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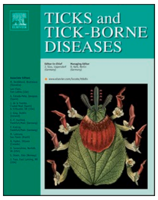

Original article

Tick hazard in a Central European country: Mapping Europe’s principal tick-borne disease vector across Germany

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ABSTRACT

The most common European tick species, *Ixodes ricinus,* is the principal vector of *Borrelia* and tick-borne encephalitis virus and several other pathogens of public health relevance in Europe. Comprehensive data on tick abundance and the underlying ecological drivers are crucial for developing awareness and control strategies and to assess future changes in tick-borne disease risk. We aimed to provide a Germany-wide map of *I. ricinus* abundance to aid in disease transmission risk assessment. During 2018–2020, questing tick density was assessed at 83 sites across the whole country by drag flagging, whereby 49,344 *I. ricinus* nymphs and adults were collected. Relationships between climate, land cover, and monthly questing *I. ricinus* nymph density were explored and used to draw an abundance map. Highest tick hazard was observed in areas near the coast with mild winters and moist springs, and in mid-elevation mountain ranges, which represent popular tourist destinations. The ticks’ seasonal activity pattern was predominantly unimodal. The fact that the observed regional differences are contradictory to a previous estimation based on a combination of regional studies illustrates the need for an extensive and coordinated sampling effort to reliably estimate tick abundance at larger spatial scales. Combined with data on tick-borne pathogens, our study enables estimating the density of infected ticks and consequently the risk of acquiring an infectious tick bite. Moreover, the observed relationships with climate and land cover can help to predict future developments of tick hazard under different climate scenarios in Central Europe.

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1. Introduction

Ticks are of global importance due to their vector function for various human- and animal-pathogenic viruses, bacteria and protozoa. In Europe, *Ixodes ricinus* is the most widespread and the most relevant tick species from a One Health perspective (Rizzoli et al., 2014). Pathogens transmitted by *I. ricinus* include, but are not limited to, tick-borne encephalitis virus (TBEV), the *Borrelia burgdorferi* sensu lato (s.l.) complex causing Lyme borreliosis, the relapsing-fever spirochaete *Borrelia miyamotoi, Anaplasma phagocytophilum*, other Rickettsiales, and several *Babesia* species (Sprong et al., 2018). Infections with these pathogens are considered (re-)emerging and constitute a considerable societal burden (Mac et al., 2019; Rizzoli et al., 2014; Semenza and Suk, 2017). For example, is has been estimated that 24 % of the European population lives in areas of high Lyme disease incidence (Burn et al., 2023).

To assess the risk of tick-borne pathogen exposure and to develop appropriate awareness and control strategies, data on the geographic distribution and prevalence of these pathogens need to be combined with data on vector abundance (Eisen et al., 2010; Hönig et al., 2019). For Germany, reliable data on *I. ricinus* abundance on a national scale are lacking, as previous studies were primarily conducted on a regional level, with a focus on southern Germany (e.g. Boehnke et al., 2015; Schulz et al., 2014). Extrapolation of *I. ricinus* abundance to a country-wide scale by combining data from different regional studies has been attempted, but suffered from challenges due to the different methodologies and sampling periods of the available studies and the lack of data from northern Germany (Brugger et al., 2016). Supra-regional data on tick abundance, collected in a standardised manner during the same time frame, are highly desirable to identify explanatory factors and to serve as a baseline for predicting future changes in tick-borne disease (TBD) risk (Diuk-Wasser et al., 2010; Kjær et al., 2019).

Ixodes ricinus is a generalist tick, occurring in many different habitats such as forests, heathland, pastures, ecotones, and urban green spaces (Kahl and Gray, 2023). Temperature and relative humidity are regarded as the principal abiotic factors influencing off-host development, survival, and host-seeking activity (Gray, 1998). These abiotic factors are dependent on regional climate, but are additionally modulated by local vegetation (Ehrmann et al., 2017). Moreover, land cover and land use may affect the density and species composition of tick hosts and thereby tick survival and reproductive success (Diuk-Wasser et al., 2020). While data on host density are often difficult to obtain, climatic and land cover data are readily available on a national scale, e.g. provided by national meteorological services and the European Commission's Coordination of Information on the Environment (CORINE) programme, and are commonly considered predictors when modelling and mapping tick abundance (e.g. Kjær et al., 2019; Li et al., 2012; Wongnak et al., 2022).

The present study was designed for two objectives: First, to provide data on *I. ricinus* abundance and seasonal activity patterns throughout Germany in order to identify regional differences and explore ecological drivers, and second, to create a Germany-wide map of relative *I. ricinus* nymph abundance to aid in TBD transmission risk assessment and highlight areas of potentially high risk. Over a period of three years, from 2018 to 2020, ticks were collected monthly from February to November by standardised drag flagging at more than 80 sample sites. Generalized linear mixed models (GLMMs) were applied to this monthly dataset to identify drivers of temporal, local and regional variation. Building on the obtained insights, appropriate long-term climatic means and land cover data were used to extrapolate nymph density to a country-wide scale by generalized additive modelling (GAM).

2. Materials and methods

2.1. Sample site selection

Twenty-eight collection areas with two to four collection sites each were selected between autumn 2017 and spring 2018. Sites were chosen according to the criteria listed in the Supplementary Methods, representing different CORINE land cover (CLC) classes, if possible. The following classes were considered: broad-leaved forest (B), coniferous forest (C), and mixed forest (M), while anthropogenically influenced areas were summarized as "agriculture" (A) (e.g. arable land, permanent crops, pastures) or "urban" (U) (artificial surfaces; e.g. urban fabric, green urban areas, sport and leisure facilities), respectively. Within agricultural or urban areas, tick collection sites were chosen e.g. within pastures, forest fragments, or parks, since *I. ricinus* does not occur on cultivated fields or paved areas.

Initially, 83 sites were chosen (Fig. 1, Supplementary Table S1). In spring 2019, ten sites had to be moved or replaced, either due to the absence of ticks, changes in accessibility, or extreme weather conditions, e.g. a heavy storm, that made the sites inoperable. The "old" and "new" locations, up to 2 km apart, were treated as separate sites in modelling analyses, resulting in a total of 93 sites.

2.2. Tick collection and morphological identification

Sampling was conducted by seven different teams, each responsible for 2–21 sites. Ticks were collected monthly from February to November in 2018–2020 by drag flagging 100 m^2 per visit using a standardized protocol (Supplementary Methods). At one site (Hasenhaege [SN1]), 120 m^2 were sampled each time to account for the vegetation characteristics (40 m^2 each in a stand of spruce, a stand of lark, and a stand of pine). For all further analyses, tick density at this site was corrected to an area of 100 m^2.

Nymphs and adult ticks were collected and stored in vials, while larval questing was only semi-quantitatively rated as absent, low, or high. Adult and nymphal ticks were identified to species level according to published keys (Estrada-Peña et al., 2017; Nosek and Sixl, 1972).

2.3. Analysis of regional differences in tick density and life stage distribution

Previous research has shown that Germany can be divided into different climate area types based on data from the climate reference period 1971–2000 (Crespi et al., 2023). Accordingly, three regions were defined for the purpose of this study: region 1 covering the coastal and north-western part of Germany, region 2 representing the driest region in eastern Germany, and region 3 covering the south of Germany (Fig. 1A).

The mean density per 100 m^2 of questing *I. ricinus* nymphs and adults was calculated for the different regions and land cover classes. Regional differences in questing nymph density were assessed in the frame of multivariable analyses to identify environmental drivers (see below), while a meaningful multivariable approach was not possible for adult ticks due to their low density. However, the ratio of nymphs to adult ticks may reveal important insights into tick population dynamics, as the stages represent different tick generations and differ in their response to environmental conditions. Therefore, monthly, regional, and land cover class differences in the nymph:adult ratio were assessed by Kruskal-Wallis tests for each sampling year, followed by Dunn's test with Bonferroni-Holm correction of *P*-values.

2.4. Assessing environmental drivers of questing *I. ricinus* nymph density

Factors correlating with monthly questing nymph density were investigated using negative binomial generalized linear mixed models (GLMMs) in R v. 4.2.1 (R Core Team, 2022). Besides sampling year and month, land cover class, elevation, and meteorological variables were considered as fixed factors, while collection site ID nested in collection area and sampling team were included as random effects.

Meteorological data from the nearest weather station of each collection site were retrieved from the German Meteorological Service [Deutscher Wetterdienst] (2022), and used to calculate mean

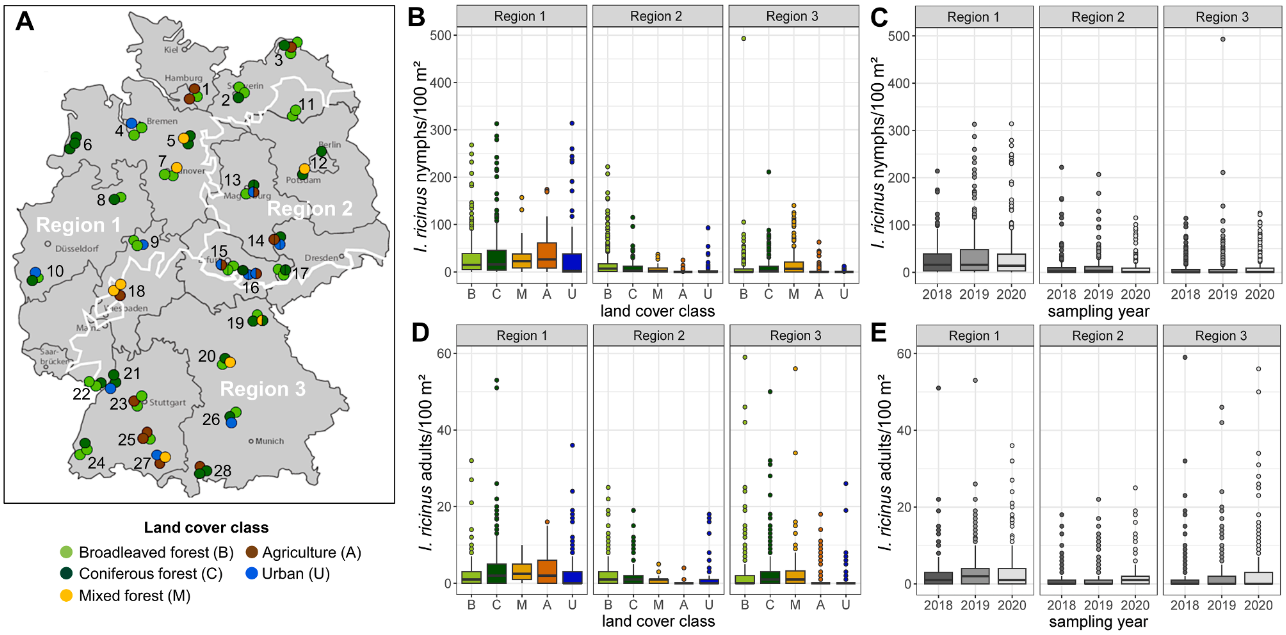

Fig. 1. Map of Germany showing the distribution of tick collection sites (A) and variation in questing nymphal (B, C) and adult (D, E) *Ixodes ricinus* density per 100 m^2 in the three different regions according to land cover class and sampling year. Regions represent climatic regions based on Kahlenborn et al. (2021). The map was created using Mapbox Studio (San Francisco, USA). The following areas were included: 1: Hamburg, 2: Schwerin, 3: Stralsund, 4: Bremen, 5: Uelzen, 6: Emsland, 7: Hanover, 8: Bielefeld, 9: Kassel, 10: Euskirchen, 11: Mecklenburgische Seenplatte, 12: Berlin, 13: Magdeburg, 14: Leipzig, 15: Erfurt, 16: Jena, 17: Chemnitz, 18: Giessen, 19: Kulmbach, 20: Erlangen, 21: Karlsruhe, 22: Suedpfalz, 23: Stuttgart, 24: Emmendingen, 25: Reutlingen, 26: Schrobenhausen, 27: Biberach, 28: Ostallgaeu.

temperature, mean relative humidity, mean soil moisture, the sum of precipitation as well as the number of frost days, ice days, days with snow cover, hot days, and rain days for different time frames: the 10-day window preceding each tick collection date, the preceding winter half-year, the previous year's spring, and previous year's summer. Details on the definition of these variables are shown in Supplementary Table S2. As weather stations were located at some distance of the tick collection sites, elevation may explain additional variation and was therefore also included.

Models were calculated for the entire dataset, including region as a fixed factor, as well as separately for the three different climatic regions. Two sets of models were fitted, differing in the assignment of collection area no. 11 (Figure 1/Supplementary Table S1) to climatic region 1 or 2, respectively. Based on the map of climatic regions (Crespi et al., 2023), this area would belong to region 2 (the driest region in the east), however, rather high tick numbers were encountered there, similar to results from region 1. Therefore, we explored whether assigning this area to region 1 would fit the data better. Model fitting and model selection procedures are described in detail in the Supplementary Methods.

2.5. Modelling Germany-wide relative abundance of I. ricinus

To generate a map of relative *I. ricinus* abundance for Germany, a generalized additive modelling (GAM) approach was employed in R v. 4.2.1 (R Core Team, 2022). As response variable, the mean questing nymph density per 100 m^2 during April to June, i.e. during the peak of *I. ricinus* nymphal and adult activity, was calculated per site. Sites visited only in a single year (due to changes in collection sites) were excluded, resulting in 83 locations used for predictive modelling. Preparation of environmental datasets is described in detail in the Supplementary Methods. Based on the GLMM results, the CLC class, elevation and multi-annual (1991–2020) means of the following climatic predictor variables were explored: winter temperature, number of frost and ice days, number of days with snow cover, spring temperature, annual precipitation, spring precipitation, spring soil moisture, annual drought index, and actual evaporation during April–June. Correlations between these variables were evaluated based on variance inflation factors (VIF), which were estimated using the usdm::vif function (Naimi et al., 2014). Variables with VIF exceeding ten were removed manually in a stepwise manner, whilst considering their ecological relevance, i.e. where several variables exceeded the VIF threshold, the least ecologically relevant were removed first, and VIF reassessed.

The mgcv R package (Wood, 2011) was used for implementation of GAMs with negative binomial error distribution, which were subjected to spatial and random cross-validation as detailed in the Supplementary Methods. The best-performing model was then fitted to the entire dataset and used to create a Germany-wide map of predicted questing nymph densities/100 m^2.

3. Results

3.1. Collected ticks

Between 2018 and 2020, 2,422 of 2,490 planned excursions took place, while 68 excursions were cancelled due to unsuitable weather (e.g. snow cover), inaccessibility of collection sites (e.g. due to flooding), or operational constraints. The total area flagged per year amounted to 78,100 m^2 in 2018, 82,400 m^2 in 2019, and 82,300 m^2 in 2020. A total of 50,064 ticks was collected (Table 1). As expected, *I. ricinus* was the most

Table 1
Species and stage distribution of ticks collected by flagging in a Germany-wide tick abundance study during the years 2018–2020.

Species	Nymphs	Females	Males	Total
Ixodes ricinus	43,676	2,747	2,921	49,344
Ixodes frontalis	32	1	1	34
Ixodes festai	0	1	1	2
Dermacentor reticulatus	0	351	282	633
Dermacentor marginatus	0	32	19	51
Total	43,708	3,132	3,224	50,064

abundant species representing 98.6 % of all collected ticks (49,344/50,064), 99.9 % of nymphs (43,676/43,708), and 89.2 % of adult specimens (5,668/6,356). The second most frequent species was *Dermacentor reticulatus* (1.3 %; 633/50,064), representing 10.0 % of adult ticks (633/6,356). All further analyses refer exclusively to *I. ricinus*.

3.2. I. ricinus density and life stage distribution according to land cover class, region, and year of sampling

Across Germany, questing *I. ricinus* nymphs and adults were encountered at higher average densities in broad-leaved, coniferous, and mixed forests as compared to agricultural and urban collection sites (Table 2). Moreover, the average density of questing nymphs was approximately threefold higher in region 1 than at more eastern (region 2) and southern (region 3) sites. The regional difference in questing nymph density applied to all land cover classes and remained consistent across years, while regional differences in the density of adult ticks were less pronounced (Fig. 1B and D, Table 2). The nymph:adult ratio was calculated for each combination of collection site, month, and year (Supplementary Figure S1), except for six sites in 2018, seven sites in 2019, and three sites in 2020, as no nymphs were collected at these sites in the respective year. Significant monthly differences in the nymph:adult ratio were observed in 2018 and 2020, but not in 2019 ($\chi^2 = 35.6/15.4/34.8$, df = 9, $P < 0.001/= 0.081/< 0.001$). In 2018, the nymph:adult ratio was significantly higher in April–June compared to November, and in July compared to April (Bonferroni-Holm corrected *P*-values all < 0.05). In 2020, the ratio was significantly higher in April–May compared to August and October (Bonferroni-Holm corrected *P*-values all < 0.05). The nymph:adult ratio also differed significantly between the regions in all sampling years ($\chi^2 = 11.2/23.8/23.8$, df = 2, *P*-values all < 0.05), with significantly lower values at collection sites in region 3 than in region 1 (Bonferroni-Holm corrected *P*-values all < 0.05; Fig. 2, Supplementary Figure S1). Additionally, a significantly lower nymph:adult ratio was observed in region 3 vs. region 2 in 2019 (Bonferroni-Holm corrected $P = 0.001$) and in region 2 vs. region 1 in 2020 (Bonferroni-Holm corrected $P = 0.021$). In contrast, no significant differences were observed between nymph:adult ratios of the different land cover classes in either year ($\chi^2 = 5.5/4.2/5.9$, df = 4, $P = 0.239/0.382/0.206$).

Seasonal patterns of questing *I. ricinus* nymph density at each collection site across the study period are illustrated in Fig. 3, while separate graphs for each land cover class are available as Supplementary Figures S2–S6. Seasonal patterns were highly variable between sites, but the predominant pattern was unimodal, with a peak between March and June, while a potential bimodal pattern with a smaller autumn peak only occurred at few sites (areas 4, 11, 15, 17, 19 in Fig. 3) and was not consistent across years. At a few collection sites in south-western Germany, where questing nymph density was generally rather low, higher nymph activity in the autumn compared to spring of 2020 was observed (areas 21, 23, 24 in Fig. 3).

3.3. Environmental drivers of questing I. ricinus nymph density

After exclusion of some sampling events due to missing meteorological data, the dataset analysed by GLMMs included 2,392 monthly observations from 93 collection sites, accounting for the relocation of ten sites in spring 2019. The final model for all sites contained the predictors region, sampling year, sampling month, land cover class, elevation, and several meteorological variables (Table 3). Although mean temperature and saturation deficit on the collection day as well as mean temperature and the number of snow days during the preceding winter half-year were highly correlated (Pearson ρ of 0.81 and -0.78, respectively), they were each retained in the final model based on their relevance for *I. ricinus* biology, as all VIFs were below ten, indicating no collinearity issues. Significant differences were observed between regions 1 and 2, sampling years, sampling months, and land cover classes, with significantly lower questing nymph densities in agricultural and urban areas as compared to broadleaved forests. Mean temperature on the sampling date, during the ten days before sampling, and during the previous year's spring showed a significant non-linear relationship with nymph density (Fig. 4). Precipitation during the ten days before sampling, as well as mean soil moisture during the previous spring were significantly positively correlated with questing nymph density, while soil moisture on the sampling date had the opposite effect (Table 3, Fig. 4). Regarding the preceding winter half-year, the number of days with snow cover was positively associated with nymph density, while neither mean winter temperature nor frost or ice days showed a significant effect (Table 3). Assigning area no. 11 to region 1 instead of region 2 resulted in a similar model, except for an additional significant difference between regions 1 and 3 and an additional significant effect of spring precipitation (Supplementary Table S3). Both models showed a similar fit to the data (AICc of 13,933.7 vs. 13,931.3). Either model explained 72 % of the variation (conditional R^2_{GLMM}), with 53 % explained by the fixed factors (marginal R^2_{GLMM}).

The models for the three different climatic regions, based on 878, 567, and 947 observations, respectively, revealed interesting differences, although sampling month, land cover class, mean temperature on the sampling day and during the ten days before sampling were significant predictors in all three regions. Elevation became non-significant in the regional models, as did the mean temperature during the previous year's spring (Table 3). When area no. 11 was included in region 1, however, the model indicated a significant effect of elevation in both

Table 2
Total number of collected nymphal and adult *I. ricinus* and their mean density per 100 m² according to the different land cover classes and climatic regions in Germany during 2018–2020.

Category (no. of collection sites)	*I. ricinus* nymphs		*I. ricinus* adults		*I. ricinus* total		Percentage of nymphs/adults
	total no.	mean density/100 m² (min.-max.)	total no.	mean density/100 m² (min.-max.)	total no.	mean density/100 m² (min.-max.)	
Land cover class							
Broadleaved forest (31)	17,472	19.88 (0 – 493)	1957	2.23 (0 – 59)	19,429	22.10 (0 – 535)	89.93/10.07
Coniferous forest (27)	14,111	19.10 (0 – 313)	2072	2.82 (0 – 53)	16,183	21.90 (0 – 366)	87.20/12.80
Mixed forest (8)	4,591	21.86 (0 – 157)	606	2.89 (0 – 56)	5197	24.75 (0 – 165)	88.34/11.66
Agriculture (14)	4,194	12.59 (0 – 174)	486	1.46 (0 – 18)	4680	14.05 (0 – 184)	89.62/10.38
Urban (13)	3,308	11.94 (0 – 314)	547	1.97 (0 – 36)	3855	13.92 (0 – 350)	85.81/14.19
Climatic region							
Region 1[a] (30)	28,837	32.12 (0 – 314)	2667	2.97 (0 – 53)	31,504	35.09 (0 – 366)	91.53/8.47
Region 2[b] (29)	6,363	11.16 (0 – 222)	925	1.62 (0 – 25)	7288	12.79 (0 – 240)	87.31/12.69
Region 3[c] (34)	8,476	8.79 (0 – 493)	2076	2.15 (0 – 59)	10,552	10.95 (0 – 535)	80.33/19.67

[a] Region 1: coastal and north-western Germany.
[b] Region 2: eastern Germany.
[c] Region 3: southern Germany.

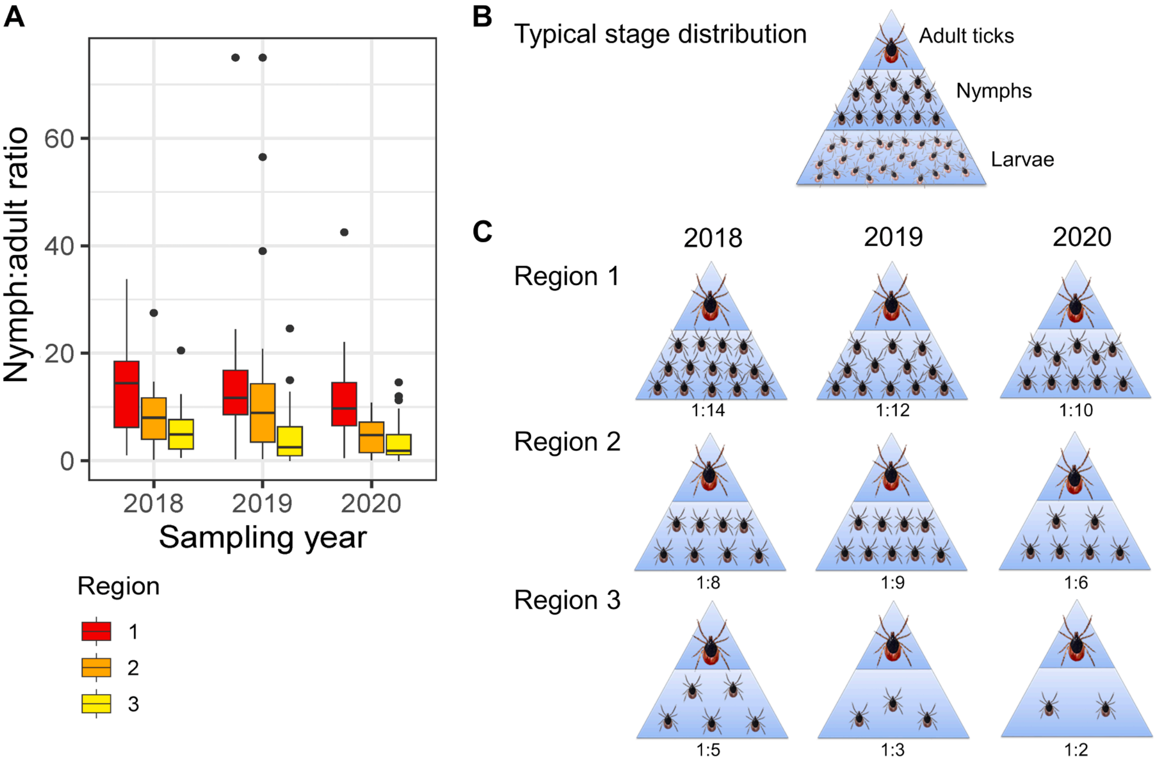

Fig. 2. Variation in the *Ixodes ricinus* nymph:adult ratio according to region and sampling year (A). The pyramid in panel B illustrates the typical stage distribution, while pyramids in panel C visualize the median nymph:adult ratio per region and study year.

region 1 and 2 (Supplementary Table S3).

In regions 1 and 3, no significant annual differences were observed, while in region 2, nymph density was significantly higher in 2019 vs. 2018, but only when area no. 11 was assigned to region 2 (Table 3).

Urban areas had significantly lower nymph densities than broad-leaved forests in all three regions, while agricultural areas additionally showed significantly lower densities in regions 2 and 3. Mean saturation deficit on the sampling day was only significant in region 1, with higher values associated with lower nymph densities, and was excluded from regional models 2 and 3. Soil moisture on the sampling date was significantly negatively associated with nymph density in regions 1 and 2, but not in region 3. Mean soil moisture during the previous spring was a significant predictor in regions 1 and 3, while no correlation with the previous spring's climate was apparent in region 2. The effect of mean winter temperature was mediated by land cover class, with different relationships in the three regions (Table 3).

The three regional models also differed considerably regarding the amount of variance explained (conditional R^2_{GLMM}), which was higher in regions 1 and 2 (83 and 88 %, respectively) than in region 3 (51 %). The amount of variance explained by the fixed factors (marginal R^2_{GLMM}) amounted to 53 % in region 1, to 53–60 % in region 2 (depending on whether area no. 11 was included), and to 38 % in region 3.

3.4. *Germany-wide relative abundance of I. ricinus*

The final selection of environmental variables used to predict *I. ricinus* abundance across Germany included land cover, and 30-year averages of winter temperature, spring temperature, and spring soil moisture. Correlation coefficients among these variables ranged between 0.07 (CLC ~ spring soil moisture) and 0.74 (winter temperature ~ spring temperature), and VIF ranged between 1.7 and 2.7. Random cross-validation showed adequate model performance, with a mean Spearman rank correlation coefficient between predicted and observed values of 0.61 (range: 0.50–0.80) and mean absolute deviance of 26.74 nymphs/100 m^2 (range: 16.73–37.37). Correlations were slightly lower in spatial block cross-validation, with a mean correlation coefficient of 0.55 (range: 0.39–0.74), and mean absolute deviance of 27.16 nymphs/100 m^2 (range: 16.34–42.55). Partial effects plots and observed vs. predicted values for the final model (Spearman's $\rho = 0.74$) are shown in Fig. 5. The model predicted high average questing nymph densities for regions near the coast and mid-elevation mountain ranges, while lower nymph densities were estimated in eastern and in many parts of southern Germany (Fig. 6A), with low standard errors of predictions except for some regions in the high mountain ranges (Fig. 6C).

4. Discussion

The goal of this extensive three-year field study was to provide a Germany-wide map of *I. ricinus* abundance to support public health risk assessment and development of counter-strategies against TBDs. More than 80 collection sites were visited over the course of three years – an unprecedented sampling effort compared to previous studies on tick abundance (Diuk-Wasser et al., 2010; Ehrmann et al., 2017; Wongnak et al., 2022), particularly considering the rather limited size of Germany. Previous studies on *I. ricinus* abundance in Germany have mainly focused on southern parts of the country (e.g. Boehnke et al., 2015; Schulz et al., 2014), with a few exceptions (Gethmann et al., 2020; Hauck et al., 2020). The probable reason for this unequal sampling effort is the much higher TBE incidence in southern than in northern federal states (Robert-Koch-Institute, 2023). The present study filled this gap, revealing a higher *I. ricinus* abundance in Germany's north-west in all three study years, particularly in the northernmost areas with a coastal climate, than in the eastern and southern parts of the country. This was somewhat unexpected, as an opposing pattern with higher tick densities in southern Germany was previously suggested based on different regional studies performed between 2006 and 2014 (Brugger et al., 2016). However, in congruence with the present result, higher habitat suitability for *I. ricinus* in the north-west compared to the east and the south of Germany was already estimated in the frame of a Europe-wide

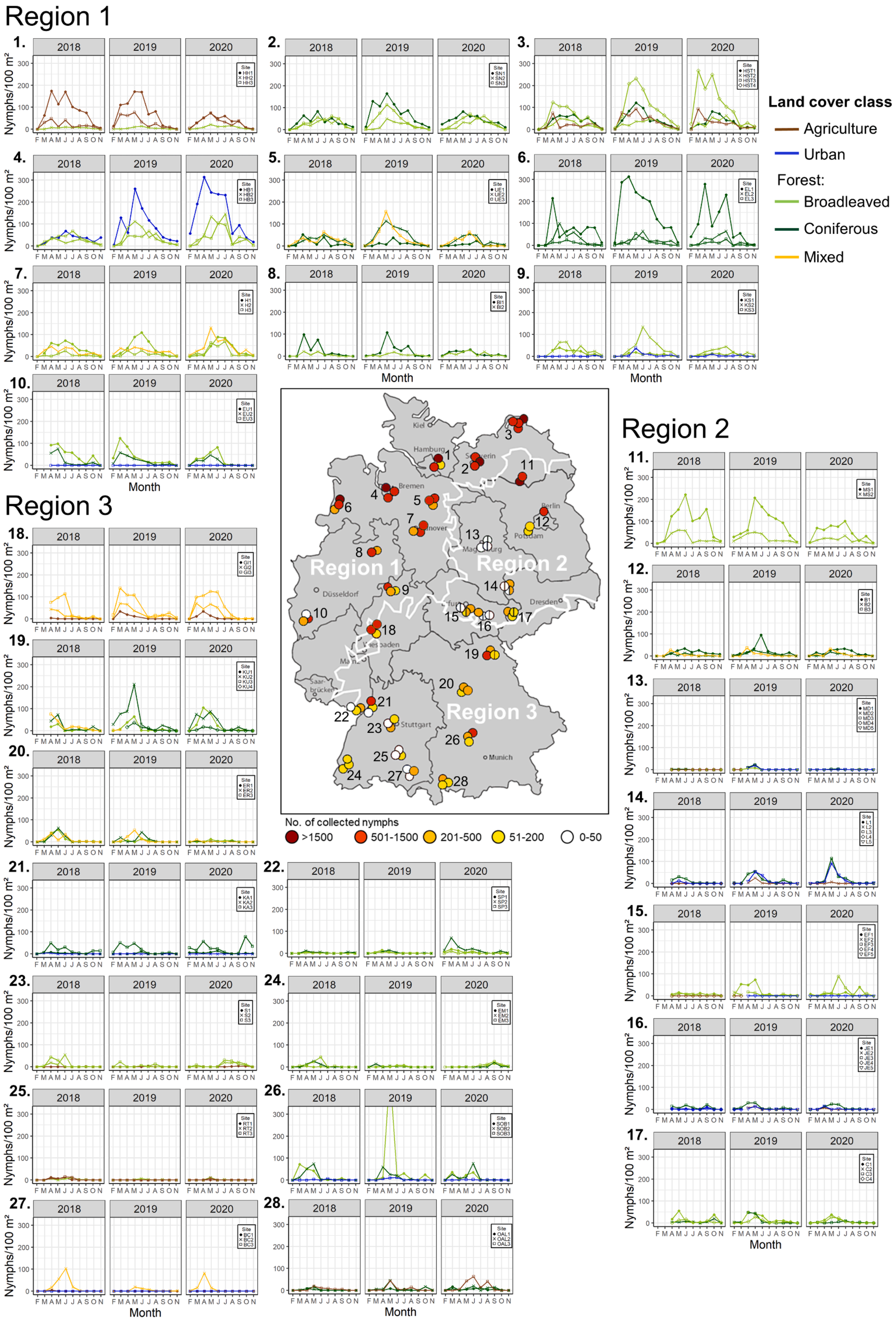

Fig. 3. Seasonal patterns of questing *Ixodes ricinus* nymph density in 28 collection areas across Germany during the years 2018–2020. Each collection site's land cover class is indicated by colour, while symbols represent the different collection sites. The y-axis is cropped at 350, i.e. one outlier is not shown. A heatmap of the total number of collected *I. ricinus* nymphs during 2018–2020 is shown in the centre (created using Mapbox Studio, San Francisco, USA). Note that vertically divided points in the map/discontinuous lines within a sampling year indicate a change of the collection site. Regions represent climatic regions based on Kahlenborn et al. (2021). The following areas were included: 1: Hamburg, 2: Schwerin, 3: Stralsund, 4: Bremen, 5: Uelzen, 6: Emsland, 7: Hanover, 8: Bielefeld, 9: Kassel, 10: Euskirchen, 11: Mecklenburgische Seenplatte, 12: Berlin, 13: Magdeburg, 14: Leipzig, 15: Erfurt, 16: Jena, 17: Chemnitz, 18: Giessen, 19: Kulmbach, 20: Erlangen, 21: Karlsruhe, 22: Suedpfalz, 23: Stuttgart, 24: Emmendingen, 25: Reutlingen, 26: Schrobenhausen, 27: Biberach, 28: Ostallgaeu.

Table 3
Overview of results from negative binomial generalized linear mixed models assessing the influence of various predictor variables on the number of *I. ricinus* nymphs/100 m^2 collected by drag sampling in Germany during 2018–2020. Shown are fixed effect estimates of final models ± their standard errors and *P*-values, with significant *P*-values printed in bold.

	Overall[a] (*N* = 2392)	Region 1 (coast/ north-west)[b] (*N* = 878)	Region 2 (east)[c] (*N* = 567)	Region 3 (south)[d] (*N* = 947)
Intercept	2.29 ± 0.37 (< **0.001**)	1.45 ± 0.42 (< **0.001**)	2.19 ± 1.31 (0.094)	1.73 ± 0.63 (**0.006**)
Region (ref.: Region 1)				
Region 2	−1.00 ± 0.38 (**0.008**)	–	–	–
Region 3	−0.86 ± 0.44 (0.054)	–	–	–
Year (ref.: 2018)				
2019	0.37 ± 0.12 (**0.003**)	0.16 ± 0.17 (0.359)	0.78 ± 0.39 (**0.044**)	0.03 ± 0.22 (0.905)
2020	0.28 ± 0.22 (0.191)	0.01 ± 0.26 (0.972)	0.67 ± 0.70 (0.338)	0.34 ± 0.4 (0.396)
Month (ref.: February)				
March	1.70 ± 0.13 (< **0.001**)	1.97 ± 0.13 (< **0.001**)	1.00 ± 0.27 (< **0.001**)	1.49 ± 0.32 (< **0.001**)
April	1.56 ± 0.17 (< **0.001**)	1.96 ± 0.17 (< **0.001**)	1.26 ± 0.39 (**0.001**)	1.27 ± 0.43 (**0.003**)
May	1.63 ± 0.19 (< **0.001**)	1.90 ± 0.19 (< **0.001**)	1.63 ± 0.40 (< **0.001**)	1.35 ± 0.48 (**0.005**)
June	1.32 ± 0.23 (**<0.001**)	1.70 ± 0.24 (< **0.001**)	0.83 ± 0.50 (0.094)	0.93 ± 0.54 (0.087)
July	0.80 ± 0.23 (< **0.001**)	1.42 ± 0.24 (< **0.001**)	0.31 ± 0.52 (0.558)	0.13 ± 0.57 (0.824)
August	0.25 ± 0.25 (0.327)	0.95 ± 0.28 (< **0.001**)	−0.70 ± 0.54 (0.198)	−0.49 ± 0.6 (0.410)
September	−0.18 ± 0.22 (0.412)	0.38 ± 0.23 (0.132)	−0.29 ± 0.45 (0.517)	−1.01 ± 0.51 (**0.049**)
October	−0.24 ± 0.18 (0.190)	0.29 ± 0.19 (0.106)	−0.35 ± 0.40 (0.383)	−0.79 ± 0.42 (0.059)
November	−0.63 ± 0.17 (< **0.001**)	−0.29 ± 0.17 (0.086)	−0.77 ± 0.37 (**0.038**)	−1.08 ± 0.42 (**0.010**)
Land cover class (ref.: broadleaved forest)				
Mixed forest	0.52 ± 0.46 (0.257)	0.34 ± 0.78 (0.663)	−0.72 ± 0.78 (0.355)	0.72 ± 0.55 (0.189)
Coniferous forest	−0.10 ± 0.31 (0.742)	0.11 ± 0.44 (0.808)	−0.21 ± 0.42 (0.615)	0.15 ± 0.37 (0.680)
Agricultural area	−1.78 ± 0.39 (< **0.001**)	0.26 ± 0.67 (0.697)	−3.29 ± 0.56 (< **0.001**)	−1.32 ± 0.54 (**0.015**)
Urban area	−2.08 ± 0.40 (< **0.001**)	−1.95 ± 0.67 (**0.004**)	−1.66 ± 0.52 (**0.001**)	−3.13 ± 0.63 (< **0.001**)
Sample site elevation	−0.65 ± 0.23 (**0.004**)	−0.72 ± 0.39 (0.065)	1.98 ± 1.09 (0.069)	−0.74 ± 0.44 (0.094)
Meteorological variables of the sampling date				
Mean temperature	0.31 ± 0.09 (< **0.001**)	0.28 ± 0.09 (**0.002**)	0.22 ± 0.12 (0.068)	0.33 ± 0.15 (**0.032**)
Mean temperature, squared	−0.31 ± 0.05 (< **0.001**)	−0.21 ± 0.05 (< **0.001**)	−0.31 ± 0.07 (< **0.001**)	−0.37 ± 0.09 (< **0.001**)
Saturation deficit	−0.07 ± 0.07 (0.274)	−0.16 ± 0.08 (**0.038**)	–	–
Soil moisture	−0.28 ± 0.04 (< **0.001**)	−0.30 ± 0.06 (< **0.001**)	−0.46 ± 0.11 (< **0.001**)	–
10-day gliding window before sampling				
Mean temperature	0.11 ± 0.08 (0.183)	0.12 ± 0.10 (0.215)	0.18 ± 0.17 (0.302)	0.19 ± 0.19 (0.317)
Mean temperature, squared	−0.28 ± 0.04 (< **0.001**)	−0.22 ± 0.06 (< **0.001**)	−0.24 ± 0.09 (**0.006**)	−0.26 ± 0.09 (**0.006**)
Sum of precipitation	0.13 ± 0.03 (< **0.001**)	0.10 ± 0.04 (**0.023**)	0.26 ± 0.07 (< **0.001**)	0.05 ± 0.06 (0.369)
Meteorological variables of the previous spring				
Mean temperature	−0.24 ± 0.12 (**0.045**)	–	–	–
Mean temperature, squared	−0.04 ± 0.03 (0.240)	–	–	–
Sum of precipitation	0.15 ± 0.08 (0.058)	–	–	–
Mean soil moisture	0.24 ± 0.07 (< **0.001**)	0.17 ± 0.08 (**0.027**)	–	0.79 ± 0.16 (< **0.001**)
Meteorological variables of the preceding winter half-year				
Mean temperature	0.04 ± 0.15 (0.795)	0.36 ± 0.18 (**0.039**)	−0.63 ± 0.41 (0.121)	0.48 ± 0.43 (0.259)
Days with snow cover	0.31 ± 0.10 (**0.002**)	0.30 ± 0.10 (**0.003**)	–	0.43 ± 0.18 (**0.015**)
Interactions				
Mixed forest*winter temperature	–	−0.28 ± 0.17 (0.104)	0.36 ± 0.33 (0.271)	−0.84 ± 0.36 (**0.021**)
Coniferous forest*winter temperature	–	−0.23 ± 0.10 (**0.018**)	0.19 ± 0.17 (0.273)	0.14 ± 0.23 (0.538)
Agricultural area*winter temperature	–	−0.19 ± 0.13 (0.135)	0.33 ± 0.53 (0.535)	−0.06 ± 0.32 (0.846)
Urban area*winter temperature	–	0.57 ± 0.19 (**<0.001**)	1.02 ± 0.31 (**0.001**)	−0.47 ± 0.47 (0.319)
R^2_{GLMM} (conditional/ marginal)	**72 %/53 %**	**83 %/55 %**	**88 %/53 %**	**51 %/38 %**

[a] The model was significantly different from a null model containing only the random factor ($\chi^2 = 1442.3$, Df = 31, $P < 0.001$).

[b] The model was significantly different from a null model containing only the random factor ($\chi^2 = 885.5$, Df = 30, $P < 0.001$).

[c] The model was significantly different from a null model containing only the random factor ($\chi^2 = 420.6$, Df = 27, $P < 0.001$).

[d] The model was significantly different from a null model containing only the random factor ($\chi^2 = 415.8$, Df = 28, $P < 0.001$).

study published in 2014 (Boeckmann and Joyner, 2014). Moreover, a similar result was generated based on modelling a composite dataset obtained by a literature survey (Noll et al., 2023). Climate data from 1971 to 2000 show that the coastal and north-western regions are characterized by the lowest variability in temperature, with mild winters and few hot summer days, while the highest temperature variability occurs in the south and the driest conditions prevail in the east (Crespi et al., 2023). Thus, the mild and moist coastal subatlantic climate likely favours a high *I. ricinus* abundance, in line with the significant impact of climatic variables on questing nymph density in this and in previous studies (e.g. Daniel et al., 2015; Hauser et al., 2018; Wongnak et al.,

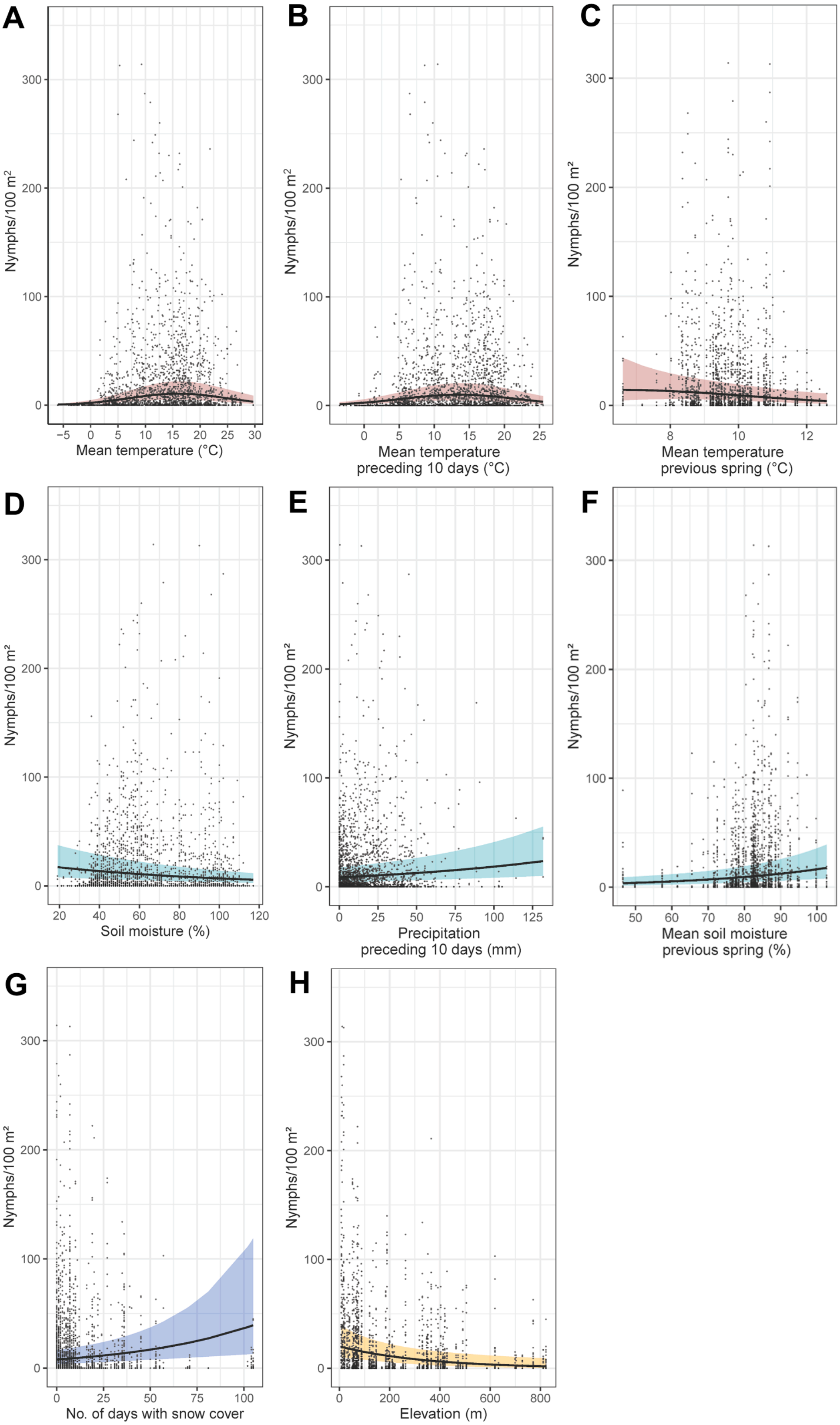

Fig. 4. Marginal effects of meteorological variables significantly associated with monthly *Ixodes ricinus* nymph density/100 m^2 at 93 collection sites in Germany based on a negative binomial generalized linear mixed model. Original data points, regression lines, and 95 % confidence intervals are shown for A) mean temperature on the day of sampling, B) mean temperature during the 10-day window prior to sampling, C) mean temperature during the previous year's spring, D) soil moisture on the day of sampling, E) precipitation during the 10-day window prior to sampling, F) mean soil moisture during the previous year's spring, G) number of days with snow cover during the preceding winter half-year, H) elevation. Note that the y-axis is cropped at 350, i.e. one outlier is not shown.

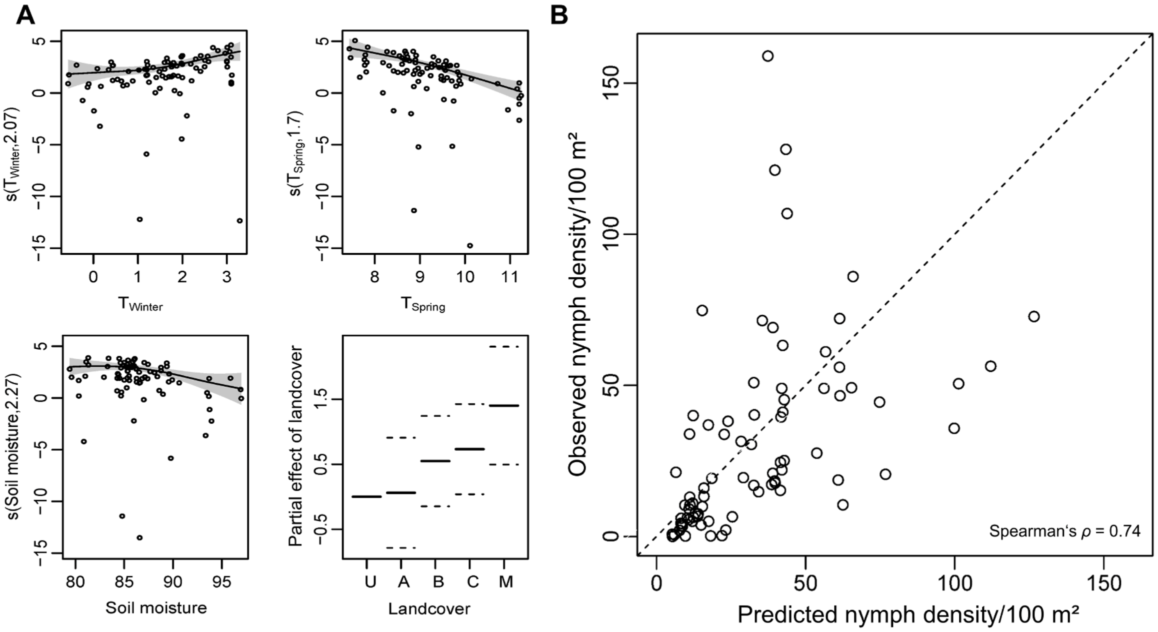

Fig. 5. Generalized additive model (GAM) plots showing the partial effects, i.e. the contribution to the model predictions, of the explanatory variables (mean winter temperature, spring temperature, soil moisture, and landcover class) (A) and predicted vs. observed mean (April−June) *Ixodes ricinus* nymph density (B) at 83 sites in Germany. Points in panel A represent model residuals, shaded bands and dashed lines, respectively, indicate the 95 % confidence intervals. The dashed line in panel B indicates a 1:1 relationship as reference.

2022), while the conditions in the east and in the south of Germany are apparently less favourable for this tick species. These climate clusters seem to be temporally stable and apply also to future climate scenarios (Crespi et al., 2023).

The previous estimation by Brugger et al. (2016) included only few tick collection sites in northern Germany and suffered from the limitation that the underlying data were collected during different time spans, introducing a potential bias due to interannual differences. The potential impact of this is highlighted in the present study, which found the survey year was significantly associated with nymph density, although the general pattern of regional differences was consistent across the three study years. The discrepancy between the two studies may have been partially driven by changes in tick density between the study periods, but, nevertheless, underlines the need for a spatially extensive and temporally coordinated sampling effort to provide public health agencies with reliable estimates of tick abundance at larger spatial scales. Such estimates should be regularly reassessed, particularly as interannual climate variability and the frequency of climatic extremes are expected to increase. Moreover, not only changes in climate, but also in other environmental factors, e.g. landscape features and tick host populations, are likely to entail changes in tick abundance.

In addition to the general differences in tick abundance between the study regions, the magnitude of the observed gradient may have been further intensified by a recent population decline of *I. ricinus* in eastern and southern Germany. This hypothesis may be supported by the surprisingly low nymph:adult ratio at eastern and southern compared to north-western sites. Commonly, far more nymphal *I. ricinus* are collected by flagging as compared to adults (Ehrmann et al., 2017; Gethmann et al., 2020; Schulz et al., 2014), whereas adult ticks dominated at various eastern and southern collection sites of the present study, particularly in 2019 and 2020. In light of the multi-year life cycle of *I. ricinus* (Kahl and Gray, 2023), this might indicate particularly adverse conditions for the survival of *I. ricinus* eggs and/or larvae, translating with a time lag into lower numbers of nymphs, while the adult stage was not as strongly affected. Previous research has shown that hatching success of *Ixodes* eggs declines after heat stress (Ajayi et al., 2024), and *Ixodes* larvae are more prone to desiccation than nymphal or adult ticks (Brunner et al., 2023; Stafford, 1994). The southern and eastern parts of Germany were affected by a long-lasting drought during the year 2015, with a water storage deficit that did not recover until mid-2016, while the coastal region and the north-western half of Germany received enough precipitation (Boergens et al., 2020). This was followed by a multi-year drought from 2018 to 2020 (Rakovec et al., 2022), i.e. during the present field study, which was most severe in central, eastern, and southern parts of Germany, while the coastal regions were less affected (Boergens et al., 2020). In addition to impairing egg and larval survival, the dry conditions may have also affected the nymph:adult ratio via tick behaviour, as nymphs are more likely to suspend questing during dry conditions than adult ticks (Perret et al., 2004). Thus, the cumulative effects of these drought events, which are expected to occur at increased frequency in the future due to climate change (Hari et al., 2020), may have contributed to the particularly low questing nymph densities in eastern and southern compared to north-western Germany. However, within these regions, a further decline in nymph density across the three sampling years was not observed. In contrast, the models revealed a significant increase from 2018 to 2019 in the east, but no annual differences at the north-western and southern collection sites. This might indicate a normalization of the population structure after a period of particularly adverse conditions in this region generally characterized by lower climate suitability for *I. ricinus*.

As expected, land cover class was a relevant predictor of questing nymph density, with higher values observed in forests compared to agricultural and urban sites. Consequently, in addition to coastal regions, a rather high relative abundance was also predicted for the mid-elevation mountain ranges, which are characterized by a rather cool and wet climate (Crespi et al., 2023) and a high proportion of forest cover. However, the CORINE land cover dataset used for the present analysis dates from 2018, and does not yet account for recent forest loss due to drought and accompanying bark beetle (*Ips typographus*) infestations (Thonfeld et al., 2022). The impact of forest stress on tick density has been little studied so far and should receive more attention in further studies. Future development of tick density will not only be affected by changes in climate, but also by de- and reforestation, illustrating the need for regular reassessments of prediction maps.

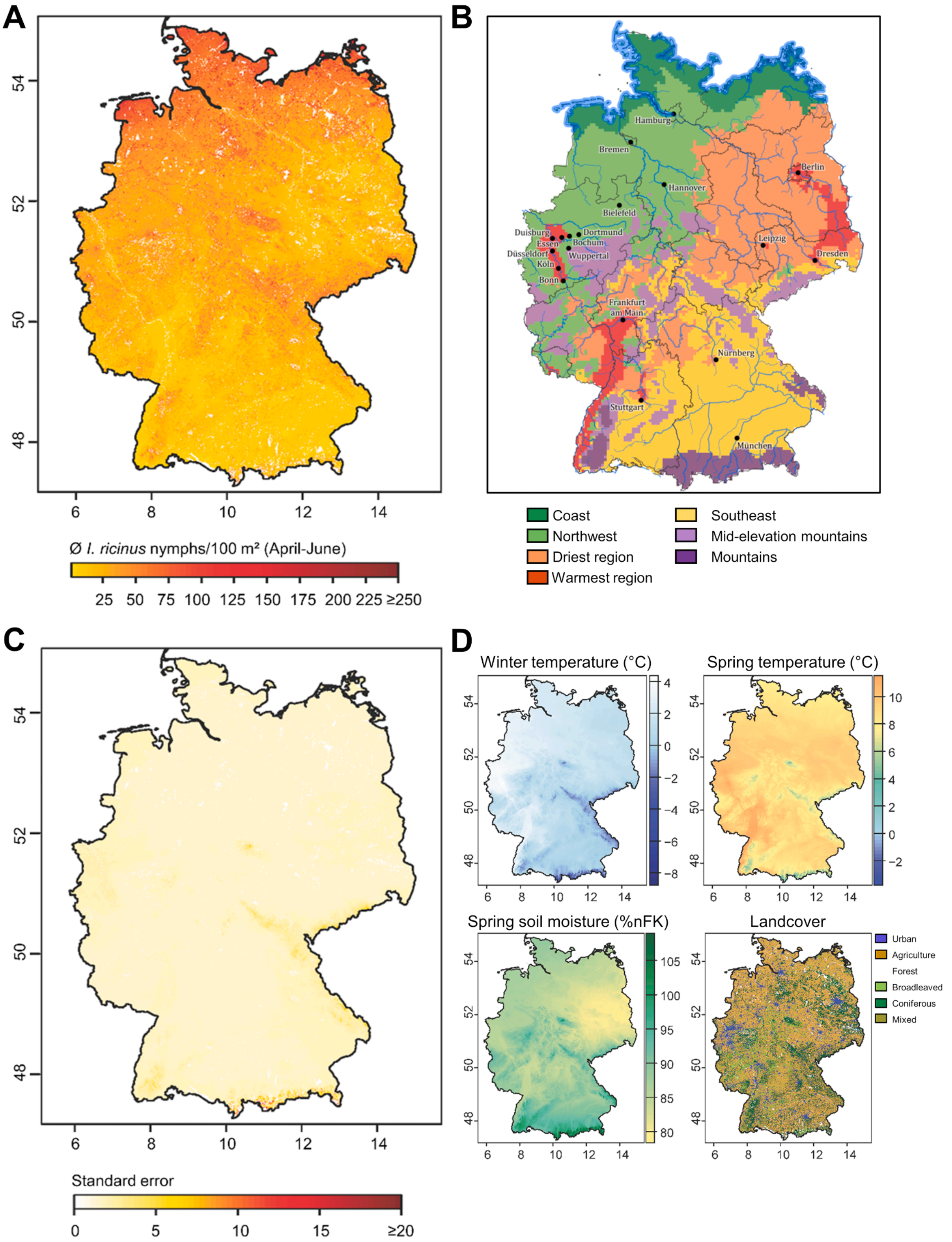

Fig. 6. Map of estimated mean (April–June) *Ixodes ricinus* nymph density in Germany (A) in comparison to German climate area types (map reproduced with permission from Kahlenborn et al. (2021)) (B). The bottom panels show standard errors of model predictions (C) and maps of the explanatory variables used to fit the model (D; 30-year average winter temperature, spring temperature, spring soil moisture, and CORINE land cover class).

Considering seasonal patterns, a high level of variability was observed between sites as well as between years. Most frequently, questing *I. ricinus* nymph activity peaked between March and June, although the peak lasted until July at some sites, particularly in the north. A bimodal pattern with a distinct autumn peak only occurred at a few sites and was inconsistent across years. Both unimodal and bimodal activity patterns have been described in previous studies from Germany (Hauck et al., 2020; Schulz et al., 2014; Schwarz et al., 2009; Vollack et al., 2017). Schulz et al. (2014) explained the unimodal pattern in their study with increased precipitation, preventing a decrease in tick abundance during the hot summer months and thus a distinct separation between a spring and autumn peak. However, as described above, the years 2018–2020 were characterized by drought, so this explanation might only be relevant for areas near the coast which received more precipitation during these years than the rest of the country (Boergens et al., 2020). At many eastern and southern collection sites, the spring peak ended in June, with no or only very low autumn activity, indicating that the autumn peak might have been prevented by drought conditions. Interestingly, in the autumn of 2020 higher nymph activity compared to spring was observed at a few sites in south-western Germany, where questing nymph density was generally rather low. The reasons for this remain unclear. It may be speculated that local conditions might have prevented questing activity at these sites during the spring, so that the ticks shifted their activity to autumn in order to find a host before depletion of their energy reserves. Alternatively, this pattern may indicate a recovery of the tick population after a period of particularly harsh circumstances, with improved conditions for engorged *I. ricinus* larvae during spring 2020, which then moulted in summer and became active as nymphs in autumn. This latter hypothesis is supported by the observation that a small stream at one of these sites was completely dried out in 2018 and 2019, but not in 2020. The same site also showed a higher questing tick density in the year 2021 as compared to the previous years (own unpublished data), indicating a recovery of the tick population.

The multivariable models confirmed the importance of temperature and moisture-related variables for explaining questing *I. ricinus* nymph density, similar to previous studies (Daniel et al., 2015; Hauser et al., 2018; Wongnak et al., 2022). Next to temperature, saturation deficit, and precipitation, soil moisture was also included in the analysis to better reflect the hydration status of the ticks' microhabitat. In the final models, mean soil moisture during the previous year's spring showed a significant positive correlation with questing nymph density, except in the dry eastern region. This likely reflects favourable conditions for the survival of tick larvae, which then may become active as nymphs in the following year. In contrast, soil moisture on the day of sampling was negatively correlated with nymph density, although the amount of precipitation during the previous ten days had a positive effect. Ticks might avoid questing when the ground and the low vegetation are still wet from recent rainfall, as water drops may represent an obstacle for them. Moreover, the efficiency of the flagging method may be impaired if the cloth becomes wet, which may have contributed to the observed negative relationship.

Conditions during the preceding winter also showed a significant association with questing nymph density. Winter temperature may have a direct effect on tick survival, as well as an indirect effect on tick density by modulating host abundance (Daniel et al., 2008; Paul et al., 2016). Due to a lack of fine-scaled, reliable data, it was not possible to explicitly include host abundance in the models, especially as multiple host species are likely to play a role due to the wide host spectrum of *I. ricinus*. While mean winter temperature had no significant effect in the overall model, the regional models indicated that it was modulated by land cover. It should be kept in mind that the climate data were derived from weather stations, as data measured directly at the collection sites were not available. Therefore, possible interactions between land cover and climate variables were explored, as local vegetation creates a microclimate which may be inadequately reflected by the weather station measurements (Boehnke et al., 2017). In the northern region, the positive effect of a mild winter was weaker in coniferous forests but stronger in urban areas as compared to broadleaved forests. In the east, significantly higher questing nymph densities after mild winters were only observed in urban areas. Temperatures in towns and cities are generally higher than in surrounding areas, a phenomenon termed the "urban heat island" effect (Oke, 1982), which may have amplified the positive effect of a mild winter on tick density. In addition, the number of days with snow cover was positively associated with nymph density in both the north-western and the southern region, confirming the protective effect of an insulating snow cover on *I. ricinus* ticks (Dautel et al., 2016; Vollack et al., 2017).

Overall, the fixed factors included in the GLMMs explained approximately 50 % of the variance, although this value reached only 38 % in the model for the southern region. The landscape in southern Germany is more heterogeneous in terms of elevation compared to the plains covering much of the northern half of the country. Thus, weather station measurements may have been less representative for the sample sites in southern compared to north-western and eastern Germany due to small-scale variation in climate, e.g. between different valleys. Moreover, further factors may also contribute to the variation in questing nymph density, e.g. wildlife abundance (Tagliapietra et al., 2011; Takumi et al., 2019) or understorey characteristics (Ehrmann et al., 2017), which were not taken into account here. However, the principal goal of the present study was to model *I. ricinus* abundance at a country-wide scale, which requires high-resolution gridded data covering the entire country. Such datasets are most readily available in the form of land cover and climate variables interpolated from local weather stations. Thus, even if more detailed insights into the relationship between microclimate, host abundance or habitat characteristics and tick activity could be drawn from in situ observations, this would not necessarily improve spatial predictions. However, if comprehensive spatial data on wildlife densities would become available, their integration could improve the model's predictions and the resulting map, which is currently based on the assumption of homogeneous host availability.

The present predictive model was evaluated by Spearman rank correlation between predicted and observed values, i.e. the model's ability to correctly order the sites according to their tick density, and by mean absolute deviance between predicted and observed values. Although both aspects are important, the former is especially relevant with regard to highlighting areas of high tick density, whereas the absolute deviance may arguably be less decisive. Moreover, both random cross-validation, which gives an impression of overall performance, and spatial block cross-validation, which indicates geographic transferability, were applied. Although both methods indicated adequate model performance, the correlation between predicted and observed values was slightly higher in random than in spatial block cross-validation, underlining the existence of regional differences, although the mean absolute deviance was comparable between both methods. The standard errors of model predictions were generally low, except in some mountainous areas, particularly the Alps, where the terrain causes a high level of local variability in climate.

5. Conclusions

The present study provides the first map of *I. ricinus* abundance in Germany based on a geographically balanced, temporally coordinated, and standardised tick collection scheme. The underlying sampling effort is unprecedented in tick ecology, given the large number of collection sites in relation to the rather limited size of Germany, and the large number of visits performed over the course of three years. The map shows a higher tick hazard in Germany's north-west compared to the east and south, which has important implications for the potential TBD infection risk. The fact that this result is contradictory to a previous estimation based on extrapolation of regional studies (Brugger et al., 2016) illustrates the need for such an extensive and coordinated sampling effort to provide public health agencies with reliable estimates of tick abundance at larger spatial scales.

When combined with data on tick-borne pathogen prevalence in ticks, the obtained results allow estimating the density of infected ticks and consequently the risk of acquiring an infectious tick bite. In this context, the high tick density observed near the coast as well as in the mid-elevation mountain ranges is especially concerning, indicating a potentially high risk of exposure to *I. ricinus*-borne pathogens such as *Borrelia* spp. or *A. phagocytophilum* in these regions, which are also popular tourist destinations. Finally, the present dataset and the observed relationships with climate and land cover can serve as a basis for predicting future developments under different climate scenarios, also beyond the borders of Germany. Nevertheless, the results of such climate-driven models should be interpreted with caution, as *I. ricinus* is a highly adaptable species (Nolzen et al., 2022). Therefore, there will be a continuous need for the collection of field data to re-evaluate model predictions.

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Declaration of competing interest

OK is a CEO of tick-radar GmbH. He occasionally acted as a consultant for pharmaceutic companies and is an unpaid member of the ESCMID study group ESGBOR. UM, LCD, CS and MP declare that they repeatedly have lectured for and acted as consultant for diagnostic and (veterinary) pharmaceutical companies and have previous and ongoing research collaborations with various diagnostic and (veterinary) pharmaceutical companies. Study conceptualization, investigation and data interpretation is completely independent of any companies' opinions. The remaining authors declare that they have no conflict of interest.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2025.102485.

Data availability

Data will be made available on reasonable request.

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