Impact of Climatic Change on the Northern Latitude Limit and Population Density of the Disease-Transmitting European Tick *Ixodes ricinus*

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We examined whether a reported northward expansion of the geographic distribution limit of the disease-transmitting tick *Ixodes ricinus* and an increased tick density between the early 1980s and mid-1990s in Sweden was related to climatic changes. The annual number of days with minimum temperatures above vital bioclimatic thresholds for the tick's life-cycle dynamics were related to tick density in both the early 1980s and the mid-1990s in 20 districts in central and northern Sweden. The winters were markedly milder in all of the study areas in the 1990s as compared to the 1980s. Our results indicate that the reported northern shift in the distribution limit of ticks is related to fewer days during the winter seasons with low minimum temperatures, i.e., below -12°C. At high latitudes, low winter temperatures had the clearest impact on tick distribution. Further south, a combination of mild winters (fewer days with minimum temperatures below -7°C) and extended spring and autumn seasons (more days with minimum temperatures from 5 to 8°C) was related to increases in tick density. We conclude that the relatively mild climate of the 1990s in Sweden is probably one of the primary reasons for the observed increase of density and geographic range of *I. ricinus* ticks. *Key words*: climate change, geographic distribution, *Ixodes ricinus*, Lyme disease, temperature, tick, tickborne encephalitis. *Environ Health Perspect* 108:119–123 (2000). [Online 29 December 1999]
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The northern distribution limit of the European tick *Ixodes ricinus* reportedly shifted northward in Sweden between the early 1980s and the mid-1990s (Figure 1) (*1*). Ticks reportedly also became more abundant in the 1990s (*1*) as compared to the 1980s (*2*).

In northern Europe *I. ricinus* ticks are the primary vectors of the agents causing tickborne encephalitis (TBE) and Lyme disease (*3–5*). Other studies on tickborne diseases have shown that disease incidence is dependent on climatic variations and that the milder climate of the 1990s was related to increases in TBE incidence (*6,7*). The geographic distribution and population density of *I. ricinus* and other closely related vector species are influenced by several interacting abiotic and biotic factors (Figure 2). Access to potential host animal species (*2,8*) and adequate vegetation cover (*3,5,9–11*) are of importance for the survival and development of the tick. The climate sets the absolute limit for the possible geographic distribution of ticks and also may influence population density both directly and indirectly (*12–19*), as illustrated in Figure 2.

Bioclimatic threshold temperatures influence the transmission of vectorborne diseases (*20*), as shown in studies on climatic change and certain mosquitoborne diseases such as malaria and dengue fever (*21*). Studies on the incidence of TBE in relation to daily minimum and maximum temperatures and precipitation during four decades in central Sweden have shown significant correlation between TBE incidence and the seasonal number of days with minimum temperatures above the lower bioclimatic thresholds for *I. ricinus* activity, development, and survival (*6,7*). These findings demonstrate the importance of bioclimatic thresholds for the dynamics of transmission of tickborne disease agents.

The primary aim of this study was to determine whether the observed shift in the northern distribution limit of *I. ricinus* ticks and the increase in tick population density in central and northern Sweden from the early 1980s to the mid-1990s were related to climatic changes.

Materials and Methods

Tick data. We studied tick data from central and northern Sweden. These data were based on the geographic distribution of *I. ricinus* in Sweden (*2*) and on the results of a combined questionnaire and field study (*1*). Tälleklint and Jaenson (*1*) used a 1994 questionnaire that was published in periodicals aimed at hunters, cat and dog owners, and house and cottage owners living in central and northern Sweden. The questionnaire included the following questions: *a*) Are ticks present within 1 km of your home? *b*) Were ticks present in the vicinity of your home in the early 1980s? and *c*) How many ticks have you found on yourself, your cat, or your dog in 1992 and 1993?

Information on ticks found on cats and dogs in the 1990s, and on tick occurrence in both the 1980s and the 1990s, was retrieved and analyzed based on the answers of > 1,000 participants (*1*). "Ticks" in this context are almost always *I. ricinus*—a study of 1,739 ticks collected from cats and dogs throughout the Swedish mainland showed that > 99% of these ticks were *I. ricinus* (*2*). For each positive response, the median number of ticks found on cats and dogs in the 1990s was calculated and classified into one of the following groups: 1–5, 6–10, 11–20, 21–50, 51–100, and > 100 ticks/year. The home locations of the study participants were then grouped and analyzed according to their tick density category and their reported percent change in tick occurrence between the 1980s and the 1990s (*1*). The information given by the study participants on tick occurrence in the early 1980s (*1*)—shown in Figure 1A—is in accordance with other studies on tick distribution and limits in central and northern Sweden (*2*). When information on tick occurrence in the 1990s was compiled, a northern shift of the distribution limit appeared as compared to the 1980s (*1*) (Figure 1B). To check the validity of the 1990s questionnaire answers, the existence of a hypothetical boundary zone in north-central Sweden, where tick density was reported to decrease dramatically on dogs and cats when going from south to north of the boundary, was corroborated by standardized cloth dragging collection of *I. ricinus* at 54 areas located to the south or north of the boundary zone (*1*).

For this study we selected 20 districts in northern and central Sweden that had different combinations of reported tick density in the 1990s and percent changes in tick occurrence over time (Table 1) (*1*). For

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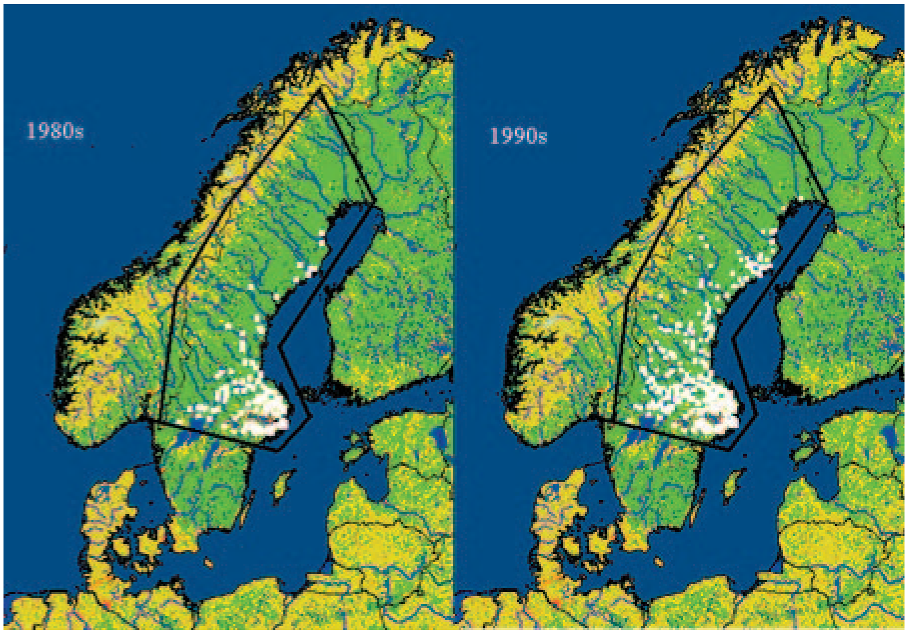

Figure 1. White dots illustrate districts in Sweden where ticks were reported to be present (*A*) in the early 1980s and (*B*) in the mid-1990s. The study region is within the black line.

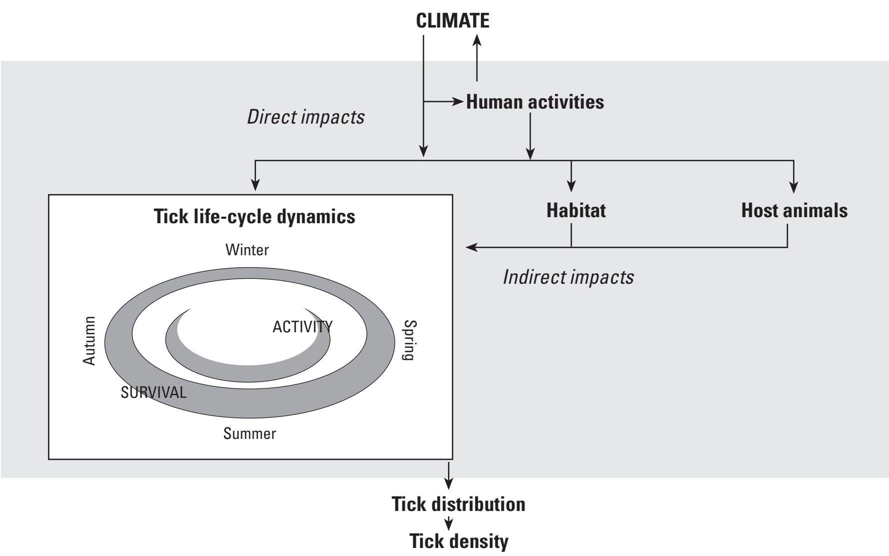

Figure 2. Schematic illustration of direct and indirect climatic impacts on tick distribution and population density.

Table 1. Zone classification with reported changes in tick occurrence and the number of ticks found on cats and dogs specified for each zone.

Zone	Meteorological station/study district	Tick occurrence (%)/ % increase[a]	Median ticks (n)[b]
1	Stensele, Luleå, and Storfinnforsen	22/(5)	1–5
2	Umeå, Frösön, Härnösand, Sundsvall, Mora, Falun	38/(15)	1–5
3	Delsbo, Edsbyn, and Söderhamn	46/(31)	1–5
No zone	Torsby	41/(48)	6–10
4	Lindesberg, Gävle, and Avesta	23/(71)	11–20
No zone	Karlstad	36/(58)	21–50
5	Västerås and Uppsala	22/(74)	21–50[c]
No zone	Stockholm	16/(84)	> 100

[a]Regional average percentage increase in tick occurrence, 1980s to 1990s (1980s value in parentheses). [b]Reported number of ticks found on dogs and cats in the 1990s; categorized by median values. [c]Median number of ticks was 51–99 for the Uppsala station.

each district we identified the meteorological station closest to the majority of the study participants' homes (*1*).

Bioclimatic thresholds. The choice of bioclimatic thresholds was based on the results of previous studies on *I. ricinus* or on closely related tick species. For instance, bioclimatic threshold temperatures for tick activity range from 4 to 5°C, and for tick development and egg deposition 8 to 11°C [(*12,13,16,17,22*)]. Moreover, freezing temperatures during the winter season may affect the survival of ticks (*17,23*) and their ability to develop in the following spring (*17*). Nymphal and adult ticks may resist freezing temperatures well below -7°C, whereas eggs and larvae, especially if fed, are slightly more sensitive to subzero temperatures (*17,19,23*).

Climatic data. We obtained daily minimum temperatures for two 3-year periods, i.e., 1979–1981 and 1991–1993, from the Swedish Meteorological and Hydrological Institute (Norrköping, Sweden) for the 20 different meteorological stations. For each of the stations we calculated number of days with daily minimum temperatures below, between, or above important bioclimatic thresholds. These threshold temperatures were -12, -10, and -7°C, with 0°C as a reference, and 5, 8, and 10°C. For temperatures above zero we looked at the annual number of days, whereas for subzero temperatures we counted days per winter seasons (i.e., mid-November to March).

Precipitation was not included in this study. The ground plant cover seems more important for maintaining adequate humidity for ticks than precipitation (*14*).

Analyses. The different districts, represented by the meteorological stations, were divided into five zones (Table 1). The zones were based on a combination of the reported data on the average number of ticks found on cats and dogs in the 1990s and the percent change in tick occurrence between the early 1980s and the mid-1990s. To characterize the temperature differences between the zones, we conducted a discriminant analysis. For each locality and for each of the years 1979–1981 and 1991–1993, we chose a set of seven variables. The variables indicated the number of days with a minimum temperature in certain intervals, i.e., < -12, -12 to -10, -10 to -7, -7 to 0, 5 to 8, 8 to 10, and > 10°C. The averages were calculated for the first 3 years (1980s) and the last 3 years (1990s). These averages were used as predictors for the five zones in a discriminant analysis based on Mahalanobis distance (*24*).

The three southernmost study areas, i.e., Torsby, Karlstad, and Stockholm County, were not grouped into zones and therefore were not used in the discriminant analyses. Each of these areas differed markedly from the rest of the study areas with regard to tick density and change in tick occurrence (Table 1). The Stockholm County study area, which includes parts of the Baltic Sea coastline and archipelago as well as the shores of a large inland lake, had the study's highest abundance of ticks in both the 1980s and the 1990s.

Results

The climate in the various study districts and zones in the 1980s, and the differences between the 1990s and the 1980s, are shown in Figure 3. In the 1980s the most noticeable difference between the 20 districts was the decrease in the number of very cold days, i.e. < -12°C, when moving from north to south (Figure 3A). Also, the number of days with temperatures > 10°C increased when moving in the same direction (Figure 3C). The number of days with mild freezing temperatures, i.e., -7 to 0°C, increased slightly from north to south (Figure 3A), whereas the number of days with lower spring and autumn temperatures, i.e., between 5 and 8°C, decreased (Figure 3C).

The main differences between the 1990s and the 1980s were the considerably milder winters in the 1990s and the increase in the 1990s in the annual number of days with temperatures between 5 and 8°C when moving from northern districts with low tick abundance toward southern districts with high tick abundance (Figure 3B and 3D). This increase was caused by a shift from warmer to cooler temperatures as well as by a real extension of the spring and autumn seasons. Also, zones 1–3 all displayed a shift from very cold to medium cold or mild winter days, but showed only minor changes in the degrees above zero. These zones all had reported low tick densities. For zones 4–5 and Stockholm County, (districts with medium to high tick density), the most marked changes were fewer cold winter days in general and a shift from warm to cooler and more extended spring and autumn seasons; these conditions create more days that allow tick activity. The consistency in the relations between the observed climatic differences over time and the reported changes in tick occurrence and density as defined by the different zones were confirmed by the results of the discriminant analysis.

Discriminant analyses. The discriminant analyses show that the zone classifications correspond perfectly to observed differences in temperature data. The assigned zones are unambiguous in the sense that for all of the study districts, the Mahalanobis distance is shortest to the center of their own zone both in the 1980s and in the 1990s. In cross-validations (in which each station is classified on the basis of the remaining 16 stations), four districts in the 1990s were reallocated—three of them from zone 2 to zone 3—and all but one (Falun) had a rather small difference between the original and the alternative classification (Table 2). In the 1980s the zones were much closer to each other in terms of temperature patterns, and in the cross-validations, 12 of 17 districts were shifted. However, the differences between the distance to the new zone center and the old were even smaller than those presented in Table 2, with the exception of two localities, Delsbo and Edsbyn (in zone 3), which were both proposed for zone 2 in the cross-validation.

When temperatures in the 1990s are classified according to the zones as characterized by data from the 1980s, all but two of the districts fall into zone 5. This means that temperature patterns in the 1990s are comparable to those in zone 5 in the 1980s. Zone 5 is the only one where ticks were highly abundant in the 1980s. We would expect the opposite situation to be present when the 1980s temperatures are classified by the 1990s zones. However, only one-third of the study districts fall into the expected zone 1, i.e., the coldest zone of the 1990s. It is possible that the dominant feature is the total number of days with temperatures < -12°C and the total number of days with temperatures of -7 to 0°C, which obscures the expected similarity to the coldest zone.

We calculated Spearman correlation coefficients between the reported tick density (average density in each district) and temperatures (average number of days in the various temperature intervals during 3 years in each district) during the 1990s. We found significant values for the highest and the lowest temperatures (ρ = 0.60–0.85, p < 0.001). The average density of ticks as reported by observers may constitute a somewhat crude measure of the true density.

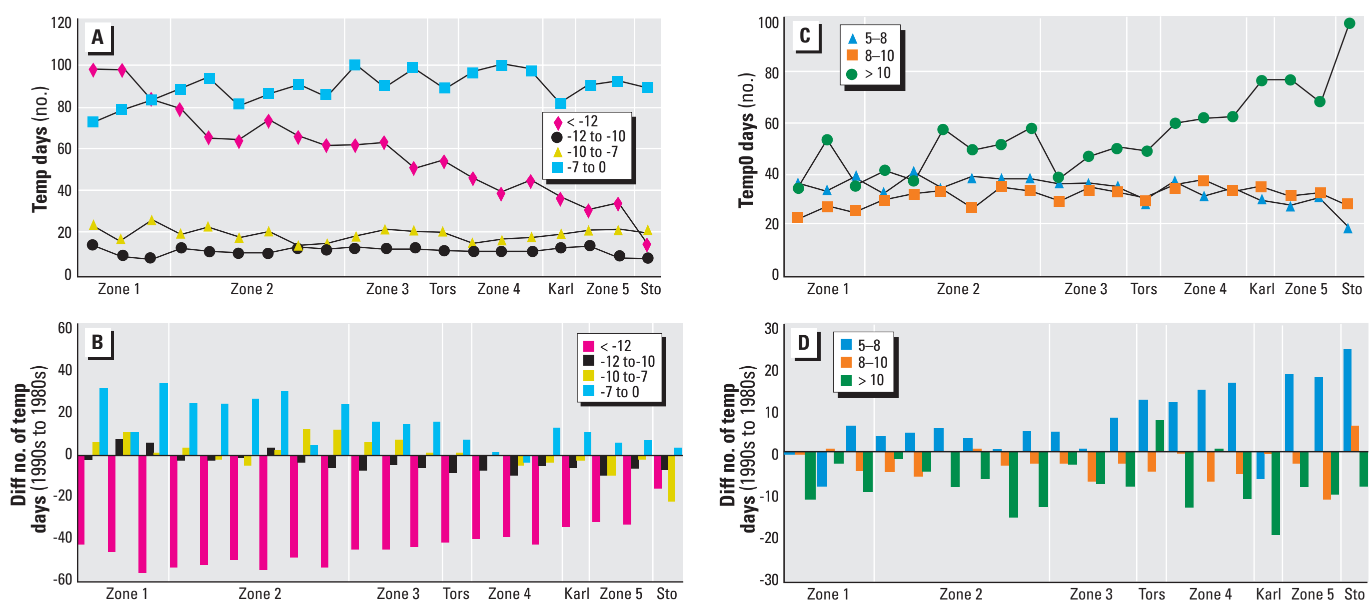

Figure 3. The climate in the various study districts and zones in the 1980s and the differences between the 1990s and the 1980s. Abbreviations: Karl, Karlstad Meteorological Station; Sto, Stockholm Meteorological Station; Tors, Torsby Meteorological Station. The average number of days during 3 years in the early 1980s with temperatures (temps) below, in between, or above bioclimatic thresholds of interest for tick distribution and density in each of the 20 study districts are shown for winter (*A*) and spring, summer, and autumn (*C*); the most northern study districts are to the left and the most southern are to the right along the *x*-axis. The difference between the 1990s and the 1980s in the average number of days for each temperature variable are shown for winter (*B*) and spring, summer,and autumn (*D*); study districts with increasing tick density and changes in tick occurrence on cats and dogs in the 1990s are shown over time from left to right along the *x*-axis.

Table 2. Mahalanobis distances for the four districts in the 1990s that were reallocated in the cross-validations.

District	1980s zone	Mahalanobis distances in cross-validations, 1990s $[\Sigma_i\Sigma_j(x_i - m_i^{(k)})c^{ij}(x_j - m_j^{(k)})]$ To zone 1	To zone 2	To zone 3	To zone 4	To zone 5
Storfinnforsen	1	88	73	147	60[a]	160
Umeå	2	142	22	10[a]	345	610
Mora	2	171	50	46[a]	245	443
Falun	2	971	440	38[a]	663	104

[a]Minimum value.

Discussion

Our results indicate that the reported northward shift of the northern distribution limit of ticks between the early 1980s and mid-1990s was related to fewer days with temperatures below -12°C during the winter. In areas with medium to high tick densities, further increases in tick abundance seemed to be related to a combination of mild winters and extended spring and autumn seasons. We also found a difference between districts with high versus low tick density, which indicated more warm nights in late spring and early autumn, and fewer cold winter days in areas with higher tick abundance.

Our results are in accordance with the findings of previous experimental and field studies on the effects of climatic factors on the lifecycle dynamics of closely related tick species (*13,16–19*). For example, the lack of importance for tick density of temperatures between -7 and 0°C is confirmed by several studies (*7*), including a Japanese study (*23*), which showed that ticks resist long-term exposures to milder subzero temperatures. Nymphs, for example, resisted exposure to -5°C during a nearly 2-month period (*23*). Snow conditions were not included in this study because snow depth may vary widely even within the same locality. The effect of snow cover on ground temperature depends on snow depth and duration, soil physical characteristics, and air temperature (*25*). In general, snow cover increases soil temperatures, sometimes by several degrees (*25*), which is why we included several winter temperature limits in our analyses (*7*). Our finding that early spring and late autumn temperatures (5–8°C) were important for increases in tick density in the more southern study areas is supported by studies on climate and tickborne diseases (*6,7*). The finding that late spring/early autumn and summer temperatures (8–10 and > 10°C) were of more importance to tick occurrence in the north is confirmed by a study from Canada (*17*). Lindsay et al. (*17*) suggested that the northern limit of the geographic distribution of *Ixodes scapularis* ticks, which are closely related to the European *I. ricinus*, is determined by annual number of days above bioclimatic threshold temperatures, i.e., median temperatures from 6 to 11°C; however, the study did not include freezing temperatures (*17*). Our observed association between winter climate and latitude shift in tick distribution limit is supported by previous studies on spatial tick distribution. For example, a central European study showed that the absence of *I. ricinus* at altitudes higher than 700 m above sea level is related to microclimatic conditions (*14*).

The climate sets the ultimate limits for the geographic distribution of ticks and for tick activity, development, and survival. Within the upper and lower bioclimatic thresholds other factors dependent (Figure 2) or independent of climatic variations may influence the spatial distribution and abundance of ticks. One such factor is land-use changes. However, between the early 1980s and the mid-1990s, no major land-use changes, such as de- or reforestation, occurred in the study districts. A factor that likely did influence tick density during our study period was a rapid increase in roe deer population from the mid-1980s. The roe deer is the main host animal for the adult developmental stage of *I. ricinus* in Sweden (*8*). The population increase was due to *a*) decreased predation from red foxes caused by a heavy scabies infestation in the fox population (*26*) (important especially in central parts of Sweden, i.e, zones 4–5 and Stockholm County), and *b*) milder winter conditions (*26*) (important for the whole study region but in particular for zones 1–3). During our study period we had a situation where adult ticks were not limited by host animal availability, and where there were favorable climatic conditions for ticks to flourish. Other studies on climate in relation to tickborne diseases in central Sweden showed that disease incidence was significantly correlated to bioclimatic thresholds both during the decades before as well as after the increase in roe deer population (*6,7*).

The tick data, which were based on the results of a questionnaire study (*1*), require some comments about their validity—possible recall bias and lack of random sampling are important issues. Recall bias in relation to tick occurrence may be accentuated by increased public awareness of tickborne diseases. However, the questionnaire information on changes in tick distribution between the 1980s and the 1990s (*1*) can be partially verified. The reported geographic distribution of *I. ricinus* ticks in the 1980s was in accordance with that of previous studies [e.g., Jaenson et al. (*2*)]. Also, parts of the hypothetical northern shift in tick distribution between the 1980s and the 1990s were corroborated in a field study, as described previously (*1*). Increased pathogen transmission in the 1990s indirectly suggests an increase in vector density. A serological confirmed increase in antibody conversion of Lyme disease has been reported in a population in southern Sweden during the beginning of the 1990s (*27*). During our study period the incidence of TBE increased significantly (*6*). These TBE data are unique in their reliability. Since the late 1950s all hospitalized encephalitis cases in endemic regions have had their blood tested for TBE virus and positive cases have been reported to a national registry at the Swedish Institute for Disease Control in Stockholm (*6,28*). There is no indication of any important differences among respondents that might cause a recall difference between districts. Considering these findings, we conclude that there is strong independent corroboration of the increases in tick density as reported in the questionnaire study (*1*). The absolute number of ticks reported in the 1990s, which could be more prone to various measurement problems as well as to sampling problems, are only used in this study as indicators of relative tick abundance in the five zones, and as such they are also confirmed by the independent findings discussed here.

A future global climate change is expected to cause a proportionally higher increase in minimum as compared to mean and maximum temperatures at high northern latitudes (*29*). Such trends have already been observed in North America (*30*). Winter minimum temperatures are also expected to increase more than spring, summer, and autumn temperatures (*29*). We suggest that changes in the distribution pattern of ticks may be expected at high northern latitudes in the decades to come. This is a new parallel to the dependence on climate in vectorborne diseases, such as malaria, dengue fever, and TBE (*6,7,20,31–35*). Climate change models have projected changes in the distribution, seasonality, and annual incidence of mosquitoborne diseases such as malaria and dengue fever (*21,36*). In conclusion, the results of this study suggest that ticks may spread into regions at higher latitudes and altitudes as well as become more abundant in established regions if the climate becomes milder. This may in turn influence the spread and seasonal range of tickborne diseases in humans, such as tickborne encephalitis or Lyme diseases, in the northern parts of both Europe and North America.

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