Northward expansion of the thermal limit for the tick *Ixodes ricinus* over the past 40 years

Daniele Da Re[1,2,3,*], Gaëlle F. Gilson[1], Quentin Dalaiden[1,4],
Hugues Goosse[1], René Bødker[5], Lene Jung Kjær[5],
Roberto Rosà[2], Nicholas H. Ogden[6,7,8], Sophie O Vanwambeke[1,*].

[1]Center for Earth and Climate Research, Earth & Life Institute, UCLouvain, Louvain-la-Neuve, Belgium
[2]Center Agriculture Food Environment, University of Trento, San Michele all' Adige, Italy
[3]Research and Innovation Centre, Fondazione Edmund Mach. San Michele all'Adige, Trento, Italy
[4]Nansen Environmental and Remote Sensing Center and Bjerknes Center for Climate Research, Bergen, Norway
[5]Department of Veterinary and Animal Sciences, Faculty of Health and Medical Sciences, University of Copenhagen, Denmark
[6]Public Health Risk Science Division, National Microbiology Laboratory Branch, Public Health Agency of Canada, Canada
[7]Groupe de recherche en épidémiologie des zoonoses et santé publique, Faculté de médecine vétérinaire, Université de Montréal, St-Hyacinthe, QC, Canada
[8]Centre de recherche en santé publique, Université de Montréal, QC, Canada
***Corresponding authors**: daniele.dare@fmach.it, sophie.vanwambeke@uclouvain.be

Abstract

The tick *Ixodes ricinus* is the main pathogen vector in Europe. Many speculations have been made about the effect of past climate change on the potential distribution of this ectothermic organism, despite a poor understanding of how climate change has resulted in distribution changes to date.

In this study, we used a public cross-sectional dataset of *I. ricinus* abundance at the northern edge of its European distribution for 2016-2017 to identify a thermal limit for *I. ricinus* distributions.

We first modelled the nymphal tick abundance as a function of cumulative annual degree days (DD) > 0°C and biogeographical regions using observations for 2016-2017. We then identified the thermal limit for each biogeographical region as the minimum DD value where the predicted nymph abundance is greater than zero. Hindcasting the identified thermal limit suggested that *I. ricinus* has expanded its range by approximately 400 km in the Boreal biogeographical region between 1979 and 2020. Despite the lack of long-term data series on tick presence, this finding helps explain numerous observations of *I. ricinus* in areas presumed to be newly colonised.

While multiple other factors affect tick distribution and abundance at the local scale (e.g., host distribution, microhabitat), our approach appears promising for understanding species distribution changes driven by recent climate change. Accounting for biogeographic regions helped consider other dimensions of habitat at a broad scale. Our results underline the relevance of long-term time series data and the risk associated with short-time series for observing changes in distribution.

Keywords: climate change, degree days, hindcast, Scandinavia

Author Contributions

Sophie Vanwambeke and Nicholas Ogden conceived the ideas and designed the methodology, with relevant contributions from Daniele Da Re, Gaëlle Gilson, Quentin Dalaiden, Lene Jung Kjær, René Bødker and Hugues Goosse. Daniele Da Re, Gaëlle Gilson, Quentin Dalaiden and Roberto Rosà analysed the data; Daniele Da Re and Sophie Vanwambeke led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

The research presented in this paper was funded by the Fonds de Recherche du Québec (FRQ), the Fonds de Recherche du Québec Nature et Technologie (FRQNT) and complementary funds from the Natural Sciences and Engineering Research Council (NSERC) of Canada and the Social Sciences and Humanities Research Council (SSHRC) of Canada as well as by the Fonds de la Recherche Scientifique (F.R.S.-FNRS, Belgium). H. Goosse is Research Director at F.R.S.-FNRS. D. Da Re was supported by the F.R.S.-FNRS ASP Grant (N. 34766961). The authors are grateful to all external contributors.

Conflict of Interest Statement

Nothing to declare.

1. Introduction

The effect of climate change on arthropod vectors is expected to be significant but has been much debated for decades. As ectothermic organisms, arthropod vectors are susceptible to temperature, which affects their development, activity, and survival[1]. Much of the discussion on the impact of climate change has focused on mosquito vectors[2], as the diseases they transmit continue to pose substantial public health burdens and have been extensively studied for a long time. The impact of climate change on ticks has also generated many studies (reviewed in Gilbert 2021[3]) and climate change as a driver of geographic range expansion of ticks has drawn attention in Europe in particular [4–7]. Europe's climate has been warming faster than the global mean temperature change and is projected to maintain this trend in the coming decades[8]. This gradual increase in temperature has already been identified as an important factor for the northward expansion of various species[9,10], including at northern latitudes, where the role of climate change on range shifts may be particularly strong[11]. Northward range expansion for *Ixodes* spp. ticks in northern latitudes are thus expected.

Ixodes ricinus is the most important tick vector of pathogens in Europe, transmitting viral, protist and bacterial pathogens to humans, livestock and companion animals[12]. As ectothermic organisms spend most of their life off-host, *I. ricinus* is sensitive to climate-driven abiotic factors such as temperature and humidity/saturation deficit[13]. Temperature affects tick survival, interstadial development rates, and activity, while humidity influences survival and activity[1,3]. Temperature and humidity also indirectly affect tick survival by affecting the availability of resources such as suitable habitat and host availability[14]. In their primary habitat, forests, ticks can find shelter from weather extremes (heat, drought, and cold) that would inhibit host finding and directly kill the ticks[1,15]. Because of their capacity to shelter and diapause when the weather is unfavourable[16], ticks may mostly be affected by long-term climate changes rather than short-term weather variations[17].

Many correlative models have been used to estimate the climatic niche of *I. ricinus* and project future geographic distributions under climate change scenarios (e.g. [18–20]), but much fewer studies have used mechanistic models[21]. In general, there is a poor understanding of past distribution changes that may or may not have been associated with climate change. However, observations of the effects of climate change on various arthropod vectors in Europe, including ticks, are accumulating[22]. Examining empirical evidence of climate-associated changes, it should be noted that data on human disease records rather than tick observations is conditional on human exposure to infectious ticks on the one hand and efficient diagnosis and reporting on the other. Both are affected by societal factors generally unrelated to tick ecology. While human cases only occur if infectious vectors are present, they represent a more visible, but often partial, part of the zoonotic iceberg[23].

Shifts in altitudinal limits, in Eastern Europe [24,25] and then the Alps [26,27], were the first evidence of the potential effects of climate change on *I. ricinus* distribution. Using a 35-year-long dataset in Russia, Korotkov et al.[28] demonstrated an increase in adult *I. ricinus* abundance that could be related to a lengthening of the tick activity season, as host abundance was found to be stable in the area. In Norway, substantial changes in an altitudinal gradient of tick abundance have been observed[29], as well as range spread along a latitudinal gradient[30,31]. However, though distributional datasets cannot fully demonstrate geographic range expansion (particularly as the absence of ticks is difficult to prove and collection efforts are rarely directed to demonstrating it), a consensus now exists that this expansion is noticed and that climate change is likely one factor driving it.

Long-term data series for *I. ricinus* are particularly lacking in areas where the health concern they bring is an emerging one. In that context, drawing conclusions on the current (or future) effects of climate change is often qualitative (using an assemblage of heterogenous or temporally biased datasets) or indirect (assessing tick-borne pathogen data in humans or animals), with the caveat that diagnostic capacity, reporting practices and disease knowledge may have changed. Disease records for humans and livestock[32] show that reported incidence has increased during the period 1995-2015 and that climate has probably played a role, likely through effects on the vector, although effects of changing reservoir host dynamics cannot be ruled out. Monitoring efforts have also been reinforced, complexifying interpretations further. Numerous studies that conclude there will be changes in distribution or risk do so from largely unvalidated projections into the future drawn from habitat suitability models, correlative associations between field observations and mostly abiotic variables obtained from datasets that are limited in terms of having small sample sizes or using presence-only data[19,33,34]. Mechanistic approaches may have more explanatory potential[21], but have only been used at small spatial scales to explore possible effects of past climate change[35] and calibration of life cycle parameters remains challenging.

In this paper, instead of using a habitat suitability model, we use cross-sectional empirical data to infer a minimum threshold of thermal suitability for *I. ricinus*, allowing us to draw a continent-wide contour line of thermal suitability/unsuitability. Then, we evaluate the changing position of the thermal limit across a period of 40 years since 1979. We adopt the use of cumulative annual degree-days above 0°C (DD > 0°C) to define the thermal suitability threshold for *I. ricinus*, following the approach used to successfully define climatic suitability for *Ixodes scapularis* in Canada[36].

2. Materials and methods

We assume that tick population survival is primarily influenced by life cycle length, as it affects interstadial development rates, with many tick-suitable habitats offering refuges that shield ticks from extreme temperatures. For that reason, average daily temperatures above 0°C are relevant for tick development and population survival. We consider a threshold on annual DD > 0°C below which the lifecycle is assumed to be so long that the population cannot persist[37]. Using a set of cross-sectional nymph count samples, we first assessed the effect of annual DD > 0°C on nymph abundance using a Generalized Linear Mixed Model (GLMM). Having found a significant and positive association between annual DD > 0°C and nymph abundance, we determined the minimum annual DD > 0°C threshold at which nymph abundance is zero. This indicates the critical temperature threshold below which conditions are unfavourable for *I. ricinus* population persistence. This threshold was obtained as the intercept of the relationships between annual DD > 0°C and nymph abundance, representing the annual DD > 0°C estimate at which nymph abundance is predicted to be zero. We then mapped these thresholds over the area of interest and assessed their latitudinal changes over the period 1979-2020. An overview of the methods is presented in Figure 1.

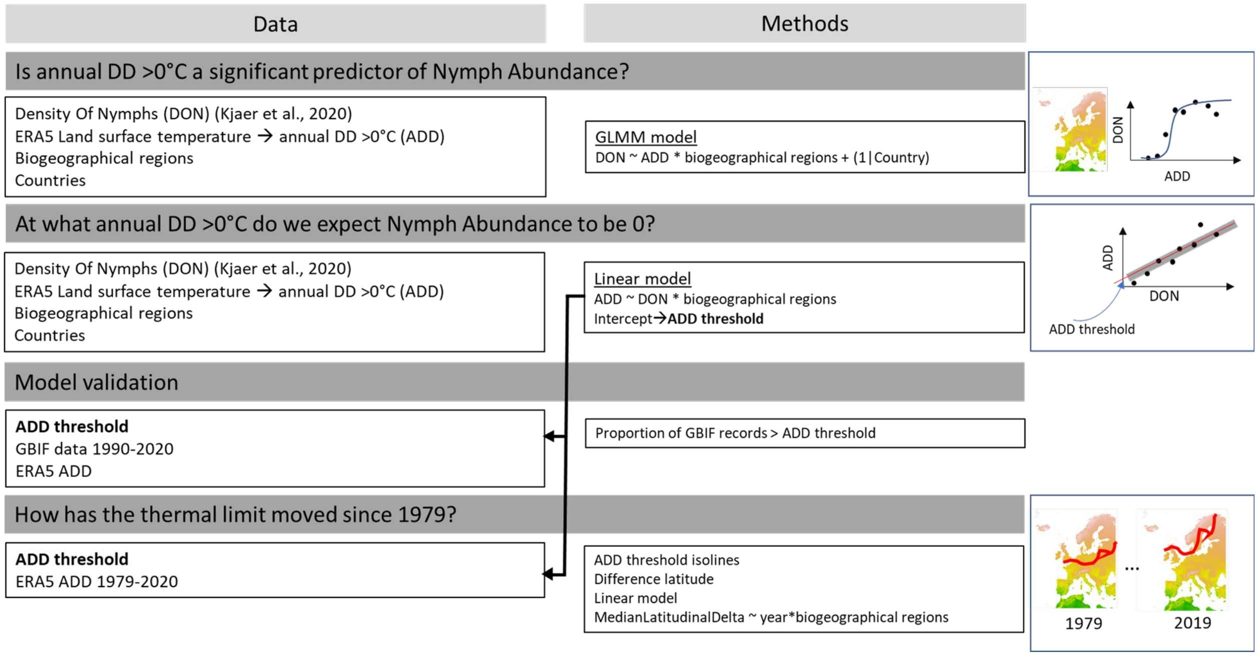

Figure 1 Summary of the methodology applied to investigate the relationship between tick nymph abundance and annual degree days > 0°C (ADD), and the ADD thresholds for ticks persistence in each biogeographical region.

2.1 Biological observations and area of interest

We used *I. ricinus* nymph counts acquired by dragging a white flannel cloth along transects as part of a survey conducted by Kjær et al. [38] across Denmark, southern Norway, and south-eastern Sweden. Kjær et al. (2020) gathered data on tick larvae, nymph and adult abundance at 159 sites in south Scandinavia during August-September 2016, with an additional sampling of 30 sites surveyed during the same months in 2017 among which 18 sites were sampled both years. To address the difference in sampling effort between 2016 and 2017, we averaged the tick abundance only for sites visited in both years, whilst the sites sampled only in 2017 were kept as sampled. Field surveillance by dragging is considered the gold-standard method for identifying the presence of reproducing, self-sustaining tick populations[39,40].

Sampling sites span from 5° to 20° East and from 54° to 64° North (Fig. 2). This area is characterised by four main biogeographical regions, namely Alpine, Atlantic, Boreal, and

Continental (Fig. 2; [41]). We limited the geographical area of extrapolation of the model to these biogeographical regions only.

2.2 Environmental covariates

We calculated the annual DD above 0°C (the daily average number of degrees centigrade above 0°C summed over a year; ADD > 0°C) from 1979 to 2020 using the daily average surface temperature estimates at 9 x 9 km spatial resolution from the land reanalysis ERA5Land[42]. Only the years 2016 and 2017, as sampled by Kjær et al., were used to inform the GLMM model and the definition of the threshold (next sections).

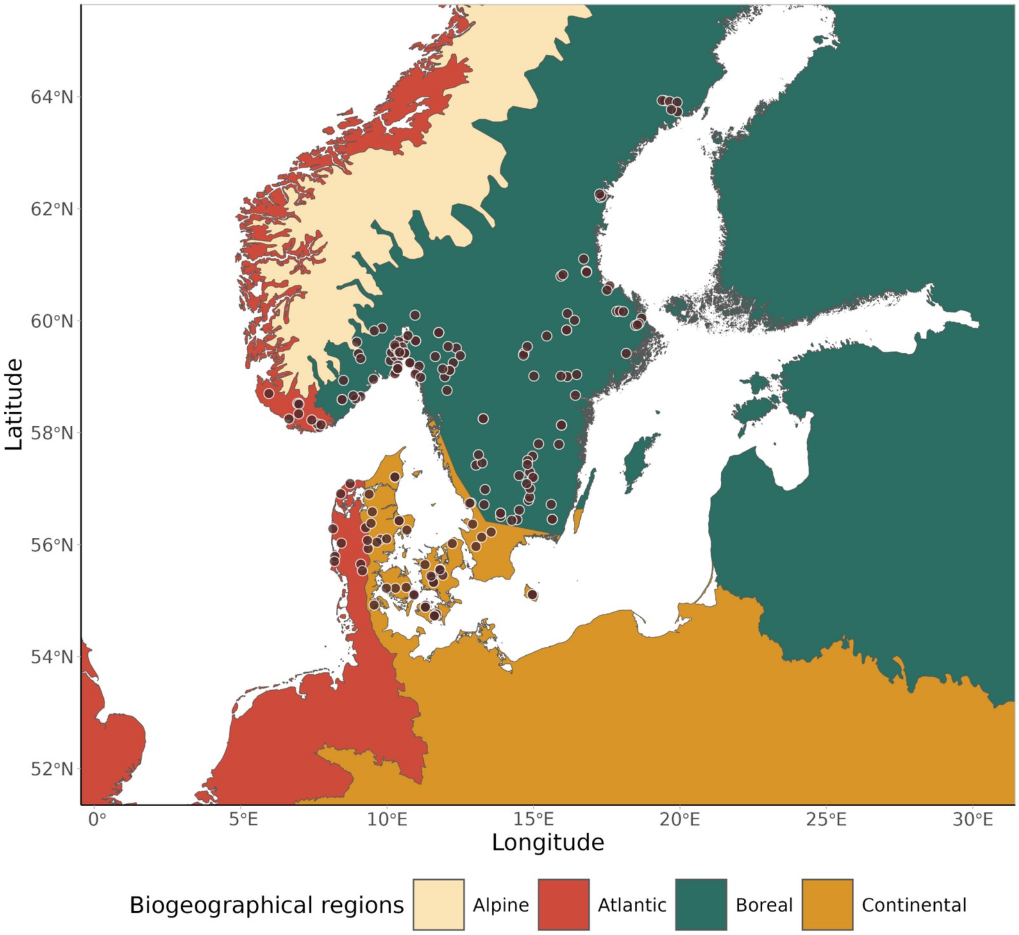

Figure 2 Biogeographical regions of Europe according to Cervellini et al., (2020) in the area of interest and the locations (brown dots) sampled in 2016-2017. The sampling locations broken down by year are available in Fig. SM1.

2.3 Modelling

We used Generalised Linear Mixed Models (GLMMs) to analyse the dependence of nymph abundance sampled in 2016-2017 on temperature, using the interaction between ADD > 0°C and biogeographical regions as predictors and country-level random effects included as a grouping factor (Eq. 1).

nymph abundance ~ ADD > 0°C * biogeographical regions + (1|Country) (Eq. 1)

Starting from a Generalised Linear Model (GLM), model selection was conducted by comparing different models. Several models were specifically tested by examining overdispersion, zero inflation, random effects, and the quadratic effect of ADD > 0°C. The final model was chosen based on the Akaike Information Criterion (AIC) and likelihood ratio test between different model formulations. Following this exploratory analysis, the final model formulation was a GLMM with a Poisson error family with a Log-link and a negative binomial distribution to account for overdispersion, and with the country as a random effect.

Summary statistics of the final model included the coefficient of determination (R^2), the root mean square error (RMSE), and the mean absolute error (MAE). Additionally, we assessed the presence of spatial correlation in model residuals using Moran’s I statistic.

All the analyses were performed in R 4.4.0[43] and the codes used are available on GitHub at https://github.com/danddr/ticks_DD_Scandinavia.

2.4 Annual Degree Days > 0°C threshold for *I. ricinus* population persistence

In the absence of substantial literature on the lower annual DD > 0°C limit for the persistence of *I. ricinus*, we defined the lower thermal limit for each biogeographical region as the intercept of the relationship between ADD > 0°C and nymph abundance as measured by et al. [38] using a linear model (Eq. 2).

ADD > 0°C ~ nymph abundance * biogeographical regions (Eq. 2)

The intercept of the linear model represents the estimated value of ADD > 0°C when nymph abundance is predicted to be zero. This can be interpreted as the critical heat threshold needed for tick development and activity to allow the completion of the tick life cycle. Below this threshold, conditions prevent a mated adult female from producing at least one surviving mated adult female, thus inhibiting population persistence.

To assess the estimated thresholds, we used an independent dataset of *I. ricinus* occurrences obtained from the Global Biodiversity Information Facility (GBIF) for the period 1979-2020 in our area of interest[44]. The occurrence data were filtered removing missing or incorrect coordinates, and occurrences located in the sea or the city centres of major cities. We subsequently linked each occurrence to its corresponding biogeographical region and annual DD > 0°C for the sampling year. Each occurrence was identified as below or above the threshold identified for that region. We defined GBIF occurrences above each threshold as True Positives and GBIF occurrences below each threshold as False Positives and computed sensitivity. Although not a formal significance test, this approach provides a practical measure to evaluate the predictive performance of each threshold.

2.5 Spatio-temporal trends in Cumulative Degree Days > 0°C thresholds

We computed the geographic position of the ADD > 0°C threshold for each of the three sampled biogeographical regions for every year spanning from 1979 to 2020 by computing the latitudinal difference between the position of the threshold in each year compared to that in 1979 within each biogeographical region. This involved determining the contour line of each ADD > 0°C threshold for each year, from which we obtained a distribution of latitudinal values belonging to the pixels intersected by the contour line. We then retrieved the yearly median latitude of each threshold and computed the difference between the median latitude of each year and that of 1979. We then utilised linear regression to analyse the relationship between the median latitudinal delta and the corresponding year (Eq. 3), aiming to discern any systematic changes in the latitudinal range of thermal limits over the study period for different biogeographical regions.

MedianLatitudinalDelta ~ year*biogeographical regions (Eq. 3)

We mapped the threshold as isolines, connecting points of equal ADD > 0°C value for 1979 and 2020.

3. Results

After the data curation, we utilised 171 unique locations out of the 189 total locations from the Kjær et al.[38] dataset. These locations were distributed across three biogeographical regions: Atlantic (n = 19), Boreal (n = 114), and Continental (n = 38). We obtained 1820 raw *I. ricinus* observations from the GBIF database in the area of interest, which were reduced to 836 after data cleaning. Following the exclusion of observations located in the alpine biogeographical region, the GBIF dataset was further refined to 809 observations, with 135 occurrences in the Atlantic, 547 in the Boreal, and 127 in the Continental biogeographical regions.

The GLMM identified statistically significant associations between nymph abundance and both ADD > 0°C and biogeographical regions (Table 1). In the Atlantic region, ADD > 0°C showed a positive association with nymph abundance (estimate = 0.001, p = 0.020), meaning that an increase of 1000 ADD > 0°C corresponds to an increase of 1 nymph in abundance. A similar positive association was observed in the Boreal region (estimate = 0.003, p = 0.006), although overall, the Boreal region was associated with lower nymph abundance than the reference Atlantic region (estimate = -5.949, p = 0.020). In contrast, the Continental region exhibited higher nymph abundance than the Atlantic reference (estimate = 8.659, p = 0.007) but showed a negative association with ADD > 0°C (estimate = -0.002, p = 0.010).

A graphical representation of the estimated relationship between nymph abundance and DD > 0°C is displayed in Fig. SM3 for each biogeographical region. Random effects analysis revealed significant variation in nymph abundance across different countries, with a variance of 0.058 and a corresponding standard deviation of 0.241.

The model performance metrics indicate that the conditional R-squared value, the proportion of the variance explained by the fixed and random effects, is 0.418. The marginal R-squared value, representing the variance explained by fixed effects alone, is 0.383. Additionally, the RMSE and MAE are 34.99 and 22.78, respectively, expressed in the number of individual nymphs. The observed Moran's I value was found to be 0.0224 (p = 0.2148) indicating that there is no significant global spatial autocorrelation in the residuals of the GLMM.

The linear regression model designed to identify the ADD > 0°C threshold values achieved an R-squared value of 0.555, with a significant intercept, which we interpret as the ADD > 0°C thresholds below which tick persistence is not possible, in each biogeographical region (Tab. 2). The Continental biogeographical region showed the highest ADD > 0°C threshold (3387 ADD > 0°C) followed by the Atlantic (2847 ADD > 0°C). The Boreal biogeographical region, instead, showed the lowest threshold equal to 2673 ADD > 0°C.

Table 1 Estimates of the fixed effects of the Generalized Linear Mixed Model showing the effects of annual Degree Days above 0°C (ADD > 0°C) and biogeographical regions on nymph abundance.

Predictor	Estimate (95% CI)	Std. Error	z value	p-value
Intercept (Atlantic)	-0.961 (-4.354, 2.431)	1.731	-0.555	0.579
ADD > 0°C	0.001 (0.000, 0.002)	0.001	2.319	0.020
Boreal	-4.988 (-9.187, -0.788)	2.143	-2.328	0.020
Continental	9.620 (2.619, 16.620)	3.572	2.693	0.007
ADD > 0°C:Boreal	0.002 (0.001, 0.003)	0.001	2.741	0.006
ADD > 0°C:Continental	-0.003 (-0.005, -0.001)	0.001	-2.566	0.010

Table 2 Linear Model identifying the ADD > 0°C threshold values; fixed effect estimates the tick nymph abundance and biogeographical regions on Degree Days above 0°C (ADD > 0°C).

Predictor	Estimate (95% CI)	Std. Error	z value	p-value
Intercept (Atlantic)	2847.436 (2698.286, 2996.587)	75.540	37.694	p < 0.01
NymphAbundance	6.995 (2.343, 11.647)	2.356	2.969	0.003
Boreal	-174.477 (-335.084, -13.871)	81.343	-2.145	0.03
Continental	539.915 (349.986, 729.845)	96.194	5.613	p < 0.01
NymphAbundance:Boreal	-3.935 (-8.910, 1.040)	2.520	-1.562	0.12
NymphAbundance:Continental	-6.711 (-11.609, -1.813)	2.481	-2.705	0.008

The sensitivity metric based on the *I. ricinus* GBIF observations scored 0.36 for the Atlantic region but was higher for the Boreal and Continental regions (0.83 and 0.60, respectively; Tab. 3 and Fig. 3A).

The model analysing the relationship between the median latitudinal difference between a given year and the reference year (1979) for each biogeographical region showed an R^2 of 0.39, and positive significant interaction terms for both the Atlantic and Boreal regions (Tab. 4). We focus only on the Boreal region as the threshold with the highest sensitivity values obtained using the GBIF data. Overall, in the period of interest, the Boreal DD > 0°C threshold moved north by 0.082 degrees of latitude/year (~9 km; Fig. 3B), corresponding to a northward shift of ~400 km between 1979 and 2020. The threshold isolines for the other regions are presented in Fig. SM4-5.

Table 3 Cumulative annual Degree Days > 0°C (ADD) thresholds for each biogeographical region and the sensitivity metrics for GBIF observations above (True positive) and below (False positive) the respective threshold.

Biogeographical regions	**ADD > 0°C Threshold (95% CI)**	**GBIF observations**	**GBIF ADD > 0°C median**	**True positives**	**False positives**	**Sensitivity (± SE)**
Atlantic	2852 (2703, 3002)	135	2745	49	86	0.363 (± 0.041)
Boreal	2673 (2363, 2983)	547	2997	455	93	0.832 (± 0.016)
Continental	3387 (3048, 3726)	127	3460	76	51	0.598 (± 0.044)

Table 4 Latitudinal differences estimated for Biogeographical Regions with Confidence Intervals and Statistical Significance.

Predictor	Estimate (95% CI)	Std. Error	z value	p-value
Intercept (Atlantic)	-87.885 [-137.066, -37.705]	25.357	-3.466	0.001
year	0.045 [0.02, 0.07]	0.013	3.540	0.001
Boreal	-75.317 [-146.282, -4.351]	35.860	-2.100	0.038
Continental	-26.909 [-97.875, 44.056]	35.860	-0.750	0.454
year:Boreal	0.038 [0.003, 0.073]	0.018	2.119	0.036
year:Continental	0.014 [-0.022, 0.049]	0.018	0.767	0.445

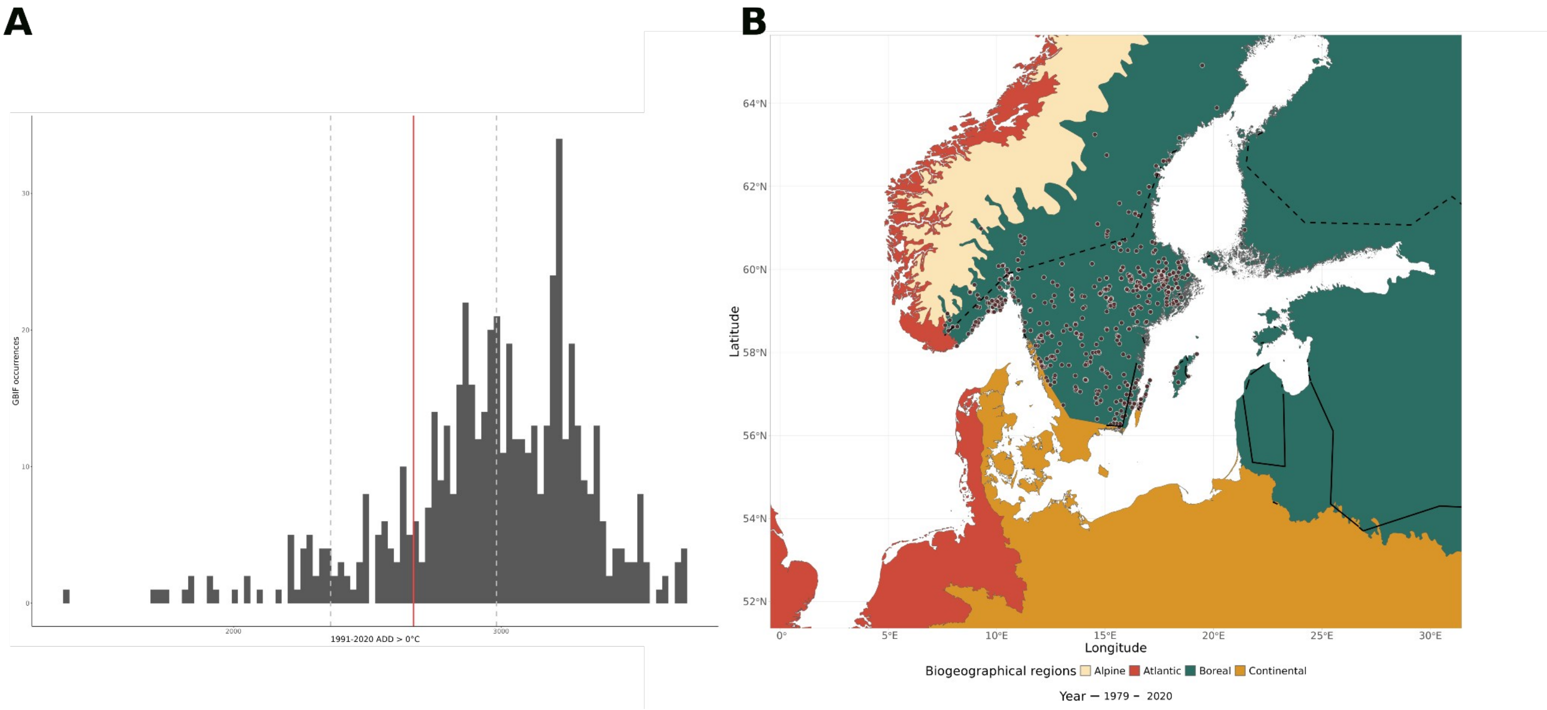

Figure 3 A) Distribution of GBIF occurrence over annual DD > 0°C (histogram) and ADD > 0°C threshold (red line; grey dashed lines represent the confidence interval) in the Boreal region and B) Mapped annual DD > 0° isoline threshold of the Boreal region for the reference years 1979 (full line) and 2020 (dashed line). Brown dots represent the GBIF observations for the Boreal biogeographical region only.

4. Discussion

In this study, we investigated the northward expansion of *I. ricinus* in relation to temperature changes over 40 years. By analysing the association of tick abundance with annual cumulative temperature (ADD > 0°C), we aimed to assess the role of rising temperatures observed since 1979 in shaping tick distribution. Our results show a northward expansion of the thermal limit for *I. ricinus* in Scandinavia over the past 40 years, corroborating observations of ticks in new areas [30,31,45–48]. We believe our estimate of range expansion is conservative compared to previous studies that based their conclusions on presence observations, which may not differentiate between ‘adventitious’ ticks that may represent ticks dispersed by migratory birds rather than the established populations from which they came[49], even though we did not account for other dimensions of habitat such as microclimate, vegetation and hosts[50].

We assessed whether temperatures are permissive for *I. ricinus* persistence using annual DD > 0°C, a useful index for understanding the effect of temperature on the tick life cycle (Ogden et al. [36]; reviewed in Ebi et al.[51]). Temperatures above 0°C determine development rates from one tick instar to the next, and thus the length of the tick life cycle, with warmer temperatures accelerating (to a point) development[1]. With a constant per capita daily mortality rate for ticks during non-parasitic phases, when ticks develop very slowly, populations cannot persist. A threshold temperature condition thus exists, below which the lifecycle is so long that the cumulative mortality means that the basic reproduction number of the tick is below unity[37]. Annual cumulative Degree Days > 0°C can thus be used to assess changes in temperature conditions over time that are of importance for *I. ricinus* population persistence. The focus on nymphs as the primary indicator of tick population establishment is supported, as larvae may be more difficult to identify and occur in clusters in the environment associated with the egg masses from which they hatched, while nymphs are more numerous than adults, and thus generally easier to collect.

Using a GLMM, we identified statistically significant relationships between nymph abundance, ADD > 0°C, and biogeographical regions, with significant interactions between biogeographical regions and ADD > 0°C. We thus proceeded to identify a temperature threshold for development, by geographical region, using a linear model (Fig. 1). Thresholds differed between regions, reflecting the challenge to capture a specific threshold through field-collected data, as well as the importance of factors to buffer temperature conditions. This was also found in Canada, where the temperature threshold for *I. scapularis* has been identified as a range, rather than a specific value[52]. This could relate to the genetic diversity of *I. ricinus* populations if this has an impact on temperature-dependent interstadial development rates (i.e. if life cycles are longer or shorter in different populations given the same temperature conditions), or results in differences in daily per-capita mortality rates. If daily per-capita mortality rates in the predominant habitats of biogeographic region A are higher than in the habitats of biogeographic region B, the threshold ADD > 0°C value for *I. ricinus* persistence will be higher in region A than in region B. While plasticity has been observed[53], what drives observed differences in host questing behaviour in ticks is not clear. Our threshold values are comparable to values identified for *I. scapularis* in Central and Eastern Canada[36].

Using our biogeographical region-specific thresholds, we found that the thermal limit identified for the Boreal region, which covers the greatest extent of our study area, progressed northward. In 1979, thermal conditions were unsuitable throughout Norway, most of Sweden, and Finland. In contrast, conditions are now suitable in the Boreal region from the southeastern shore of Norway to the southern and central regions of Sweden and the south of Finland, suggesting an overall northward shift of the limiting conditions of tick persistence of ~400 km over the 1979-2020 period. Our results are corroborated through a comparison with the proportion of GBIF observation recorded above this threshold (sensitivity = 0.83) and are coherent with other studies that have used similar approaches based on seasonal length[6,31] or climatic thresholds[54]. Mechanistic approaches assessing changes in the speed of tick development concluded that it increased substantially, in the Boreal region in particular, without identifying a threshold[55].

Further investigation into the Atlantic and Continental portion of our study area may confirm the validity of the estimated thresholds. Various reports exist confirming the recently observed presence of *I. ricinus* along the Norwegian coast[30,31,56], but the ruggedness of the coastline and the coarseness of the climate data employed here create challenging conditions for our methodology (Fig. SM5-7). Similarly, in the Continental region, no clear spatial patterns were observed (Fig. SM5, SM7). Nonetheless, we detected a positive latitudinal difference between each year and the reference year over the period of interest (Fig. SM6). Qualitatively, the areas with annual DD > 0 exceeding the respective threshold appeared to expand during the period 1979–2020 (Fig. SM7). It is important to consider the low sample size for this region, which could influence the robustness of observed trends. Furthermore, interannual fluctuations likely play a significant role in these patterns. Interestingly, the observed changes in threshold position over time, extending beyond our study areas, align with field observations, suggesting that the thermal limit has shifted mostly along an altitudinal gradient rather than a latitudinal one[25,57].

Several elements in our results (low effect size and no statistical validation) as well as in tick biology emphasise that while temperature is a key factor, other environmental variables shape the ecological niche of *I. ricinus*. Our assumptions focus on the role of temperature in accelerating development rates, but tick persistence relies on the presence of a diversity of habitat resources provided by vegetation cover and vertebrate hosts. In Scandinavia, complex relationships exist with host distribution[32], a factor that has also changed substantially across the European continent over the past century[58]. While humidity may not be the limiting factor in the Boreal region, precipitation regimes may also affect tick habitat suitability[59]. Complex interactions exist between all habitat dimensions at various spatial and temporal scales that still remain to be fully established. Understanding the long-term effects of environmental changes will require understanding the complex interactions of habitat factors.

The lack of long-term data series remains a significant challenge for studying the effects of environmental change such as climate change, as long-term data are needed to better understand the mechanisms driving tick population dynamics. This lack of data could explain the limited validation observed in our findings using GBIF data. The potential biases associated with passive surveillance and citizen science and science methods also challenge the use of GBIF data for model validation[60] as GBIF data may include non-established ticks. It is possible that spuriously low ADD > 0°C thresholds (or spuriously variable thresholds amongst biogeographic regions) could be obtained from GBIF data if numerous observations of adventitious ticks are included. Such observations could be ticks dispersed northwards by migratory birds into locations where habitat allows survival over one winter and moulting followed by questing and host finding, but where temperature conditions are too cold for the tick to complete its life cycle[36].

Our results highlight the importance of standardised abundance and longitudinal data, as demonstrated by the VectorByte (https://www.vectorbyte.org/) platform and the VectAbundance database[61]. While promoting open data, these resources enhance modelling reliability and contribute to better public health preparedness by providing standardised, high-quality datasets that allow for more accurate analysis of vector population dynamics.

5. Conclusion

We found that the northern temperature limit for *Ixodes ricinus* has moved northward by about 400km in the Boreal region since 1979, corroborating much circumstantial evidence that this pathogen vector has been observed in recently colonised habitat. Like other species, there are other features of the European climate that matter for *I. ricinus* ticks, such as extremes in temperature and changes in precipitation distribution across the seasons, and other ecological variables, such as host distribution and abundance, but here we focus on the effect of gradual temperature increase at the northern limit range. Our method made use of nymphal abundance data collected over a large area in a robust fashion and climate data reanalysis. While our thresholds were not designed as a predictive tool and should not be used as such given the low sample size of the dataset employed, they shed striking light on the changes in thermal suitability in the north of Europe.

6. References

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Supplementary materials of

Northward expansion of the thermal limit for the tick *Ixodes ricinus* over the past 40 years

Daniele Da Re[1,2,3,*], Gaëlle F. Gilson[1], Quentin Dalaiden[1,4],
Hugues Goosse[1], René Bødker[5], Lene Jung Kjær[5],
Roberto Rosà[2], Nicholas H. Ogden[6,7,8], Sophie O Vanwambeke[1,*].

[1]Center for Earth and Climate Research, Earth & Life Institute, UCLouvain, Louvain-la-Neuve, Belgium

[2]Center Agriculture Food Environment, University of Trento, San Michele all' Adige, Italy

[3]Research and Innovation Centre, Fondazione Edmund Mach. San Michele all'Adige, Trento, Italy

[4]Nansen Environmental and Remote Sensing Center and Bjerknes Center for Climate Research, Bergen, Norway

[5]Department of Veterinary and Animal Sciences, Faculty of Health and Medical Sciences, University of Copenhagen, Denmark

[6]Public Health Risk Science Division, National Microbiology Laboratory Branch, Public Health Agency of Canada, Canada

[7]Groupe de recherche en épidémiologie des zoonoses et santé publique, Faculté de médecine vétérinaire, Université de Montréal, St-Hyacinthe, QC, Canada

[8]Centre de recherche en santé publique, Université de Montréal, QC, Canada

***Corresponding authors**: daniele.dare@fmach.it,

sophie.vanwambeke@uclouvain.be

Supplementary materials

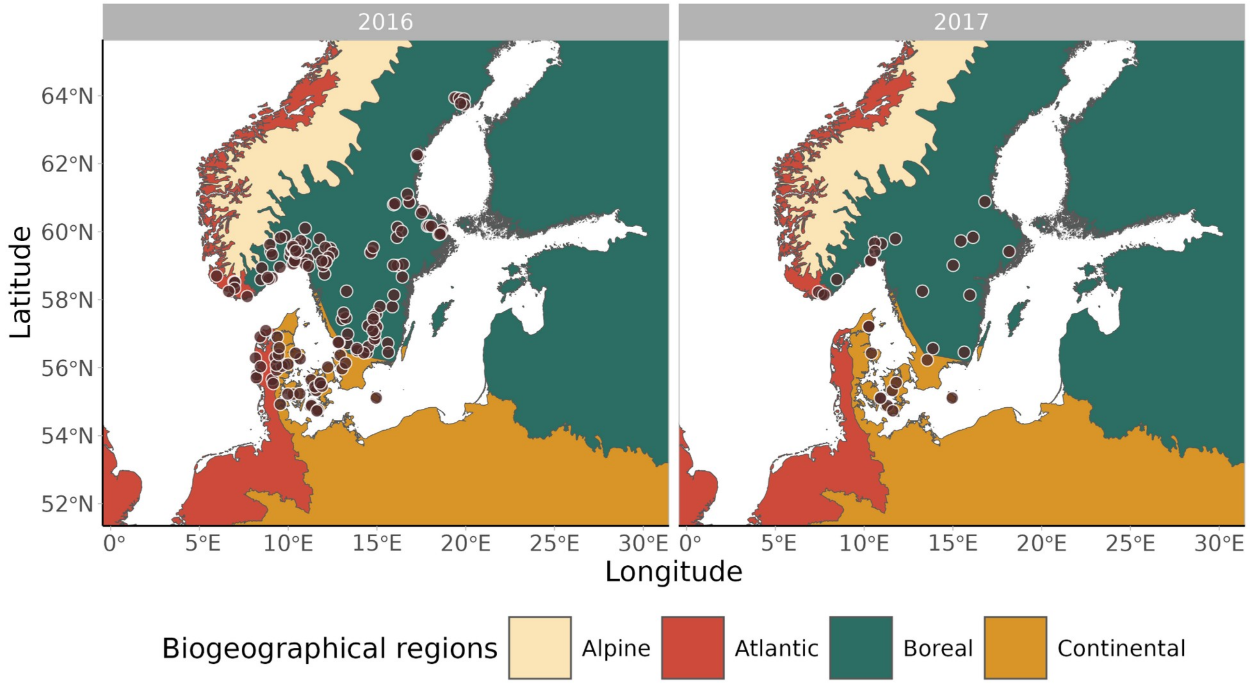

Figure SM1: Biogeographical regions of Europe according to Cervellini et al., (2020) in the area of interest and the location (brown dots) of the locations sampled in 2016 and 2017.

Table SM2: Contingency table of the observations broken down by country and biogeographical region.

	Denmark	Norway	Sweden
Atlantic	9	10	0
Boreal	0	-	73
Continental	32	0	6

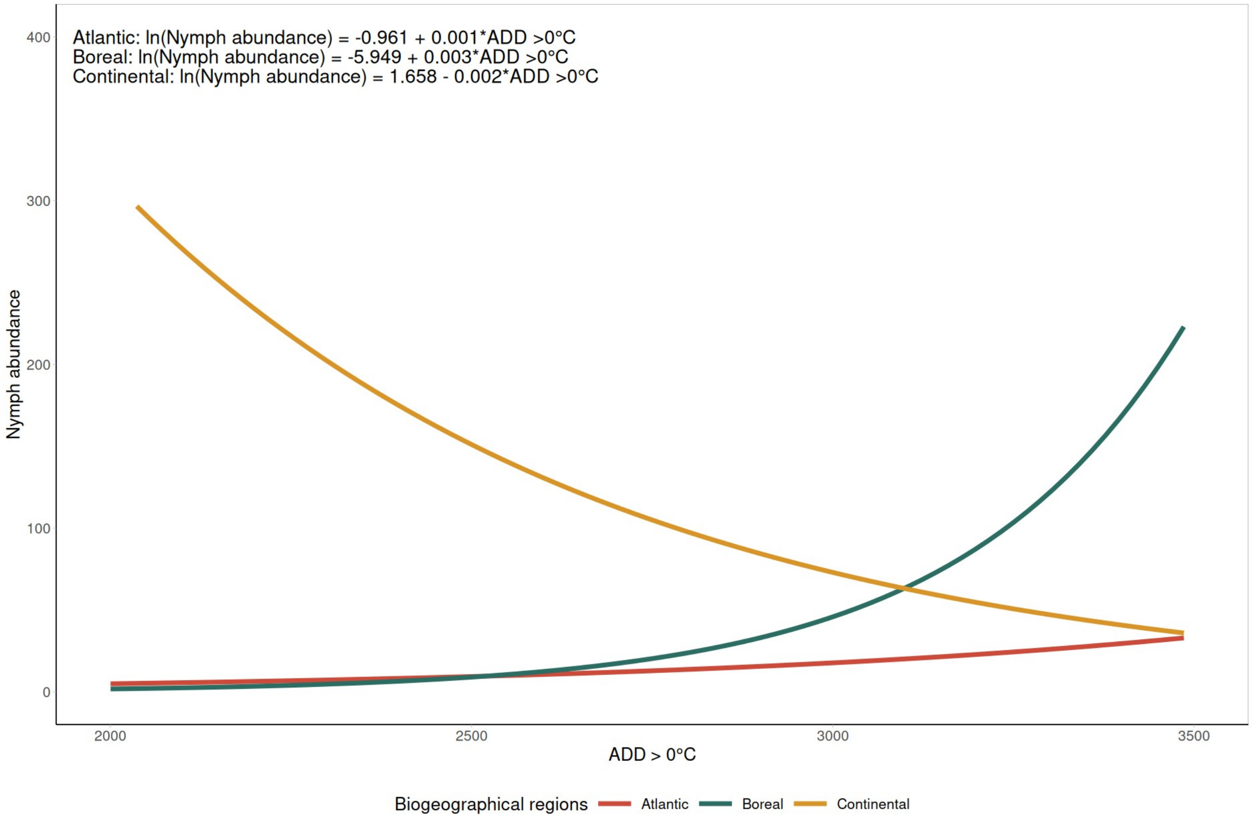

Figure SM3: Relationships between the *Ixodes ricinus* nymph abundance and the annual degree days > 0°C (ADD) for each biogeographical region as estimated by the generalised linear mixed model defined in Eq. 1.

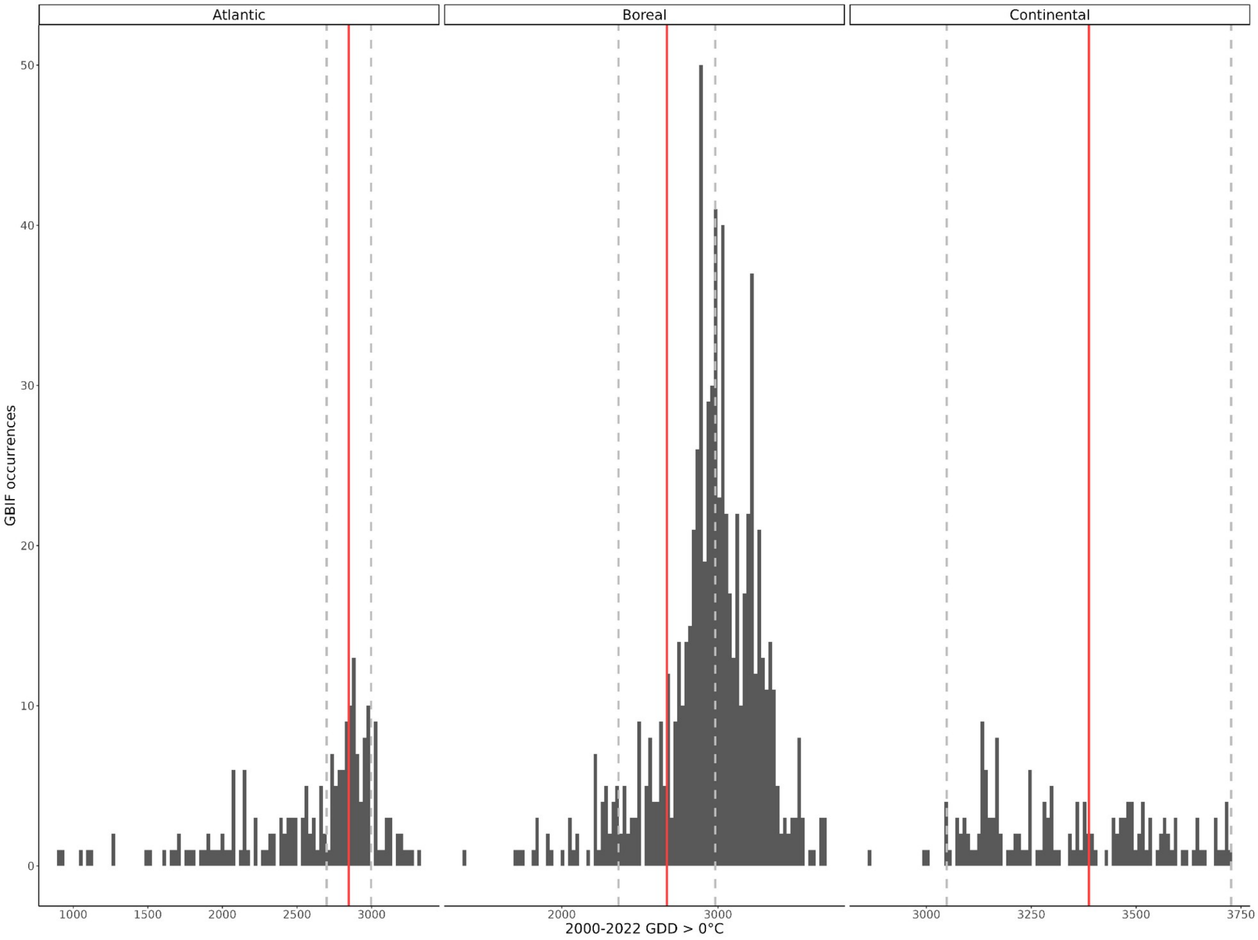

Figure SM4: Distribution of GBIF occurrence over annual DD > 0 °C (histograms) and annual DD > 0 °C threshold (red line; dashed grey lines represent the confidence interval).

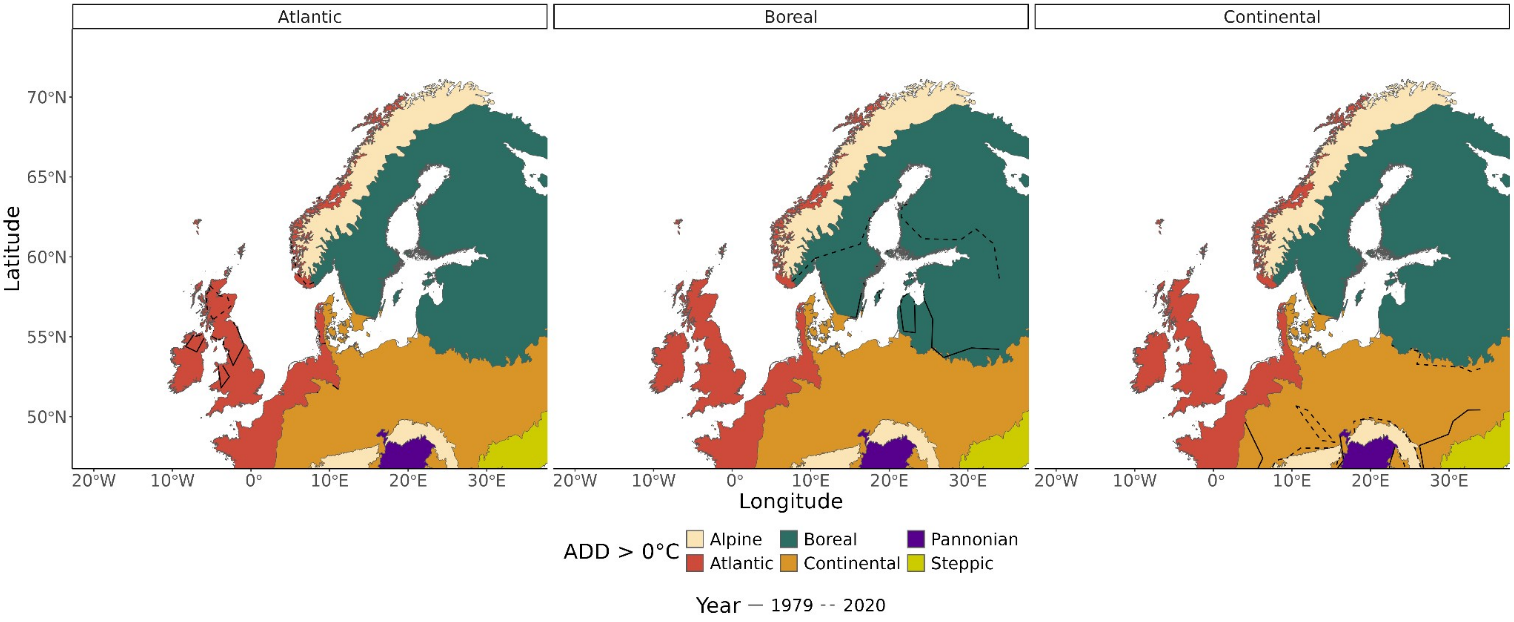

Figure SM5 Mapped annual DD > 0 °C isolines thresholds across a larger portion of continental and northern Europe for the reference years 1979 and 2020.

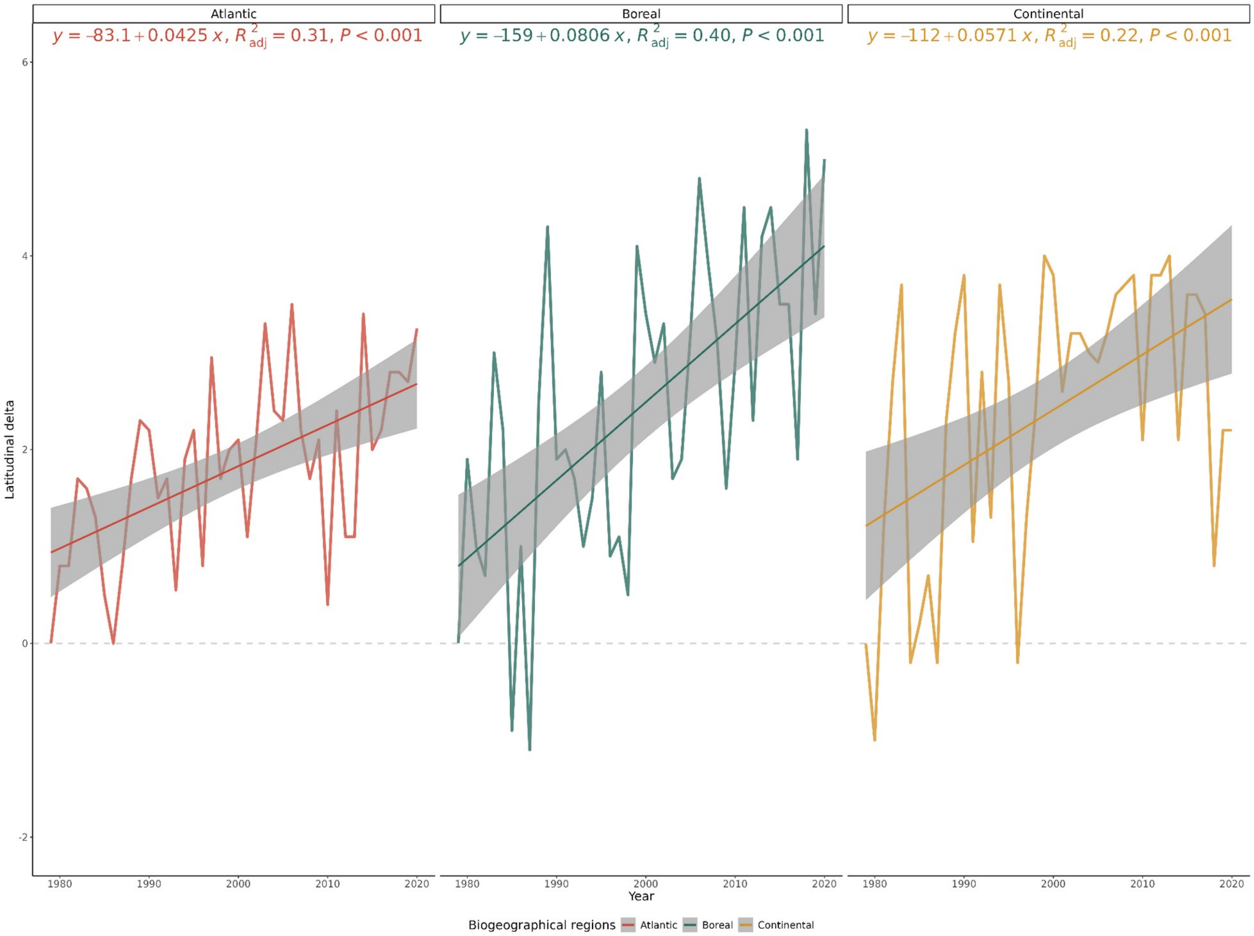

Figure SM6 Variability of the Latitudinal delta between each year and the reference year 1979 in each biogeographical region.

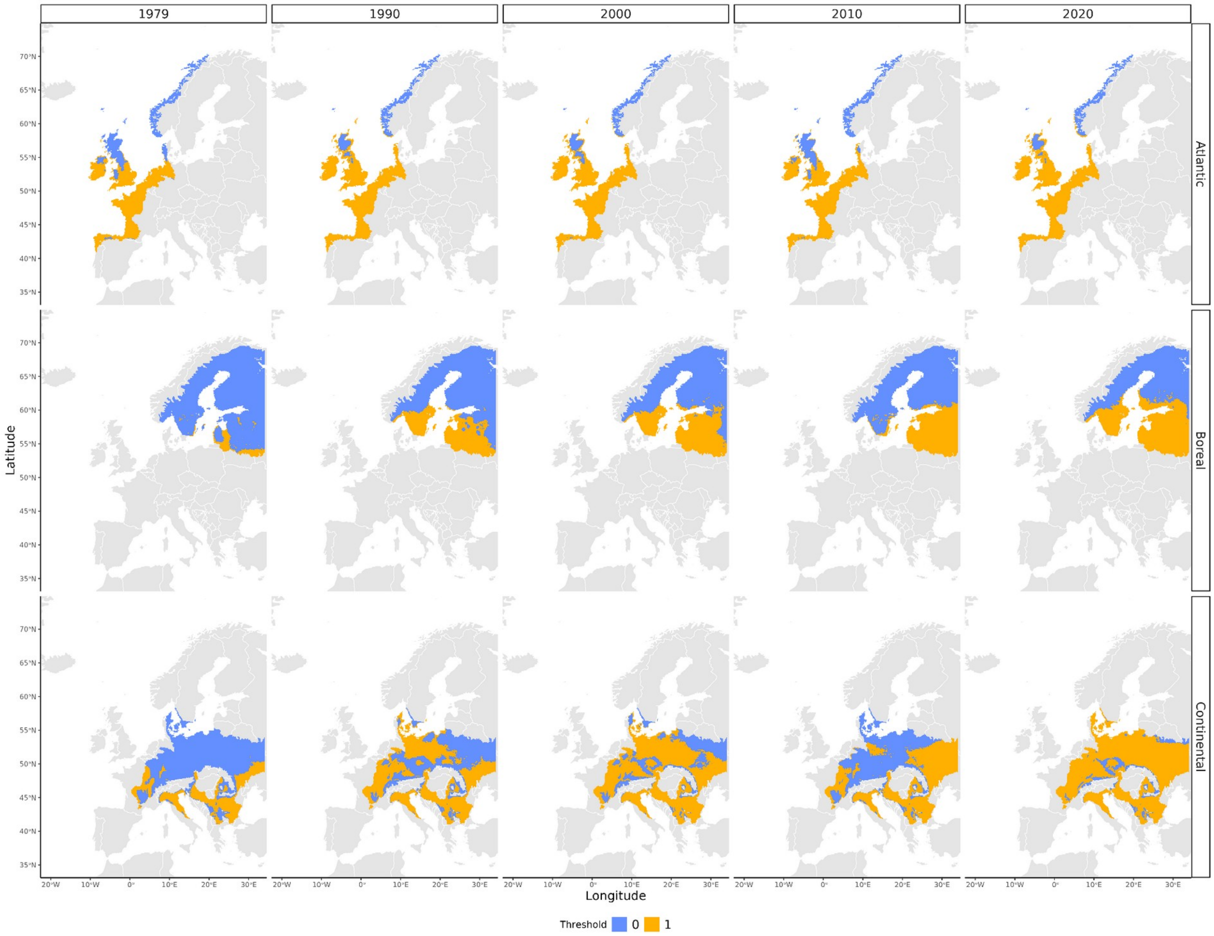

Figure SM7 Areas of Europe with annual Degree Days > 0°C values exceeding the thresholds for the three biogeographical regions (rows) and five reference years (columns): 1979, 1990, 2000, 2010, and 2020.