoileus virginianus*), in the 1800s resulted in a substantial contraction in the northern portion of the tick's range. In the early 1900s, *I. scapularis* was documented from numerous locations in the southeastern US, but the tick appeared to be relegated to a few focal refugia sites in the Upper Midwest and Northeast where forest remained intact and deer populations endured. Dramatic expansion from these sites

was noted, primarily from the 1980s onward, as the tick started to reclaim its historical range. In the northern part of the eastern US, the tick's range expanded in all geographic directions radiating out from focal relic populations, several of which were located far to the north (e.g., in northern Wisconsin and coastal New York and Massachusetts), rather than via unidirectional spread from south to north (Eisen and Eisen 2023; see also Section 2). Understanding the relative importance of climate, versus landscape and hosts, as a driver for the observed changes in the distribution and abundance of *I. scapularis* in the US is complicated by simultaneous changes, presumably favorable for the tick, occurring over the last century in the form of climate warming (Contosta et al., 2019), reforestation (Li et al. 2023), and spread and population increase of white-tailed deer (Adams and Hamilton, 2011; Hanberry and Hanberry, 2020).

High-quality, fine-scale data are available for climate factors and land cover from the 1980s onward in the US (NOAA, 2023b; USGS, 2023), whereas data of similar quality and spatial resolution are lacking for key tick hosts (such as rodents, shrews, and white-tailed deer) and for the tick itself. Consequently, modeling-based efforts in the US to describe associations between environmental factors and presence or abundance of *I. scapularis*, or to predict current and future tick presence and abundance patterns, have tended to focus on climate and land cover without accounting for tick hosts. Moreover, as efforts to standardize tick surveillance were implemented only recently in the US (Eisen and Paddock, 2021), models have generally utilized *I. scapularis* surveillance data of uneven quality. In the following sections, we summarize the evidence for spread and proliferation of *I. scapularis* within the US over the last century being driven by resurgence of white-tailed deer (Section 2; see also Eisen and Eisen, 2023 for a more in-depth review) and climate warming (Section 3).

2. White-tailed deer as a driver for spread and proliferation of *I. scapularis*

We recently described the known history of the geographic distribution of *I. scapularis* in the US from the description of the species in the early 1800s to present, in relation to concurrent changes in land cover and populations of white-tailed deer (Eisen and Eisen, 2023). The white-tailed deer, which is recognized as a key species for establishment and proliferation of *I. scapularis* (Spielman, 1994; Telford, 2017), underwent dramatic population changes in the US over the last two centuries. White-tailed deer were decimated through deforestation and hunting following the European colonization of the eastern US, reaching a low point by the late 1800s to early 1900s when they had become scarce to absent across most of the Northeast, Upper Midwest, and Ohio Valley regions (Adams and Hamilton, 2011; Li et al., 2023). The tide then turned over the 1900s due to reforestation, legislation to protect white-tailed deer, and development of deer population management programs. Natural spread of white-tailed deer from local refugia where they had persisted through the nadir of the species, combined with translocation of deer by humans to new areas (McDonald and Miller, 2004), led to a resurgence resulting in white-tailed deer now being ubiquitous in forested areas of the northern part of the eastern US. With regards to the late 1900s, populations of white-tailed deer were still increasing from 1982 to 2003 in virtually all northern states (Hanberry and Hanberry, 2020). In the coldest portions of the eastern US, this resurgence also likely was facilitated in recent decades by climate warming as milder winters and

reduced snow depth favor survival of white-tailed deer (Nelson and Mech, 1986; Lavigne, 1999; DelGiudice et al., 2002).

Very few records of *I. scapularis* were published in the 1800s and the first map of its geographic distribution in the US was published in the early 1900s (Hooker et al., 1912), at a time when the white-tailed deer was at a historically low population size and confined to local refugia in the northern part of the eastern US. We therefore do not consider the primarily southern geographic distribution presented for *I. scapularis* in the eastern US up to the 1940s (Hooker et al., 1912; Bishopp and Trembley, 1945) to be representative of its historical distribution prior to and in the early stages of the European colonization, but rather a reflection of a trend of deforestation and deer depredation in the northern part of the eastern US during the 1800s and early 1900s. Without careful consideration of the history of *I. scapularis* records, it is tempting to assume a northward spread of the species from the 1950s onward into areas of the eastern US where the tick had never previously been present. However, the earliest documented populations of *I. scapularis* in the Northeast and Upper Midwest, respectively, were reported as far north as coastal Massachusetts, in the 1920s (Larrousse et al., 1928; Bequaert, 1945); and in northwestern Wisconsin, near the border with Canada, in the 1960s (Jackson and Defoliart, 1970). Notably, the population of *I. scapularis* in northwestern Wisconsin persisted in one of the coldest forested parts of the eastern US. Following the recognition of *I. scapularis* as a vector of the causative agent of Lyme disease (Burgdorfer et al., 1982), increased surveillance led to populations of this tick being described in many areas across the Northeast and Upper Midwest in the 1980s, including in additional locations close to the Canadian border in Michigan's Upper Peninsula (Strand et al., 1992) and coastal Maine (Ginsberg and Ewing, 1988).

The documented spread patterns of *I. scapularis* from the 1980s onward in the northern part of the eastern US are directionally multifaceted rather than reflecting largely unidirectional spread from south to north, as observed for *I. scapularis* in southeastern Canada. As outlined by Eisen and Eisen (2023), there are examples of spread of *I. scapularis* in the Northeast, Upper Midwest, and Ohio Valley regions from the 1980s to present in all cardinal directions, except when spread was impeded by presence of large water bodies (e.g., the Atlantic Ocean or the Great Lakes). Moreover, numerous studies across the northern part of the eastern US where hunter-killed white-tailed deer were used as sentinels to detect the presence of *I. scapularis* documented the importance of this species for the spread and proliferation of the tick (see Eisen and Eisen, 2023). We find it likely that *I. scapularis*, similar to the white-tailed deer, now is in the latter stages of reclaiming a historical distribution spanning the forested portions of the northern part of the eastern US rather than invading areas where it has never previously occurred.

3. Climate factors as drivers for spread and proliferation of *I. scapularis*

The threat to human health posed by *I. scapularis* has come into sharper focus as northern populations of this tick (accountable for the majority of human infections associated with *I. scapularis*) continue to expand geographically and new human pathogens they spread have been discovered (Eisen et al., 2017; Eisen and Eisen, 2018, 2023). The geographic distributions and spread patterns of northern versus southern populations of *I. scapularis*

were described previously by Eisen and Eisen (2023). Statistical and machine learning models have been used to estimate the full range of suitable environments for the tick in order to predict in which areas humans presently are at risk for encounters with *I. scapularis*, or where they might be placed at risk in the future. Climatic variables are often used to explain or predict the distribution and abundance of tick species. However, the accuracy of those predictions is highly dependent on the quality of input data used to train the models, the strength of the relationship between the climate predictors and the measured outcomes, and the consistency of that relationship into the future as other variables potentially impacting tick population dynamics change. In the sections below, we first outline general impacts of climate variables on the life history of *I. scapularis* ticks and then review models aimed at predicting the geographic distribution and abundance of tick populations in the eastern US based on climatic variables. We found that although temperature and humidity impact tick survival and reproduction, there was a lack of consistency in specific climate variables identified as correlated with or predictive of the geographic distribution or local abundance of *I. scapularis*. The observed lack of consistency may arise from 1) utilization of incomplete tick presence and abundance data sets, 2) varying modeling methods and spatial scales employed across studies, or 3) a limited role of climate variables in modulating tick presence or abundance relative to other variables including landscape factors (e.g., forest cover) or deer density.

3.1. Impacts of climate variables on *I. scapularis* life history traits

There is a rich literature on the impacts of climate variables on the life history of *I. scapularis*, including recent reviews (Ostfeld and Brunner, 2015; Eisen et al., 2016a; Ogden et al., 2021). Several experimental laboratory studies have demonstrated a positive relationship between relative humidity and survival of *I. scapularis* immatures and adults (Yuval and Spielman, 1990; Stafford, 1994; Rodgers et al., 2007; Ginsberg et al., 2017; Nielebeck et al., 2022). Other laboratory studies explored cold hardiness of *I. scapularis* (Vandyk et al., 1996) and relationships between temperature (i.e., for different temperatures held constant during the experimental period) and reproduction by females or development of immatures (Ogden et al., 2004; Rand et al., 2004). Female oviposition was inhibited or inefficient below 6–8 °C and egg masses failed to produce larvae below 12 °C. Molting of fed larvae and nymphs was inhibited below 12 and 16 °C, respectively. Not surprisingly, increasing temperature reduced the number of days required for fed females to oviposit (within a range of 8–28 °C), their eggs to hatch (within a range of 12–28 °C), or for fed larvae or nymphs to molt (within a range from 12 or 16 to 28 °C). A temperature of 32 °C resulted in failure of egg masses to produce larvae and prevented fed larvae and nymphs from molting. Together, these laboratory results indicate that *I. scapularis* requires temperatures above 16 °C, for at least some part of the year, and high humidity to complete the life cycle, and that excessively high temperatures (above 30 °C) or low humidity could be detrimental. However, it should be noted that all laboratory studies to date were based on relative humidity or temperature held constant rather than reflecting natural variation during the 24 h diel cycle.

Experimental field studies in Connecticut indicated that the daily survival rate of unfed *I. scapularis* ticks in the warm part of the year is negatively related to temperature and

vapor pressure deficit (Bertrand and Wilson, 1996, 1997). That is, mortality of unfed ticks was greater when the warm part of the year was warmer and drier. With regards to overwintering success in the field, experimentally placed unfed nymphs (the life stage expected to overwinter as unfed ticks) typically had high levels of overwinter survival (> 70 %) in studies conducted in Connecticut, New York, and Maine in the northeastern US, although a lower level of survival (20–30 %) was recorded in some years for sites in Maine (Linske et al., 2019; Brunner et al., 2012, 2023; Volk et al., 2022). Two of these studies (Linske et al., 2019; Volk et al., 2022) also explored the impact of experimental removal of leaf litter and/or snow on the over-winter survival of unfed nymphs. Not surprisingly, removal of insulating leaf litter and/or snow above the tick-holding containers resulted in decreased temperatures within the containers, especially for snow removal, and tended to reduce overwinter survival compared to the controls where leaf litter and snow were not manipulated. In other words, unfed nymphs can survive low ambient temperatures during the coldest part of the year if they are protected from lethal cold temperature through insulation afforded by snow and leaf litter cover. In Germany, Dautel et al. (2016) reported that an extreme winter cold spell in the absence of snow cover appeared to result in reduced abundance of *I. ricinus* nymphs in the following warm season. The finer details of specific events causing mortality of overwintering ticks, such as cold snaps in the absence of snow cover or repeated freezing and thawing, remain poorly understood. We conclude that existing data are inadequate to fully understand the impact of climate variables on *I. scapularis* population dynamics, considering the tick's multi-year life cycle, the phenology of unfed versus fed larvae, nymphs, and adults, and the impacts of natural seasonal and diel variation in temperature and humidity on survival of questing ticks and developmental and reproductive processes.

Multiple longitudinal observational studies have attempted to link field-estimated densities of host-seeking *I. scapularis* to climate data in the US. This type of study should be interpreted bearing in mind that (1) there is considerable uncertainty in estimates for density of host-seeking ticks based on drag or flag sampling, (2) questing ticks also are removed by hosts as their active season progresses, and (3) there are complex interactions between climate and host abundance impacting different life stages in the multi-year tick life cycle. Nevertheless, some long-term studies merit mention here. A 14-year study covering 37 forested locations across Rhode Island indicated a negative relationship between the annual density of host-seeking *I. scapularis* nymphs and the number of occasions during the early part of the nymphal season (June) when the relative humidity in leaf litter fell below 82 % for more than 8 h (Berger et al., 2014). That is, as the number of dry days in early summer increased, density of host-seeking nymphs decreased. A similar finding of a negative impact of dry summer weather on the annual density of host-seeking *I. scapularis* nymphs was reported in an 18-year study from New York (Burtis et al., 2016). Another long-term (25-year) study on host-seeking *I. scapularis* nymphs in Connecticut found their annual density to be positively associated with a standardized precipitation index for January of the same year, indicating that nymphal tick density in the spring increased with precipitation in the preceding winter (Hayes et al., 2015).

Notably, climate warming may change the phenology of the different life stages of *I. scapularis*, potentially leading to longer periods of questing activity of immatures from

spring to fall, increased winter activity of adults, and changes to the levels of overlap in the peak host-seeking periods for different life stages (Ogden et al., 2008b, 2018; Levi et al., 2015). A previous evaluation of meteorological influences on the seasonality of Lyme disease in high incidence states in the eastern US found that the start and peak of the Lyme disease season were associated with growing degree days in the early part of the calendar year, saturation deficit and precipitation, but none of the included weather variables adequately explained the timing of the end of the transmission season (Moore et al., 2014). However, when considering the impact of a warming climate on the phenology of *I. scapularis*, the primary driver for the tick to enter and exit winter diapause also should be taken into account. There is evidence for photoperiodic control of winter diapause in *I. scapularis* (reviewed by Gray et al., 2016) and the potential for temperature to override the photoperiodic control is unclear.

3.2. Modeling to estimate the geographic distribution of *I. scapularis* across the eastern US based on county level tick collection records up to 1996

Key characteristics and outcomes of the models described below are summarized in Table 1. The earliest environmental suitability models for *I. scapularis* in the US (Estrada-Peña, 20002; Brownstein et al., 2003) were developed based on tick collection records at the county level presented by Dennis et al. (1998). In their classification of county status for *I. scapularis*, Dennis et al. (1998) included records accumulated up to 1996 and categorized a county as follows: “established” if six or more *I. scapularis* or two or more life stages of the tick had been collected by 1996; “reported” if fewer than six ticks of a single life stage had been collected by 1996; or “no records,” which may have resulted from lack of surveillance effort or true absence of the tick. The surveillance efforts underlying the county classifications for *I. scapularis* were not standardized, most likely resulting in a greater concentration of established counties where *I. scapularis* collection efforts were more intensive – typically in areas where Lyme disease cases were reported in the northeastern or upper midwestern US in the 1980s and early 1990s.

Despite utilizing the same tick surveillance data set, Estrada-Peña (2002) included both established and reported counties as presence points, whereas Brownstein et al. (2003) disregarded counties classified as reported, and considered established counties as present and attributed “no records” to absence. As a result, the assumed range of the tick used to build the model was broader for Estrada-Peña (2002) compared with Brownstein et al. (2003). The studies employed vastly different modeling approaches, used different climate data sources (e.g., 30-year monthly averages derived from daily measurements in a global data set (Brownstein et al., 2003) versus use of advanced very high-resolution radiometer sensor satellite imagery to derive surface temperatures at specific 10-day intervals (Estrada-Peña, 2002), and focused on different spatial scales (conterminous US (Brownstein et al., 2003) versus eastern US (Estrada-Peña, 2002)).

The model by Estrada-Peña (2002) included climate variables as well as a land cover variable but did not account for tick hosts. Two variables were identified as key predictors for presence of *I. scapularis*: a measure of winter temperature and the normalized difference vegetation index (NDVI), which is a measure of vegetation vitality and a proxy of rainfall

and humidity, but also an indirect predictor of forest or other vegetative cover. The study tracked retrospective geographic changes in these variables over discrete time periods to show that the amount of suitable environment for the tick, as defined in the study, increased from 1982 to 2002. By 2002, the model predicted suitable conditions for the tick to survive and reproduce over much of the eastern US. However, notable pockets of low suitability were identified in parts of the Ohio Valley, Upper Midwest, and Eastern Plains where *I. scapularis* is currently established (Eisen et al., 2016a, CDC, 2023). Projections to present day were not made and to the best of our knowledge, the Estrada-Peña (2002) model has not been recreated with data from more recent eras to assess comparability with current *I. scapularis* distribution data.

The Brownstein et al. (2003) model used a logistic modeling framework with nonlinear relationships between 30-year averages of eight climate predictors (mainly temperature measures) and tick presence (i.e., counties considered to have an established population of *I. scapularis* by 1996). The model did not include variables related to forest coverage or other measures of vegetation, or tick hosts. Variables identified as key predictors for presence of *I. scapularis*, after accounting for spatial autocorrelation in the data, included minimum monthly temperatures. The final model included seven temperature variables and a single vapor pressure variable. The functional relationship between these variables and tick occurrence was complex and their biological plausibility was not explained. Nonetheless, the model predicted the highest suitability for *I. scapularis* in the southeastern US, along the Atlantic coast in the Mid-Atlantic states, throughout the Northeast, and sporadic pockets of suitability in the Upper Midwest – primarily in Wisconsin and eastern Minnesota. Much of the Ohio Valley region (Indiana, Illinois, Kentucky, Ohio, Tennessee, and West Virginia) and lower Michigan in the Upper Midwest were classified as unsuitable for *I. scapularis*. The majority of counties in these areas now have established populations of *I. scapularis* (Eisen et al., 2016a, CDC, 2023). Despite using vastly different modeling approaches and dissimilar climate predictors, both models (Estrada-Peña, 2002; Brownstein et al., 2003) identified minimum monthly temperatures (or winter temperature), as a significant predictor and they both accurately predicted presence of the tick in counties where it was known to be established based on the build set used (high sensitivity). However, the models yielded divergent predictions of suitability in parts of the Ohio Valley region and Upper Midwest where the tick had not yet been classified as established in 1996.

3.3. Modeling to estimate the geographic distribution of *I. scapularis* across the eastern US based on county level tick collection records up to present

Key characteristics and outcomes of the models described below are summarized in Table 1. The county status classifications for *I. scapularis* based on data up to 1996 presented by Dennis et al. (1998) were later updated, following a similar classification method, based on additional tick collection records from 1997 to 2015 (Eisen et al., 2016a). The update revealed that by 2015, the number of counties in which *I. scapularis* was classified as established had more than doubled since 1996. Expansion of counties with *I. scapularis* established, from 1996 to 2015, was recorded in nearly all geographic directions in the Northeast, Upper Midwest, and Ohio Valley regions, with large bodies of water serving as the main barriers to expansion. Similar to the time period up to 1996, surveillance efforts

from 1997 to 2015 were not uniform across counties, and lack of county records should not be attributed to true absence of the tick.

Hahn et al. (2016, 2017), developed an updated environmental suitability model for the eastern US using counties considered established by Eisen et al. (2016a) to indicate counties (labeled “present” in Hahn et al., 2016, 2017) where *I. scapularis* likely can survive and reproduce. Counties classified by Eisen et al. (2016a) as having *I. scapularis* reported were not included in the “present” category because the single or few ticks recorded may in some cases have represented specimens imported from other counties via humans or domestic animals, or alternatively include records of ticks going back more than a half-century. The study evaluated multiple strategies to select candidate abiotic and biotic predictive variables and used an ensemble of modeling approaches (boosted regression tree, generalized linear model, multivariate adaptive regression spline, and maximum entropy) to minimize biases introduced by variable selection strategy or by a single modeling framework. The models included elevation and both climate and land cover variables as predictive factors but did not account for tick hosts. Each of the model types retained different predictor variables, which limits our ability to decipher which are the most biologically meaningful predictors of environmental suitability. Elevation was retained as a predictor in each model type and forest cover was retained in three of the four model types. In general, suitability was greater at lower elevations, decreased as elevation increased up to 500 m, then remained low as elevation increased. Suitability increased with increasing forest cover up to approximately 50 % of county coverage. Precipitation in the warmest quarter and maximum temperature of the warmest month also contributed considerably to three of the four model types. Although the functional relationships differed slightly among models, environmental suitability generally increased with increasing warm season precipitation and the association with maximum temperature of the warmest month was non-linear; heat generally had a negative impact on suitability between 26–30 °C. Notably, while minimum monthly or winter temperatures were leading indicators in earlier models (Estrada-Peña, 2002; Brownstein et al., 2003), cold season variables played a minimal role in the models developed using more contemporary presence data (Hahn et al. 2016); the mean temperature of the coldest month contributed only moderately to a single model in the ensemble and suitability was highest at the lowest temperatures, with a slight increase in suitability in counties where the mean temperature of the coldest quarter was greater than 10 °C.

Burtis et al. (2022) used a similar ensemble modeling approach to Hahn et al. (2016), both focusing on the eastern US, but Burtis et al. (2022) included in the model build set an additional 159 counties with established *I. scapularis* populations based on data from 2016 to 2021. Percent forest cover, maximum temperature of the warmest month, and elevation were leading predictors. Across the models (Hahn et al., 2016; Burtis et al., 2022), environmental suitability for *I. scapularis* generally increased with increasing forest cover and was highest in counties with lower temperatures in the warmest month of the year.

Two additional recent models for presence of *I. scapularis*, including but not exclusive to the eastern US, were presented by Alkische et al. (2021) and Zhang et al. (2022). These models were not restricted to county-scale data for *I. scapularis* but rather included finer scale data from various online sources and published literature. Alkische et al. (2021) unfortunately did

not clarify the spatial precision of the *I. scapularis* data used or specify which predictor variables contributed most strongly to their presented environmental suitability model. Nonetheless, the model predicted widespread stable suitable conditions for *I. scapularis* to persist in the future under various climate change scenarios. Notably, loss of suitable conditions was predicted along the Appalachian Mountains in Virginia and North Carolina, where populations of northern *I. scapularis* have expanded rapidly and Lyme disease cases have increased substantially in recent years (see review by Eisen and Eisen, 2023). Zhang et al. (2022) used point location data for *I. scapularis* from the Global Biodiversity Information Facility (<https://www.gbif.org/>), implemented with a 2.5 km buffer to eliminate closely located collection points, but included as predictor variables elevation and climate data at a more crude 20 km² (2.5 min) spatial resolution. The quality of the *I. scapularis* data points are uncertain as they appear to commonly include records with species identification made by the public. With that in mind, the leading predictors for presence of *I. scapularis* in the maximum entropy model included precipitation in May, precipitation in September, precipitation of the driest month; temperature seasonality and mean diurnal temperature range were also influential. The relative importance of precipitation in these two models might be explained by their global spatial scale; the emphasis on precipitation may be highlighting that the tick is not well adapted to very arid conditions, but it provides very little insight into variation in suitability within and surrounding the current known range of the tick. No appreciable changes in the distribution of suitable conditions for the tick were predicted by Zhang et al. (2022) into the future (2080–2100) across the eastern US when the models were extrapolated under different climate change scenarios; all of the eastern US was expected to remain climatically suitable.

Across all models mentioned above, the predicted range of suitable environment for *I. scapularis* in the US was more expansive than the recorded range of the tick. This could imply that surveillance to date has been inadequate to detect the full range of the species, or that the environmental variables used to develop the models are not limiting the distribution of the tick in most of the eastern US. Alternatively, the occupied range of suitable environment might be limited by dispersal of the tick.

3.4. Modeling to estimate presence or abundance of *I. scapularis* at regional or state scales in the eastern US based on field tick collections

Key characteristics and outcomes of the models described below are summarized in Table 1. Models to estimate presence or abundance of *I. scapularis* at state or regional scales based on data from field tick collections typically have included elevation and both climate and land cover variables as predictive factors (Diuk-Wasser et al., 2010; Johnson et al., 2016, 2018; Kopsco et al., 2023). However, such models only rarely also have accounted for host animals (Tran et al., 2021), as presence and abundance data for key hosts for *I. scapularis* immatures or adults generally are lacking across broad geographic coverages. The studies mentioned above focused on areas located in the northern part of the eastern US, where the vast majority of human infections associated with *I. scapularis* occur, and most often they have been restricted to the nymphal life stage, which is considered to account for the majority of human infections (Eisen et al., 2017; Mead, 2022). Nymphs of northern populations of *I. scapularis* commonly quest from leaf litter and vegetation, which facilitates contact with

humans, whereas nymphs of southern origin quest more cryptically and only rarely contact humans (Arsnoe et al., 2015, 2019; Tietjen et al., 2020; Eisen and Eisen, 2023).

In an early effort to determine in what parts of Maine, located in the far northeastern US, the climate would allow *I. scapularis* to establish populations, Rand et al. (2004) conducted a field experiment where fed females were placed in tick enclosures in the fall and spring in sites spread across the state and their survival, oviposition, and egg hatching success was documented. The study also documented temperature conditions in the tick enclosures and calculated degree days (above 6 and 11 °C) accumulated by the ticks in situ from placement of fed female to larval emergence. The results were then used to define a degree day threshold considered to allow *I. scapularis* to establish a population if it was reached, and a map was generated displaying areas in Maine falling below versus above this threshold. Additionally, Rand et al. (2004) explored changes in degree days from 1971–1980 to 1991–2000 in Maine; they concluded that based on the small difference in seasonal accumulation of degree days seen in Maine from 1971–1980 to 1991–2000, it was difficult to ascribe more than a supporting role for temperature in the increase seen during that time period in the state for the geographic range and abundance of *I. scapularis*, and the incidence of Lyme disease, especially considering a concurrent increase in populations of white-tailed deer (see Lavigne, 1999; Rand et al., 2003).

Diuk-Wasser et al. (2006) later conducted extensive and unbiased drag sampling in forested areas across the eastern US from 2004–2006 to document presence and density of *I. scapularis* nymphs. Based on the resulting data, elevation, monthly mean vapor pressure deficit, and seasonal variation in temperature were identified as the leading variables predictive of finding host-seeking nymphs (Diuk-Wasser et al., 2010). However, spatial autocorrelation (i.e., the known presence and abundance of host-seeking nymphs in neighboring sites), was the primary predictor of nymphal densities. That is, the likelihood of observing high nymphal density in a focal location was greater if neighboring sampling sites had nymphs present and the density of host-seeking nymphs was elevated. The highest density populations of *I. scapularis* nymphs were observed, and predicted, in the Northeast and Upper Midwest, particularly along the Atlantic Coast from New York to Massachusetts and in Wisconsin, which represent locations with early records of established populations of *I. scapularis* in these regions (Eisen and Eisen, 2023). This pattern may reflect nymphal densities being highest in areas where the tick has been established longer and a radiating decrease in density away from those locations. While climatic variables (vapor pressure deficit and seasonal variation in temperature) were found to be predictive of the presence of *I. scapularis* nymphs, density of host-seeking nymphs was best predicted based on densities at nearby locations, rather than by climate variables.

Subsequent *I. scapularis* presence and nymphal density estimation efforts in the Upper Midwest focused on Minnesota (Johnson et al., 2016, 2018). First, occurrence data for *I. scapularis* from 2005 to 2014, representing locations across the state fulfilling the Dennis et al. (1998) criteria for establishment, were used to explore associations with climate and landscape variables (Johnson et al. 2016). The resulting model identified 19 % of Minnesota as potentially suitable for establishment of the tick and indicated that the distribution of these areas was driven by land cover type, summer precipitation,

maximum summer temperatures, and annual temperature variation. Specifically, suitability increased with increased forest coverage and increasing summer precipitation (up to ~28 mm). Suitability declined in areas where maximum temperature of the warmest month exceeded 28 °C and where the annual temperature range exceeded 41 °C. As a follow-up to assess factors that influence density of *I. scapularis* in Minnesota, a statewide survey of the density of host-seeking nymphs was conducted in 81 sites in 2015 (Johnson et al., 2018). Sampling sites were selected using a conditional Latin hypercube sampling method that was used to maximally stratify the distribution of each variable into as many strata as sites sampled. The probability of finding a host-seeking nymph increased as the proportion of agricultural land cover within a 5.25 km² buffer around the sampling site decreased. The observed density of host-seeking nymphs was negatively associated with the amount of agricultural land, mean diurnal temperature range, and elevation, but annual temperature range and the amount of summer precipitation were positively associated with increased nymphal densities. Notably, in contrast to observations across the eastern US (Diuk-Wasser et al., 2010), spatial autocorrelation was not significant among density observations; sites located in close proximity to one another were not significantly more likely to share similar estimates of nymphal density (Johnson et al., 2018). Instead, the proportion of agricultural land, which was inversely related to forest cover, was the most influential predictor of nymphal density. The positive association between annual temperature range and predicted nymphal density was attributed to warmer summer temperatures favoring tick survival and reproduction.

Tran et al. (2021) modeled the probability of presence and density of *I. scapularis* across New York based on surveillance records of nymphal occurrence and density in more than 500 unique locations from 2008–2018, which represents a period of emergence of the tick in western and northern New York. This study included not only fine-scale climate and landscape factors but also county-level data for hunter harvest of white-tailed deer. Consistent with the preceding models for presence and density of *I. scapularis* in the northern part of the eastern US (Diuk-Wasser et al., 2010) and Minnesota (Johnson et al., 2018), this model from New York showed that the variables predictive of nymphal presence differed from the variables predictive of abundance, suggesting the ecological processes defining presence of nymphs differs from factors defining their abundance. Nymphal ticks were more likely to occur at elevated abundance at lower latitudes with higher degree days above 0 °C during the spring and summer months. Other climate variables were identified as uniquely predictive of either nymphal presence or abundance, but the relative importance of each variable was not clear. Bearing in mind the crude (county-level) spatial scale for the deer variable relative to the tick sampling sites (more than 500 sites spread across the 62 counties in New York) and differences across counties in hunting pressure, the number of deer harvested by hunters showed a positive correlation with density of *I. scapularis* nymphs but a negative correlation with presence of *I. scapularis* nymphs. Considering the well documented importance of the white-tailed deer as the key reproductive host for *I. scapularis* adults (see Telford, 2017), this strange result raises the question of how to meaningfully include deer-related variables into modeling approaches where other potentially predictive variables, and the response variable, represent data for much finer scales than the deer data.

A recent model from Illinois in the Ohio Valley region used 62 occurrence location records for *I. scapularis* (including data from the 1950s onward) to explore associations between tick presence and climate and landscape variables (Kopsco et al., 2023). The leading predictors of tick presence were all landscape variables (percent forest cover, percent wetland, and percent grassland), with climate variables contributing to a much lesser extent (< 8 % collective variable contribution among the five significant climate variables included). For the climate variables, occurrence of *I. scapularis* was more likely to occur with increasing precipitation in the warmest quarter and with increasing temperatures (up to 21 °C) in the wettest quarter; whereas the tick was less likely to occur with increasing maximum temperatures in the warmest month, increasing mean temperature of the driest quarter, increasing annual temperature range, and increasing precipitation in the wettest month. Given the strong dependence on land cover for describing present day distribution, it was not surprising that predictions of distributional changes in the future were based primarily on changes in landcover.

3.6. Comparison with modeling efforts for *I. scapularis* in Canada

Compared to models for the climatically highly diverse eastern US, models for the colder areas found in eastern Canada to the north appear to more uniformly include degree days as a key predictor for presence and establishment of *I. scapularis* in forested settings (Ogden et al., 2005; Leighton et al., 2012; Gabriele-Rivet et al., 2015, 2017; Clow et al., 2017; Lieske and Lloyd, 2018; Kotchi et al., 2021; Hammond-Collins et al., 2022). This is not surprising as southeastern Canada represents the northern edge of the geographic distribution of *I. scapularis* in North America, where the tick is expected to be limited in large part by temperature conditions that restrict its ability to complete the life cycle due to a shorter warm period allowing for host-seeking and development following a blood meal.

4. Conclusions and directions for future research

Tick surveillance efforts over the past half-century, albeit sporadic and non-standardized, have clearly documented expansion of the range of *I. scapularis* in the northern half of the eastern US (Eisen and Eisen 2023). However, the role of climate change in driving such an expansion remains uncertain. Numerous efforts have been undertaken to model the distribution and abundance of *I. scapularis* at state, regional, and global scales, but outcomes have been inconsistent. Across the models, the functional relationships between seasonal or annual measures of heat, cold, precipitation, and humidity and tick presence or abundance varied. The contribution of climate variables relative to landscape differed among models or was not evaluated; host composition was very rarely considered. Although it is well established that the white-tailed deer is a key host for *I. scapularis* adults and deer distribution and abundance has expanded rapidly over the last half-century, appropriately scaled data on deer distributions and abundance are lacking and therefore not included in the modeling efforts.

Lack of consistently collected, long-term data on host and tick distributions and abundance limit our ability to disentangle the relative contributions and functional relationships between climate, landscape, and host variables and tick distribution and abundance.

Although recolonization of white-tailed deer over the last century in the eastern US largely may have represented a climate-independent process (e.g., reseeding deer populations through relocation of herds, land use changes favoring reforestation, and changes in regulations related to hunting), warming temperatures conceivably contributed to increasing the population growth rates of both white-tailed deer and *I. scapularis* populations, particularly in the coldest portions of the tick's range. One potential way to tease out the impact of climate warming on population growth of *I. scapularis* would be to focus longitudinal studies specifically on forested areas where deer populations are stable and the tick is already established. We are not aware of any studies fulfilling those criteria. The impact of climate warming on spread and initial establishment of *I. scapularis* in new areas is more difficult to tease out as this process first requires a deer population to be established and then depends on the timeline for the tick being introduced by hosts into the area in sufficient numbers to establish a population.

We conclude that although laboratory and small-scale field studies provide insights into how temperature and humidity impact survival and reproduction of *I. scapularis*, scaling up these associations to predict broad scale tick distribution and abundance patterns is more challenging. Owing to the lack of consistency among the studies outlined in Section 3 for which climatic variables best predict presence or density of *I. scapularis* in the northern tier of the eastern US, it is difficult if not impossible to assess how climate dictates the geographic distribution or density of this important human-biting tick species. To paraphrase Randolph and Nuttall (1994) in the context of natural versus laboratory studies of vector-borne diseases, modeling of the current and future geographic ranges and abundance of *I. scapularis* in the US based solely on climate variables could be either nearly right or precisely wrong. Additional data are needed to better understand the impact of climate variables on the complex population dynamics of *I. scapularis*, including how natural seasonal and diel variation in temperature and humidity during the warm period of the year influences (i) survival of questing ticks of different life stages during their respective peak activity periods and (ii) molting and reproductive success.

Data availability

This review focuses on previously published data; sources are listed in the References section.

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Table 1

Overview of models to estimate the geographic distribution of *Ixodes scapularis* in the United States.

Refs.	Geographic area	Time periods for included climate data / tick data	Outcome measure for <i>I. scapularis</i>	Includes future projections	Key modeling parameters			Primary variables predictive of tick distribution or density	
					Climate data	Vegetation data	Elevation data		
					Types of data included	Spatial resolution	Deer abundance data		
Estrada-Peña (2002)	Eastern US	1982–2000/1907–1996	Presence	No	Temperature	64 km ²	Not included	Not included	Tick presence: winter temperatures and NDVI.
Brownstein et al. (2003)	Conterminous US	1961–1990 1907–1996	Presence	Yes	Temperature and vapor pressure	0.5° × 0.5°	Not included	Not included	Tick presence: complex, nonlinear relationships with 7 temperature and 1 vapor pressure variables.
Diuk-Wasser et al. (2010)	Eastern US	1986–2005/2004–2006	Presence; Nymphal density	No	Temperature and vapor pressure	64 km ²	Forest fragmentation; NDVI ^a	Included	Tick presence: elevation, monthly mean vapor pressure deficit, and seasonal variation in temperature. Nymphal density: spatial autocorrelation term was the best predictor variable.
Hahn et al. (2016)	Eastern US	1950–2000/1907–2015	Presence	No	Temperature, vapor pressure, and snow cover	25 km ²	Land cover types	Included	Tick presence: elevation, forest cover, precipitation in the warmest quarter, and maximum temperature of the warmest month.
Johnson et al. (2016)	Minnesota	1960–1990/2005–2014	Presence	No	Temperature and precipitation	1 km ²	Land cover types	Included	Tick presence: landcover type, summer precipitation, maximum summer temperatures, and annual temperature variation.
Johnson et al. (2018)	Minnesota	1980–2014/2015	Presence; Nymphal density	No	Temperature, precipitation, and vapor pressure	1 km ²	Land cover types	Included	Tick presence: landcover. Nymphal density: landcover, mean diurnal temperature range, elevation, annual temperature range, and amount of summer precipitation.
Alkhishe et al. (2021)	North America	Not specified / Not specified	Presence	Yes	Not specified in the publication	Not specified	Not included	Not clear from the publication	Not specified in the publication.

Refs.	Geographic area	Time periods for included climate data / tick data	Outcome measure for <i>I. scapularis</i>	Includes future projections	Key modeling parameters			Primary variables predictive of tick distribution or density		
					Climate data		Elevation data			
					Types of data included	Spatial resolution				
Tran et al. (2021)	New York	Not specified / 2008–2018	Presence; Nymphal density	No	Temperature, precipitation, and vapor pressure	16 km ²	Land cover types	Included	County-level deer hunt harvest	Tick presence: elevation, degree days, precipitation, vapor pressure deficit, and deer harvest ^b . Nymphal density: degree days, vapor pressure deficit, and deer harvest ^b .
Burtis et al. (2022)	Eastern US	1980–2015/1907–2021	Presence	No	Temperature, precipitation, and vapor pressure	1 km ²	Forest cover	Included	Not included	Tick presence: elevation, forest cover, and maximum temperature of the warmest month.
Zhang et al. (2022)	Global	1970–2000/Not specified	Presence	Yes	Temperature and precipitation	20 km ²	Not included	Included	Not included	Tick presence: precipitation in May and September, precipitation in the driest month, temperature seasonality, and mean diurnal temperature range.
Kopsco et al. (2023)	Illinois	1970–2000/1950–2022	Presence	Yes	Temperature and precipitation	1 km ²	Land cover types	Included	Not included	Tick presence: land cover.

^aNDVI, Normalized Difference Vegetation Index; remotely sensed measure of vegetation density. Can also be viewed as a proxy for rainfall and humidity.

^bRelationship with county-level deer hunt harvest was negative for presence of *I. scapularis*, but positive for abundance of *I. scapularis* nymphs.