Drivers of *Ixodes ricinus* population dynamics in Northeast France: a Bayesian modelling approach

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Abstract

Ixodes ricinus is the primary vector for Lyme disease and tick-borne encephalitis across Europe. To better understand the environmental and ecological drivers of its population dynamics, we collected monthly tick density data over ten years (2013–2022) in four sites in Northeast France, where *I. ricinus* has established, and developed and fitted a mathematical model using a Bayesian approach. Our model estimated oviposition, hatching, and moulting rates across a range of temperature or saturation deficit, as well as questing and vertebrate host contact rates. Furthermore, we showed the importance of diapause in reproducing the observed seasonal population dynamics. Finally, model projections indicated a significant decrease in *I. ricinus* abundance over the next 20 years under several climate change scenarios. This study elucidates *I. ricinus* population dynamics in Northeast France, provides foundations for developing models of *I. ricinus*-borne pathogen transmission, and is adaptable to other *Ixodidae* populations of public health significance.

Introduction

Ticks undergo a complex life cycle comprised of a series of key demographic processes, including oviposition, hatching, questing, feeding on vertebrate hosts, and moulting, which may occur with or without delays in development (developmental diapause) or questing (behavioural diapause)[1]. Understanding the mechanisms driving these processes is crucial for unravelling tick population dynamics, thereby allowing for the quantification of the current and future incidence of tick-borne diseases and developing effective public health strategies.

Ixodes ricinus is the most widespread tick species across Europe, transmitting pathogens that pose significant risks to both public and animal health[2]. These pathogens include *Borrelia burgdorferi* sensu lato causing Lyme disease—the most prevalent vector-borne disease in Europe[3]—and tick-borne encephalitis virus (TBEV), which can lead to fatal neurological disorders with a growing incidence throughout the continent[4]. However, our knowledge about *I. ricinus* population dynamics in natural environments remains limited, precluding formal assessments on the transmission dynamics of pathogens carried by this tick species.

Mechanistic modelling provides an ideal framework for understanding tick population dynamics by enabling explicit descriptions of tick progression through key demographic processes. For *Ixodes* ticks, although few in number, mechanistic models have been developed to capture the seasonality of questing tick density by accounting for climatic impacts on tick demographic processes[5-8], and have been further expanded to explore the transmission dynamics of tick-borne pathogens[9-11]. While providing valuable insights into the population dynamics of *Ixodes* ticks, the application of these models has been limited for a number of reasons. Firstly, most simulation studies have relied on parameter values derived from controlled laboratory or field settings[12-15]. Significant spatiotemporal variations in climate and *Ixodes* ticks' adaptability to a wide range of climatic conditions[16,17] suggest that those parameter values do not fully represent how ticks have adapted to their dynamic natural environments[18]. Secondly, relying on simulations with fixed parameter values fails to capture the variability inherent in observed data[19]. This restricts the value of mechanistic models since understanding the extent of data variability can not only provide insights into the unobserved ecological processes but also allow more reliable predictions of tick population sizes and the burden of tick-borne pathogens.

Here, we collected data on questing *I. ricinus* density on a monthly basis from four distinct sites (Dannemarie, Illkirch, Murbach, and Niedermunster) in the Alsace region of Northeast France, over the decade from 2013 to 2022. We developed and fitted a mechanistic model to this longitudinal data, using a Hamiltonian Monte Carlo (HMC) Bayesian algorithm, to estimate key demographic parameters related to tick development, questing, and

vertebrate host contact activities, and to test hypotheses regarding two key features in the life cycle of *I. ricinus* (Figs. 1 and 2). First, we assessed the functional relationship between climatic conditions and tick development, while estimating the daily rates of oviposition, hatching, larva-to-nymph moulting, and nymph-to-adult moulting according to temperature or saturation deficit (Theme 1 hypotheses). Second, we investigated the length of developmental diapause—delay between tick feeding and moulting—which influences the emergence of newly moulted and thus questing ticks (Theme 2 hypotheses). Finally, based on the best-fitting model, we assessed the potential impact of climate changes for the next 20 years on *I. ricinus* abundance in the study region by using climate change scenarios represented by Representative Concentration Pathways (RCP)[20].

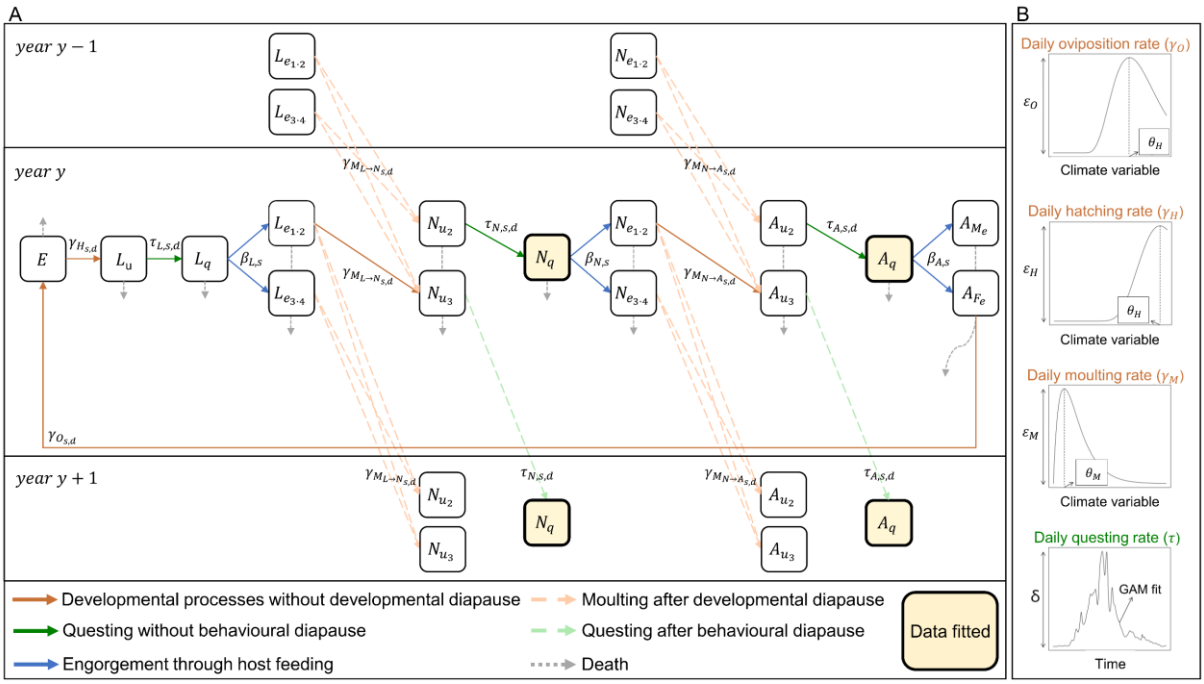

Figure 1. Schematic description of *Ixodes ricinus* population dynamics model. See Tables 1 and 2 for the definition of parameters shown in this figure. **(A) Transition of ticks through life stages.** The square boxes represent the compartments of ticks in various life stages: E=eggs, L=larvae, N=nymphs, A=adult, A_M=male adults, and A_F=female adults. The subscripts u, q, and e represent unfed, questing, and engorged statuses, respectively. The square boxes with bold outline and ivory colour represent questing nymph and adult populations to which the model was fitted. The arrows between the compartments indicate the daily rates of developmental (brown), questing (green), or host contact (blue) processes, with the subscripts s, d indicating study site and date, respectively. The dotted pale brown arrows represent a delay in moulting through developmental diapause, and dotted pale green arrows represent a delay in questing through behavioural diapause. The grey dotted arrows represent mortality through natural death. **(B) Parameters estimated for daily oviposition, hatching, moulting and questing rates.** For daily oviposition, hatching, and moulting rates, the climatic condition (temperature or saturation deficit) at their peaks (θ_O, θ_H, and θ_M) and the corresponding maximum daily rates (ε_O, ε_H, and ε_M) were estimated assuming that these rates followed the shape of a Gamma distribution under Theme 1 alternative hypothesis. Under Theme 1 null hypothesis, these developmental rates were assumed to follow the inverse of the power-law functions estimated by Ogden, Lindsay [12]. In both baseline and alternative hypotheses, daily questing rates were obtained by scaling temporal trends in questing tick density, estimated by the best-fitting generalised additive model (GAM), by parameter δ.

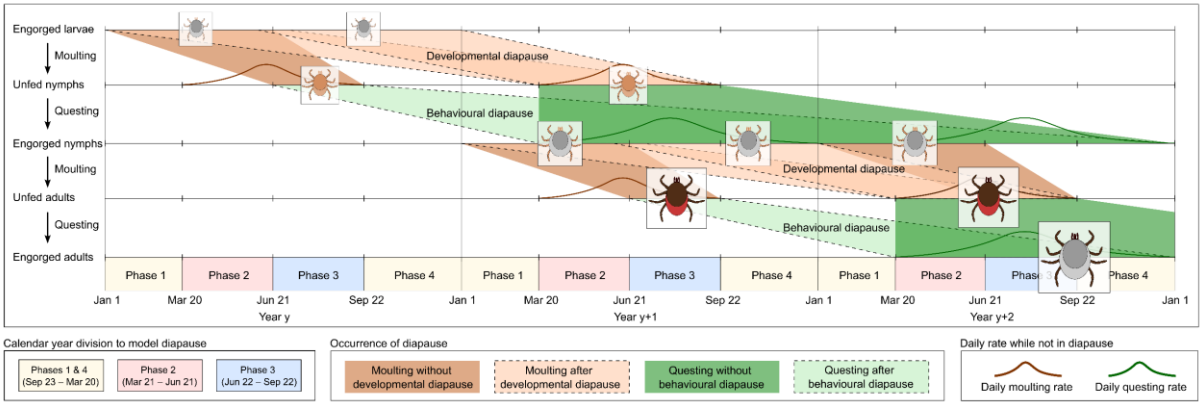

Figure 2. Occurrence of developmental and behavioural diapauses in relation to the timing of moulting and questing. The upper four rows illustrate the transition of ticks from engorged larvae to engorged adults, through moulting and questing, with or without experiencing a developmental or behavioural diapause. The bottom row displays the division of each calendar year into four phases, which govern tick demographic processes. Under Theme 2 null hypothesis, ticks that had their blood meal during Phase 2 or earlier began moulting from Phase 3 of the same year (dark brown shades). Some ticks that did not moult in Phase 3 began moulting in Phase 2 of the following year after a developmental diapause (pale brown shades with a dashed border). Additionally, ticks that had their blood meal in Phase 3 began moulting from Phase 2 of the following year after a developmental diapause (pale brown shades with a dashed border). Under Theme 2 alternative hypothesis, these ticks began moulting from Phase 3 of the following year instead (not shown in the figure). Regarding questing, ticks that moulted after a developmental diapause began questing from Phase 2 of the year they moulted (dark green shades), whereas ticks that moulted in Phase 3 without a developmental diapause began questing from Phase 2 of the following year after a behavioural diapause (pale green shades with a dashed border). While moulting and questing were permitted under these conditions, they were subject to occur according to daily moulting (brown lines) or questing (green lines) rates, as estimated under Theme 1 hypotheses.

Results

Longitudinal *Ixodes ricinus* questing density data. In the four study sites, we collected questing *I. ricinus* nymphs and adults monthly from 2013 to 2022, primarily between March and November (Fig. S1A). A total of 368 sampling campaigns were conducted. Each study site was sampled a median of 9 times a year (range: 7–11), totalling between 89 and 95 sampling campaigns during the study period. Across the study sites, questing *I. ricinus* nymphs and adults exhibited distinct annual peaks in the spring or early summer, with magnitudes that varied over the study years (Fig. 3). The highest questing tick density recorded was 426.25 per 100m^2 for the nymphs (June 24, 2013, at the Murbach site) and 18 per 100m^2 for the adults (May 18, 2016, at the Niedermunster site) (Fig. 3). Annual peak densities were predominantly observed between May 22 and June 17 for the nymphs and between May 18 and 30 for the adults (Figs. 3 and S1B). This pattern demonstrated a primarily unimodal questing activity, consistent with previous observations in this region[17,21].

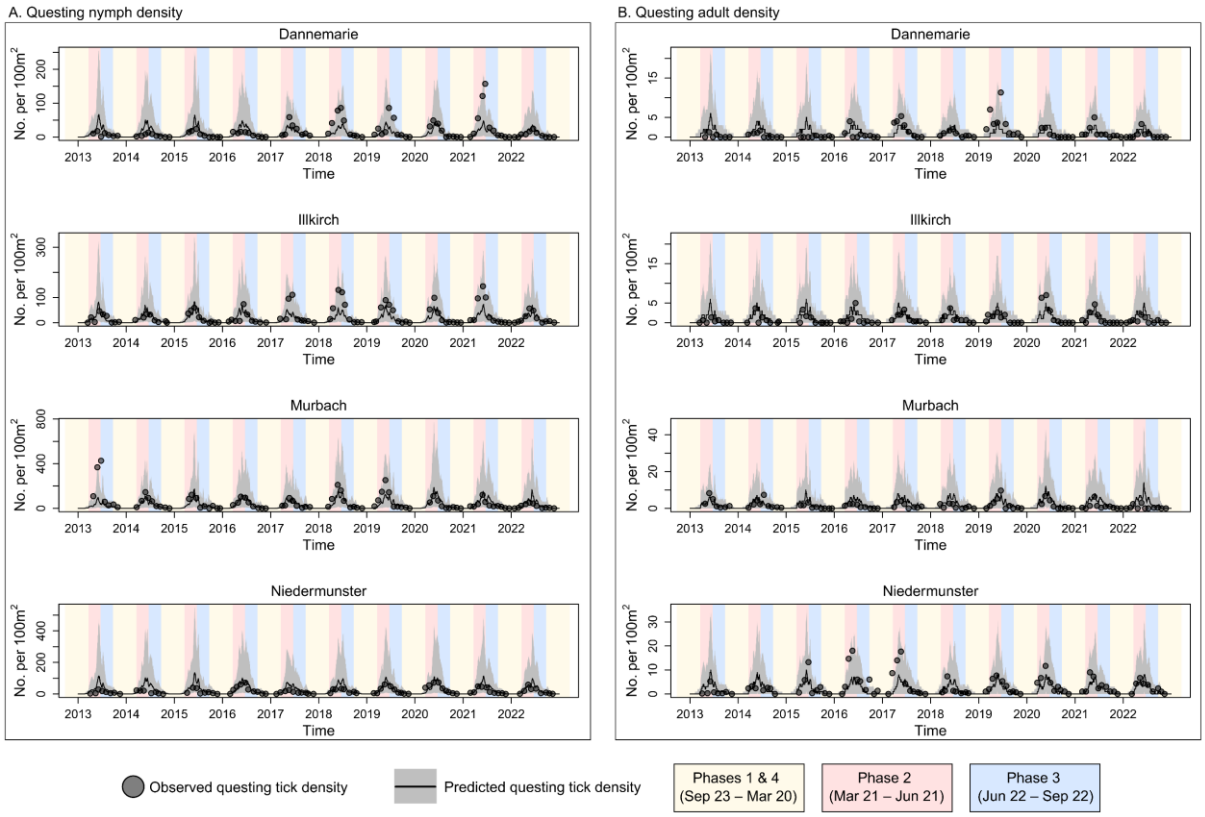

Figure 3. Observed and predicted longitudinal questing nymph and adult density. The points represent the observed numbers of questing nymphs and adults per 100m^2, respectively. The black lines and grey shades represent the median and 95% percentile intervals of these metrics predicted by the best-fitting model.

Demographic model and tick density predictions. The progression of *I. ricinus* was modelled through four life stages: eggs (E), larvae (L), nymphs (N), and adults (A). Larvae, nymphs, and adults were further categorised into three stages: unfed (L_u, N_u, A_u), questing (L_q, N_q, A_q), and engorged (L_e, N_e, A_e) compartments. Each transition between these life stages required a blood meal from a vertebrate host (apart from eggs hatching into larvae) and was influenced by environmental (climatic conditions) and ecological (developmental and behavioural diapauses) factors. In our model, these demographic processes were determined by the daily rates of oviposition, hatching, larva-to-nymph moulting, nymph-to-adult moulting, questing, vertebrate host contact, and death (Fig. 1), with or without developmental and behavioural diapauses (Fig. 2) (see the Methods and Supplementary Information for more details). The best-fitting model (Table 1) accurately predicted the observed densities of questing nymphs and adults, with the 95th percentile intervals of the predicted densities encompassing those observed in most sampling sessions across the sites (96.7% for questing nymphs and 97.6% for questing adults) (Figs. 3, S2, and S3). The observed densities followed a negative binomial distribution, with an overdispersion parameter estimated at 1.54

(95%HDI: 1.30–1.82) for questing nymphs and 2.13 (95%HDI: 1.38–2.97) for questing adults, indicating excess variability in both questing nymph and adult density data (Fig. S4F).

Estimates of key demographic processes. Our best-fitting model estimated that oviposition, hatching, larva-to-nymph moulting, and nymph-to-adult moulting rates varied across the range of climatic variables (daily mean temperature or saturation deficit) observed in the natural habitats of the ticks, following the shape of a Gamma distribution (Table 1, Theme 1 alternative hypothesis: "Gamma dist. by temperature" and "Gamma dist. by saturation deficit") as follows.

The estimated peak of daily oviposition and hatching rates were 0.05 (95% highest density interval [HDI]: 0.01–0.10) and 0.05 (95%HDI: 0.02–0.07), occurring at daily mean saturation deficit values of 7.8 (95%HDI: 3.2–10.9) and 6.5 (95%HDI: 2.8–9.0), respectively (Figs. 4A–B and S4A–B). These saturation deficit values, being near the upper end of the values recorded during the study period (median: 2.2, 95th percentile interval [PI]: 0.5–8.5), indicated moderate to high drying power of the air. These rates exhibited similar variations across the range of daily mean temperature, with oviposition and hatching rates peaking at 24.4°C (95%HDI: 10.9–27.2°C) and 24.7°C (95%HDI: 17.8–27.2°C), respectively, near the highest temperature recorded.

Furthermore, our best-fitting model estimated that the highest larva-to-nymph and nymph-to-adult moulting rates were 0.003 (95%HDI: 0.001–0.005) and 0.002 (95%HDI: 0.001–0.002), respectively, both of which were significantly lower than the upper prior limits set based on laboratory observations (Fig. S4B)[12]. These peak rates occurred at 14.2°C (95% HDI: 12.5–16.1°C), which was substantially lower than 27.3°C—the highest daily mean temperature recorded during the study period (Figs. 4C–D and S4A).

Finally, the daily rates of questing (unfed ticks looking for a host) and vertebrate host contact (questing ticks successfully feeding on a vertebrate host) were estimated, with the latter accounting for variability between the four study sites. The peak daily questing rate was 0.14 (median, 95%HDI: 0.12–0.14) (Fig. S4C), close to the upper prior limits established to allow time for ticks to harden their cuticle after moulting or hatching (hardening of 7 days). The median values of host contact rates ranged 0.12–0.35 for larvae, 0.18–0.51 for nymphs, and 0.23–0.64 for adults, across the study sites (Fig. S4E). We estimated the highest vertebrate host contact rates to be at the Murbach site, being 2.90 (95%HDI: 2.15–3.86), 2.64 (95%HDI: 1.91–3.47), and 1.34 (95%HDI: 0.94–1.78) times higher than those at the Niedermunster, Dannemarie, and Illkirch sites, respectively (Fig. S4D).

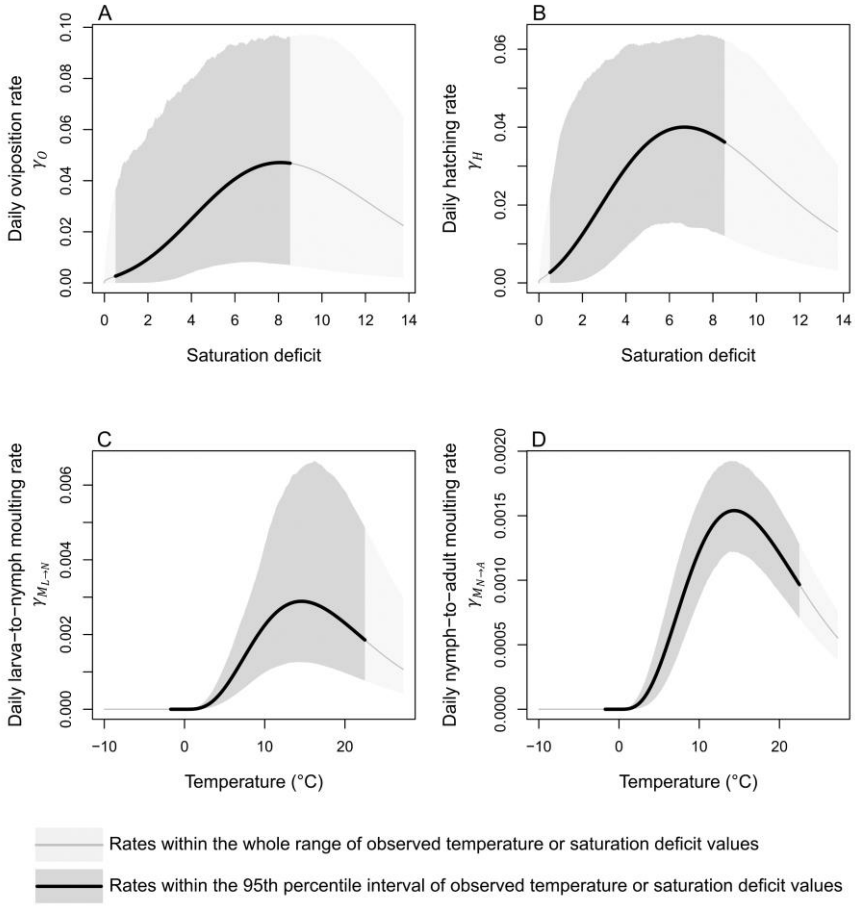

Figure 4. Functional relationship between climatic conditions and tick development. Daily developmental rates were estimated as a function of daily mean saturation deficit or temperature, under Theme 1 alternative hypothesis derived by the best-fitting model. It shows the functional relationship of daily **(A)** larva-to-nymph and **(B)** nymph-to-adult moulting rates with temperature, and the functional relationship of daily **(C)** oviposition and **(D)** hatching rates with saturation deficit. The lines and shades represent the median and 95th percentile interval of the developmental rates, respectively. The thick lines and dark shades represent the developmental rates within the 95th percentile interval of the daily mean temperatures or saturation deficit values observed across the four sampling sites, while the thin lines and pale shades represent those rates within the whole range of the climatic variables observed.

Influence of the length of developmental diapause. The scenario allowing ticks feeding in the summer of year *y* to undergo a developmental diapause and to begin moulting in the spring of year *y*+1 (Table 1, Theme 2 null hypothesis: "Phase 2 [Mar 21–Jun 21]", and illustrated in Fig. 2) exhibited a significantly better fit than the scenario assuming a later start of moulting in the summer of year *y*+1 (Table 1, T1.12 vs. T2 ΔDIC: -58.3, Theme 2 alternative hypothesis: "Phase 3 [Jun 22–Sep 22]"). Additionally, the annual peak of questing tick densities predicted by the best-fitting model were, on average, 37% higher for nymphs and 28% higher for adults compared to the model assuming a later start of moulting (Fig. S5), more accurately matching the primarily unimodal questing activity observed in the data.

Forecasting *I. ricinus* population under climate change scenarios. We chose Murbach site as a representative location for forecasting the *I. ricinus* population for the next 20 years (2023–2042), considering its higher tick densities compared to the other sites, and assuming that similar climate changes will occur in the Alsace region. Our projections based on the best-fitting model showed that, under moderate to pessimistic scenarios for reducing greenhouse gas emissions (RCP 4.5, 6.0, and 8.5[20]), the abundance of *I. ricinus* decreased over time (Fig. 5). The extent of the decrease was most noticeable under the RCP 6.0 scenario, with the annual peak of questing tick density decreasing on average by 4.64 per 100m^2 (95% confidence interval [CI]: 2.77–6.52 per 100m^2, p-value<0.001) for nymphs and 0.26 per 100m^2 (95%CI: 0.11–0.40 per 100m^2, p-value: 0.001) for adults each year (Fig. 5). These decreases corresponded to average reductions of 21.8% and 53.8% in questing nymph and adult densities, respectively, after 20 years, compared to the maximum density values observed at the Murbach site.

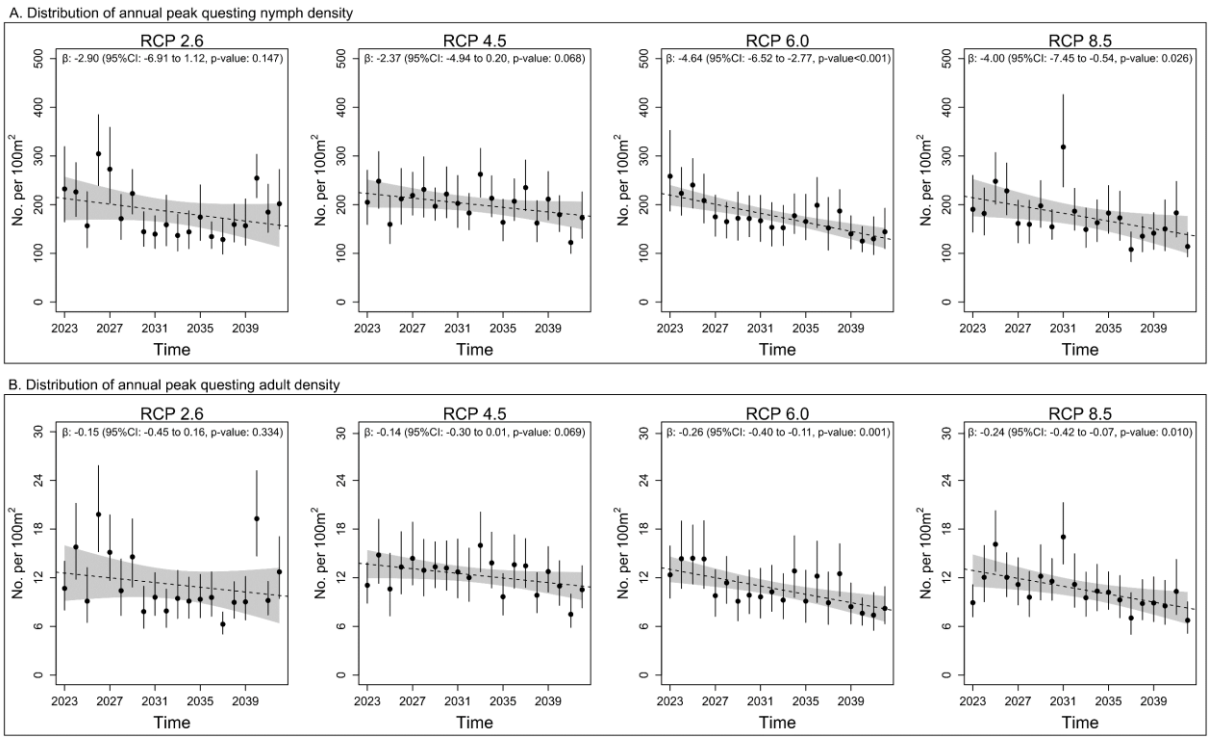

Figure 5. Forecast of questing tick density over the next 20 years until 2042 under Representative Concentration Pathways (RCP). RCP 2.6, 4.5, 6.0, and 8.5 represent climate scenarios from the most optimistic (RCP 2.6) to the most pessimistic (RCP 8.5) view on reducing greenhouse gas emission. The points and vertical lines represent the median and 95th percentile intervals of the annual peak questing **(A)** nymph and **(B)** adult densities predicted based on the joint posterior distribution of the best-fitting model and daily mean temperature and saturation deficit values predicted under respective climate scenarios. Linear regression models were fitted to the median values of these annual peak densities, and their mean and 95% confidence interval predictions are illustrated by the dotted lines and shades, respectively, with their results presented on the top of each panel.

Discussion

Our study, for the first time, quantified the drivers of *I. ricinus* population dynamics in their natural habitat by fitting a mechanistic model to longitudinal tick density data we collected from four sites in Northeast France over the decade from 2013 to 2022. Our model explicitly accounted for the functional relationship between climatic conditions and tick development, the timing of diapauses, and questing and blood-feeding processes. This approach enabled robust parameter estimation while addressing variability in data[19,22], allowing us to reproduce the observed population dynamics and, furthermore, generate the first projections of the *I. ricinus* population in one site of the study region under climate change scenarios.

I. ricinus has excellent adaptability to a wide range of climate conditions across Europe[2,16,17], suggesting that climatic conditions may influence their demographic processes differently to laboratory observations. This was also the case for the studied *I. ricinus* populations. Firstly, the daily moulting rates were estimated to peak at relatively mild temperatures (median: 14.2°C, 95% HDI: 12.5–16.1°C). This finding contrasts with the literature that presented shortening periods between feeding and moulting, and thus increasing moulting rates, with increasing temperature[7,12]. It should be noted that these results from the literature were mainly derived from laboratory experiments where different groups of ticks were exposed to different temperatures under otherwise controlled conditions[7,12,15]. Notably, the temperatures were kept constant for each group, with relative humidity maintained at or near saturation, a condition that rarely occurs in natural environments. In our study area, relative humidity tended to be low during the hot season in the study region, which may negatively affect the survival of *I. ricinus* undergoing moulting because it temporarily loses its water-absorbing capability in sub-saturated air[1,23], thereby necessitating adaptation to moult at lower temperatures.

Secondly, allowing ticks feeding in the summer of year y to start moulting only from the spring of year y+1 provided a significantly better explanation for the observed data, compared to allowing a further delayed start in moulting from the summer of year y+1. This could be explained by the observation that the studied *I. ricinus* populations exhibited a single prominent yearly peak in questing activity, typically during late spring or early summer—a pattern also frequently observed in other parts of Europe[17]. Considering this, allowing moulting from the spring, rather than the summer, after a developmental diapause, better prepares a substantial number of unfed ticks to be ready for questing before the main questing season and thereby better aligns with those prominent peaks, leading to a better model fit. Indeed, the alternative scenario of a year-long delay in moulting has been widely considered for *I. ricinus* populations that exhibit a bimodal questing pattern, characterised by an additional, smaller peak in questing activity in the fall[7,24].

In contrast with the daily moulting rates, our model suggests that the daily oviposition and hatching rates increased with increasing temperature or saturation deficit, consistent with the literature discussed above[7,12]. Following peak questing activity in the late spring or early summer, temperatures—and consequently, the drying power of the air, were high when most female adults had their blood meal and were ready for laying eggs. *I. ricinus* is known to continuously lay eggs soon after engorgement unless the temperature drops too low, at which point egg laying may cease[1]. Thus, in absence of diapause for engorged female adults and eggs, both oviposition and hatching may have predominantly occurred in the summer. Regarding model fits, saturation deficit explained the observed data significantly better than temperature when it was assumed for both oviposition and hatching processes. However, both climatic variables explained the observed data at similar levels when assumed for either oviposition or hatching. This suggests that variations in saturation deficit were more effective for explaining oviposition and hatching occurring in a synchronised manner, while temperature still remained a reliable predictor for each process individually.

Although oviposition and hatching rates were allowed to increase or decrease as functions of environmental variables, we did not explicitly assume a diapause for engorged female adults and eggs due to a lack of data indicating the emergence of eggs and larvae. While the literature suggested that diapause does not seem to occur in engorged *I. ricinus* female adults[1,25,26], some studies suggested diapause for eggs[15,25,26]. This highlights the need for additional field data on the emergence of larvae to allow for hypothesis testing regarding the presence of diapause for eggs, as well as a more robust estimation of the associated parameters. Such data would include questing larva density data, but this may require more thorough sampling efforts, for example, dragging a larger area, because larvae tend to aggregate more than nymphs and adults, having been hatched from clustered eggs.

We estimated that the daily host contact rates were highest at the Murbach site, suggesting that this study site may have provided a more ideal environment for ticks than the others. Indeed, Murbach has been known to harbour a large abundance of small mammals and, particularly, deer in Northeast France[27,28]. This suggests that the high host abundance in Murbach may have increased the likelihood of encountering a host during questing, leading to more successful progression to the next life stages and thus increased tick abundance. Interestingly, this area has also been associated with high risks of Lyme disease and tick-borne encephalitis[27,28]. This highlights the need for deeper research into the impact of host abundance on tick abundance as well as tick-borne pathogen transmission dynamics.

Climate forecasts over the next 20 years indicated that, under moderate to pessimistic climate scenarios, the abundance of *I. ricinus* at the Murbach site decreases significantly. This highlights the need for continued monitoring of the status of *I. ricinus* populations in the study region, as well as their role as reservoir and vector of Lyme disease, tick-borne encephalitis, or other zoonotic pathogens. In particular, our forecasts provide insights into the impact of temperature increases in areas where *I. ricinus* has already been established under similar climatic conditions. This needs to be considered along with the geographical expansion of *I. ricinus* towards regions at higher latitudes and higher elevations previously uninhabited by *I. ricinus*[29-31], when assessing the impact of climate change on the overall disease burden by *I. ricinus*-borne pathogens. However, caution must be exercised in interpreting this result because climatic changes would also affect tick mortality, host population dynamics and patterns of land-use, factors which were not explicitly addressed by our model. Additionally, considering ticks' adaptability evidenced in various parts of Europe[16,17], tick development may exhibit different functional relationships with future climatic conditions compared with those estimated based on the observed data.

Further points merit consideration when interpreting the study results. Firstly, our model assumed that baseline daily mortality and host contact rates remained constant throughout each year due to the lack of available information. These rates are likely to vary in response to changes in energy reserves, climatic conditions, and host availability[24,32], possibly leading to yearly variations in tick abundance, as indicated by variations in questing tick density in this study. Secondly, although our model structure allowed for assessing the timing of diapause (spring vs. summer), it was constrained by the way calendar years were divided, which may not fully reflect the field reality. This is because, although the division was made based on changes in day length, which is a primary determinant of diapause[26,32], the initiation and, particularly, termination of diapause could also be influenced by other factors, such as local climatic conditions and heterogeneities in the behaviour of individual ticks[26,32]. Thirdly, the functional relationship between climatic conditions and tick development were constrained by the fixed variance of the Gamma distributions assumed to underlie those relationships, although sensitivity analysis did not indicate major changes in the study results. These points underline the need for further demographic data to improve model inference, such as temporal variations in mortality and host abundances, as well as the emergence of newly moulted ticks or laid eggs.

In conclusion, our study elucidated the environmental and ecological drivers of *I. ricinus* population dynamics in Northeast France. While oviposition and hatching processes demonstrated similar dynamics to those suggested by laboratory experiments and field observations in other regions, moulting exhibited unique dynamics in its relationship with climatic conditions and delays through developmental diapause. These characteristics were

considered to drive the predominantly unimodal questing pattern observed in the study region. Our findings emphasise the importance of further research tailored to various regions where *I. ricinus* has established, to assess heterogeneities in the mechanisms behind *I. ricinus* population dynamics. Furthermore, our modelling framework can also be expanded to other *Ixodidae* ticks of public and animal health significance. Finally, when combined with relevant epidemiological data, our modelling framework will allow the assessment of the transmission of *Ixodes*-borne diseases, such as Lyme disease and tick-borne encephalitis.

Materials and Methods

Longitudinal questing tick density and climate data

Between 2013 and 2022, we collected host-seeking *I. ricinus* ticks (questing nymphs and adults) at four sites located in Dannemarie (47°41'56.7"N 7°09'15.1"E), Illkirch (48°31'06.3"N 7°44'35.9"E), Murbach (47°55'18.2"N 7°09'21.3"E), and Niedermunster (48°26'02.6"N 7°24'28.6"E) in the Alsace region of Northeast France. The ticks were collected through multiple sampling events per year, as part of surveillance activities conducted by the national reference centre for *Borrelia* (https://www.chru-strasbourg.fr/service/borrelia/).

At each visit, the ticks were collected from the vegetation and litter by dragging a $1m^2$ piece of white cotton sheet over an area of $10m^2$ and inspecting the cloth for ticks every $10m^2$; at each visit, a total of 30 draggings were performed in order to sample a total vegetation area of $300m^2$. The same area was collected at each visit. The captured nymph and adult ticks were removed from the cloth, identified, and counted, and the density per $100m^2$ was calculated. At least two collectors participated in each visit, which occurred every month when the weather conditions were favourable for sampling.

At each visit, the ground temperature and relative humidity were measured and recorded with an LCD digital hygro-thermometer. Additionally, for each sampling site, observed and projected daily mean temperature and relative humidity near the surface were sourced from the Copernicus Climate Change Service for the period 2008–2022[33,34] and for the following 20 years under different Representative Concentration Pathway (RCP) scenarios[20], including RCP 2.6, 4.5, 6.0, and 8.5. A higher RCP value indicated a higher level of greenhouse gas emissions, and therefore, global surface temperatures, over time.

Daily mean temperature and relative humidity from the Copernicus Climate Change Service were highly correlated with those recorded from the field. Therefore, the metrics from the Copernicus Climate Change Service were used

for fitting models and projecting *I. ricinus* tick abundance under the RCP scenarios. Additionally, these metrics were used to calculate daily mean saturation deficit, based on the formula provided by Randolph and Storey [35]. Day length was obtained using the *daylength* function of the *geosphere* package[36] in R. 4.3.2[37]. Each climate data was smoothed with a Gaussian kernel of 21 days to account for their cumulative impact on tick host demography processes.

Mechanistic model for tick population dynamics

Model structure

Figures 1 and 2 illustrate the overall model structure. Table 2 describes input parameters, and Table 3 details the estimated parameters. Here, unfed ticks (L_u, N_u, A_u) were ticks that have newly moulted or hatched but have not yet begun seeking a host, whereas questing ticks (L_q, N_q, A_q) were ticks actively seeking a host. Engorged ticks (L_e, N_e, A_e) were ticks that have fed but have not yet progressed to the next life stage.

The progression of *I. ricinus* occurs through development (oviposition, hatching, larva-to-nymph moulting, and nymph-to-adult moulting), questing, host contact, and mortality. Of these processes, development and questing are influenced by meteorological conditions and the occurrence of developmental and behavioural diapauses[26,32]. Our model accounted for these meteorological impacts by allowing ticks to advance through life stages at developmental and questing rates changing daily according to climatic variations. Additionally, our model accounted for developmental diapause (delays in moulting) and behavioural diapause (delays in questing) by allowing for moulting based on the timing of feeding, and for questing based on the timing of moulting, across four distinct phases of the year. Phase 1 (Jan 1–Mar 20) and Phase 4 (Sep 23–Dec 31) were periods when moulting processes were halted because of short daylengths (day is longer than night) and low temperatures during these months[26,32]. In contrast, Phase 2 (Mar 21–Jun 21) and Phase 3 (Jun 22–Sep 22) were periods where moulting processes could occur, divided at summer solstice when day length starts to decrease. Following this calendar, engorged larvae and nymphs were categorised into the following compartments according to the timing of feeding in the year: ticks fed in Phases 1 and 2 ($L_{e1\cdot2}$ and $N_{e1\cdot2}$), and those fed in Phases 3 and 4 ($L_{e3\cdot4}$ and $N_{e3\cdot4}$). Questing activity was allowed throughout the four phases, with its daily rate being influenced by meteorological conditions, but depending on the timing of moulting. Thus, to account for behavioural diapause, the compartments for unfed nymphs (N_u) and adults (A_u) were divided based on the timing of moulting: ticks moulted in Phase 2 (N_{u2} and A_{u2}), and those moulted in Phase 3 (N_{u3} and A_{u3}) (see *Developmental rate* and *Questing rate* below for details).

The following sections describe in detail how developmental, questing, and moulting, and mortality rates were modelled.

Developmental rate

The daily oviposition, hatching, and larva-to-nymph and nymph-to-adult moulting rates were modelled to be associated with climatic conditions under Theme 1 hypotheses. Theme 1 null hypothesis assumed that these developmental rates continued to increase with daily mean temperature, following the inverse of the power-law curves estimated by Ogden, Lindsay [12] (Table 2, $\eta_{i=1,\ldots,4}$). These curves were derived from the observed number of days required for *Ixodes scapularis* to progress to a subsequent life stage under different temperature conditions in a laboratory setting. According to these curves, peak rates occurred exclusively at the maximum temperature observed. Randolph, Green [7] derived curves describing changes in the hatching and moulting rates of *Ixodes ricinus* at different temperatures based on laboratory observations. Considering that these curves were highly correlated with those derived by Ogden, Lindsay [12] and only available for hatching and moulting, but not oviposition rates, we chose to use the Ogden, Lindsay [12] curves as the underlying functions for Theme 1 null hypothesis.

In contrast, Theme 1 alternative hypothesis allowed that these developmental rates increased, peaked, and decreased across the range of a given climatic condition observed in the ticks' natural habitats, following the shape of a Gamma distribution (Table 2, $\gamma_{i=1,\ldots,4}$). Temperature is recognised as the primary factor influencing tick development[12,38,39], and saturation deficit is determined by both temperature and relative humidity. Therefore, we also considered saturation deficit in modelling developmental rates under Theme 1 alternative hypotheses, along with temperature.

For example, the daily rate of developmental process i (γ_{i_t}) was hypothesised to vary with daily mean temperature *t*, following the shape of a Gamma distribution defined by its mode (θ_i) and variance (ε_i):

Eq. 1 $$\gamma_{i_t} = \varepsilon_i \frac{f(t;\theta_i,\sigma_i)}{f(\theta_i;\theta_i,\sigma_i)}$$

Here, $f(t;\theta_i,\sigma_i)$ represented the probability density of a Gamma distribution at temperature t, with θ_i and σ_i being its mode and standard deviation, respectively, derived from the shape and rate parameters of a Gamma distribution. This probability density was normalised by the maximum probability density, $f(\theta_i;\theta_i,\sigma_i)$, and then converted into a rate using a scaling parameter ε_i. Thus, ε_i represented the peak rate of developmental process i occurring at a temperature of θ_i. Under this hypothesis, θ_i and ε_i were estimated through model fitting, while σ_i

was fixed to a value that covered a reasonably wide temperature range within which ticks were considered to be active (Table 1 in the main text). We assumed that larva-to-nymph and nymph-to-adult moulting rates peaked under the same climatic condition ($\theta_3 = \theta_4$), but at different levels of intensity ($\varepsilon_3 \neq \varepsilon_4$).

The timing of developmental diapause (Theme 2) was assessed as follows. The null hypothesis assumed that ticks that fed during Phase 2 (when day length increases, Mar 21–Jun 21) moulted in Phase 3 of the same year (dark brown shades in Fig. 2) or Phase 2 of the following year (pale brown shades in Fig. 2), based on climatic conditions (see Theme 1). Ticks that fed during Phase 3 (when day length decreases, Jun 22–Sep 22) moulted in Phase 2 or Phase 3 of the following year (pale brown shades in Fig. 2), still based on climatic conditions (see Theme 1). In Theme 2 alternative hypothesis, these ticks were allowed to moult only from Phase 3 of the following year, whilst the same assumption was made for ticks that fed during Phase 2.

Questing rate

The daily questing rate ($\tau_{l,s,d}$) was defined as the rate at which unfed ticks are active and looking for a host, and modelled as follows. First, for life stage l, sampling site s on day d, a generalised additive model fit value, $GAM\ fit_{l,s,d}$, was obtained as a function of the photoperiod, daily mean temperature, and daily mean relative humidity recorded on day d in site s (see Supplementary Information for details). Second, this value was normalised, divided by the maximum GAM fit value observed across all sites during the study period, $GAM\ fit_{l_{max}}$. Finally, this normalised value was converted into a rate, multiplied by a scaling parameter δ.

Eq. 2 $$\tau_{l,s,d} = \delta \frac{GAM\ fit_{l,s,d}}{GAM\ fit_{l_{max}}}$$

δ was estimated, assuming that it was the same across the sites and life stages, given that the GAM fit values were derived after accounting for these differences. Therefore, it represented the maximum questing rate observed. Because GAM fit values were not available for larvae, it was assumed that larvae and nymphs exhibit identical questing rates, distinct from those of adults.

In addition, our model accounted for behavioural diapause (delays in questing) by allowing ticks to start questing based on the timing of their moulting. Firstly, ticks that moulted in Phase 3 were modelled to start questing from Phase 2 of the following year (pale green shades in Fig. 2). In contrast, those that moulted in Phase 2 were allowed to begin questing without a behavioural diapause (dark green shades in Fig. 2).

Host contact rate

Questing ticks were modelled to take a blood meal following a daily host contact rate, $\beta_{l,s}$, as follows:

Eq. 3 $$\beta_{l,s} = \varphi_l \rho_s$$

where $\beta_{l,s}$ was assumed to vary between the life stages (subscript l) and across the four study sites (subscript s). The baseline host contract rates (φ_l) was assumed different for larvae, nymphs, and adults, but with the same ratios as estimated by Dobson, Finnie and Randolph [5], and were scaled differently (ρ_s) across the four sampling sites, to account for the between-site variability resulting from tick and host densities and host species. β was assumed constant over time, with the premise that temporal changes in the daily questing rate would explain temporal changes in the probability of feeding on a host.

Mortality rate

The daily background mortality rates, m_0, were derived by Daniel, Cerný [13] through the observations of *I. ricinus* within containers placed in fields, for unfed and questing ticks in each life stage. In the present study, these daily background mortality rates were assumed for unfed and questing ticks in each life stage (subscript l), linearly increasing with population size, becoming twice m_0 when population size reached its threshold value, ω_l. It was assumed that the maximum questing nymph density observed across the study period was proportional to the threshold value for nymphs, allowing the estimation of the questing population size at this limit using a sampling fraction of 6.0%[40]. Following this, the thresholds for larvae and adults were derived from the nymph threshold, taking into account theoretical survival probabilities between life stages[41]. For unfed or questing ticks in life stage l on site s and day d, with population of N, density-dependent mortality, $m_{1_{l,s,d}}$, was determined as follows:

Eq.4 $$m_{1_{l,s,d}} = m_{0_l}\left(1 + \frac{N_{l,s,d}}{\omega_l}\right)$$

For engorged ticks, mortality (m_2) was set to 1/365 to ensure that, on average, these ticks either progressed to subsequent life stages within one year after having their blood meal or died (overwintering no more than once).

Model fitting and hypothesis testing

The model was fitted to the longitudinal questing tick density data within an HMC Bayesian inference framework using the *RStan* package[42] in R version 4.3.2[37]. The HMC sampling was iterated with multiple chains until convergence was considered achieved, based on visual inspection of the trace plots, Gelman-Rubin convergence diagnostic (<1.01), and the number of effective sample size (>500). Briefly, after the tick population was simulated

with a given set of parameter values, the predicted number of questing ticks per 100m^2 was calculated assuming a sampling fraction of 6.0%[40]. Then, for site s and day d, the probability of the observed number of questing ticks per 100m^2 was assessed under a given probability distribution. Assuming an excess variability (overdispersion) in the observed data[43], we used a negative binomial distribution. The model was, therefore, fitted with the following likelihood function:

Eq. 5 $$L = \prod_{s,d} NB(k_{N_q,s,d}; \mu_{N_q,s,d}, \emptyset_{N_q}) NB(k_{A_q,s,d}; \mu_{A_q,s,d}, \emptyset_{A_q})$$

For nymphs and adults, respectively, $k_{N_q,s,d}$ and $k_{A_q,s,d}$ were the observed and $\mu_{N_q,s,d}$ and $\mu_{A_q,s,d}$ were the predicted number of questing ticks per 100m^2 on site s and day d, and $\emptyset_{N_q}$ and $\emptyset_{A_q}$ were the overdispersion parameters.

Model fits under different assumptions on the functional relationships between climatic conditions and tick development (Theme 1) were assessed based on the deviance information criterion (DIC) as follows. The baseline model (Table 1, T0) assumed that (i) all types of developmental rates increased with temperature following the inverse of the power-law curves estimated by Ogden, Lindsay [12] (Theme 1 null hypothesis) and (ii) ticks that fed a blood meal in Phase 3 moulted from Phase 2 of the following year after undergoing a developmental diapause (Theme 2 null hypothesis).

During model fit comparison, one specific type of developmental rate was assumed to vary with temperature or saturation deficit, following a Gamma distribution shape (Table 3, T1.1–T1.6), in contrast to the power-law function assumed in the baseline model. If this alternative assumption resulted in a decrease in DIC greater than 5 units, it was considered to indicate a significantly better explanation of the observed data and replaced the null hypothesis assumed in the baseline model. Subsequently, other types of developmental rate were assessed in the same manner (Table 1, T1.7 – T1.12), and the best-fitting mechanistic model—a model with a set of hypotheses that best explains the questing tick density data—was determined when no alternative hypotheses led to a DIC reduction greater than 5 units.

As a posterior predictive check, the densities of questing nymphs and adults were simulated based on the joint posterior distribution of the best-fitting mechanistic model and compared with the observed densities. For a given developmental process i, its functional relationship with the climatic variable selected in the best-fitting mechanistic model was described based on θ_i and ε_i. If daily mean saturation deficit was selected in the best-fitting model, the functional relationship with daily mean temperature was also explored in a separate model fitting

to help the interpretation of study results. Finally, to explore how the length of developmental diapause on a model fit (Theme 2), we compared the best-fitting model to the scenario that allowed extended delays in moulting for ticks that fed in Phase 3 (Table 1, T2).

Projections under different climatic scenarios

We forecast the *I. ricinus* population at the Murbach site until 2042 based on the climate changes predicted under the RCP 2.6, 4.5, 6.0, and 8.5 scenarios—corresponding to optimistic to pessimistic view on reducing greenhouse gas emission—and the parameter estimates from the best-fitting mechanistic model. The *I. ricinus* population at the Murbach site was chosen as it exhibited higher tick densities in the observed data. For each RCP scenario, forecasting was performed by simulating the *I. ricinus* population for each set of joint posterior parameter estimates, based on the predicted changes in the climatic variable selected in the best-fitting model. For each iteration, we recorded the annual peak questing tick densities as an indicator of tick abundance. After the simulation, we computed their median values for each year and then fitted a linear regression model to these median values over the forecasted years.

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Competing interests

The authors declare no competing interests.

Table 1. Comparison of mechanistic models under different sets of Theme 1 and 2 hypotheses

Model no.	Functional relationship between meteorological conditions and tick development			Moulting start after diapause	No. of parameters estimated	DIC	ΔDIC [a]
	Moulting rate	Hatching rate	Oviposition rate				
T0	1/power-law curve	1/power-law curve	1/power-law curve	Phase 2 [Mar 21–Jun 21]	7	4107.4	231.7
T1.1	Gamma dist. by temperature	1/power-law curve	1/power-law curve		10	3933.5	57.9
T1.2	Gamma dist. by saturation deficit	1/power-law curve	1/power-law curve		10	3933.2	57.5
T1.3	1/power-law curve	Gamma dist. by temperature	1/power-law curve		9	4097.9	222.2
T1.4	1/power-law curve	Gamma dist. by saturation deficit	1/power-law curve		9	4095.7	222.2
T1.5	1/power-law curve	1/power-law curve	Gamma dist. by temperature		9	4095.6	219.9
T1.6	1/power-law curve	1/power-law curve	Gamma dist. by saturation deficit		9	4097.0	221.3
T1.7	Gamma dist. by temperature	Gamma dist. by temperature	1/power-law curve		12	3929.5	53.8
T1.8	Gamma dist. by temperature	Gamma dist. by saturation deficit	1/power-law curve		12	3929.3	53.7
T1.9	Gamma dist. by temperature	1/power-law curve	Gamma dist. by temperature		12	3928.2	52.5
T1.10	Gamma dist. by temperature	1/power-law curve	Gamma dist. by saturation deficit		12	3920.7	45.0
T1.11	Gamma dist. by temperature	Gamma dist. by temperature	Gamma dist. by saturation deficit		14	3888.0	12.4
Best-fitting model: T1.12	Gamma dist. by temperature	Gamma dist. by saturation deficit	Gamma dist. by saturation deficit		14	3875.7	0
T2	Gamma dist. by temperature	Gamma dist. by saturation deficit	Gamma dist. by saturation deficit	Phase 3 [Jun 22–Sep 22]	14	3934.0	58.3

a difference in DIC to the best-fitting model (T1.12)
DIC: deviance information criterion
1/power-law curve: a developmental rate continued to increase with temperature, following the inverse of the power-law curves estimated by Ogden, Lindsay[12] based on laboratory observations.
Gamma dist. by temperature (or saturation deficit): a developmental rate increased, peaked, and decreased across temperature (or saturation deficit), following the shape of a Gamma distribution.

Table 2. Input parameters for the mechanistic model. Notations, definitions, values and sources or assumptions.

Notation	Definition	Value		Source or assumption
$n_{new\ eggs}$	Number of eggs laid by one female adult	1,597		Macleod [44], Sonenshine [45]
m_{0_l}	Daily background mortality for unfed and questing ticks by life stage [a]	0.02618 (egg) 0.0067 (larva), 0.0021 (nymph), 0.0014 (adult)		Dobson, Finnie and Randolph [5]; Daniel, Cerný [13]
m_2	Daily background mortality for engorged ticks	0.00274		Engorged ticks survive for one year if not moulting or laying eggs [1,26].
φ_l	Baseline daily host contact rate by life stage	0.0493 (larva), 0.071 (nymph), 0.09 (adult)		Dobson, Finnie and Randolph [5]
σ	The standard deviation of the Gamma distribution, which specified changes in the developmental rates by climate conditions	Temperature: 8°C Saturation deficit: 4		The standard deviation was set to encompass reasonably wide ranges of either temperature or saturation deficit values.
$GAM\ fit_{l,s,d}$	Temporal trends in daily question rates by life stage and site	see Supplementary Information		Temporal trends in daily questing rates were assumed to follow daily questing tick density predicted by the best-fitting generalised additive model (GAM).
$GAM\ fit_{l_{max}}$	The maximum predicted tick density by life stage	see Supplementary Information		
η_{O_t}	Daily oviposition rate at temperature *t* under Theme 1 null hypothesis	$1/(1300t^{-1.42})$		Ogden et al. (2004). Temperatures below zero were assumed zero when daily developmental rates were determined by these functions.
η_{H_t}	Daily hatching rate at temperature *t* under Theme 1 null hypothesis	$1/(34234t^{-2.27})$		
$\eta_{M_{L\to N_t}}$	Daily larva-to-nymph moulting rate at temperature *t* under Theme 1 null hypothesis	$1/(101181t^{-2.55})$		
$\eta_{M_{N\to A_t}}$	Daily nymph-to-larva moulting rate at temperature *t* under Theme 1 null hypothesis	$1/(1596t^{-1.21})$		
Climate condition (2008–2022) [b]		**median**	**95th percentile interval**	
Daily mean 2m temperature [c]		10.2°C	-10.0–27.3°C	Daily statistics calculated from ERA5 data.
Daily mean relative humidity [c]		77.1%	42.1–97.3%	Daily statistics calculated from ERA5 data.
Daily mean saturation deficit		2.2	0.15–13.7	Computed based on ERA 5 daily mean temperature and relative humidity using the equation in Randolph and Storey [35]
Day length		12.3 hrs	8.3–12.3 hrs	The data were extracted for each day and each site using the *daylength* function of the *geosphere* package.

a The overall mortality, m_1, was assumed to increase with population size from these daily background mortality rates.
b The climate conditions were smoothed with a Gaussian kernel of 21 days to account for their cumulative impact on tick host demography processes.
c Daily mean 2m temperature and relative humidity data under climate change scenarios between 2023 and 2042 were sourced from the Copernicus Climate Change Service under the following settings. Experiment: RCP 2.6, 4.5, 6.0, and 8.5, Model: IPSL-CM5A-LR (IPSL, France), Ensemble number: r1i1p1

Table 3. Parameters estimated by the mechanistic model. Notations, definitions, priors, and assumptions

Notation	Definition	Prior	Assumption
Daily questing rate			
$\tau_{l,s,d}$	Daily questing rate by life stage, site, and day	NA (computed from other parameters)	Larvae and nymphs were assumed to have same questing rates.
δ	A scaling parameter for the daily questing rate	Uniform (0, 0.143)	The upper prior limit was set to ensure that ticks remain unfed for at least 7 days after moulting, to account for the hardening process [1].
Daily host contact rate			
$\beta_{l,s}$	Daily host contact rate by life stage and site	NA (computed from other parameters)	For each life stage and study side, β was derived by scaling the baseline daily host contact rate (Table 1) using the parameter ρ.
ρ_s	A scaling parameter for the daily host contact rates by site	Uniform (0, 11.1)	The upper prior limit is set to ensure that β remains below 1.
Developmental rate under Theme 2 alternative hypothesis			
γ_{O_x} γ_{H_x} $\gamma_{M_{L\to N_x}}$ $\gamma_{M_{N\to A_x}}$	Daily oviposition, hatching, and larva-to-nymph and nymph-to-adult moulting rates at temperature or saturation deficit x	NA (computed from other parameters)	The daily developmental rate was assumed to vary with climatic conditions following the shape of a Gamma distributions.
θ_O θ_H θ_M	A temperature (or saturation deficit) at which a given daily developmental rate peaks following a gamma distribution shape	Temperature: Uniform (0, 27.3°C) Saturation deficit: Uniform (0, 14.6)	The daily developmental rate was assumed to peak between 0°C (or a saturation deficit of 0) and the maximum temperature (or saturation deficit) observed during the study period. Larva-to-nymph and nymph-to-adult moulting rates were assumed to peak at the same temperature (or saturation deficit).
ε_O ε_H $\varepsilon_{M_{L\to N}}$ $\varepsilon_{M_{N\to A}}$	A scaling parameter for daily oviposition, hatching, and larva-to-nymph and nymph-to-adult moulting rates	Uniform (0, 0.105) Uniform (0, 0.066) Uniform (0, 0.043) Uniform (0, 0.057)	The peak daily developmental rates, estimated to occur within the observed temperature ranges according to the power-law functions of Ogden, Lindsay [12], were increased by an additional 25% to accommodate possibly species differences. These values were set as the upper prior limits.
Parameters for model fitting based on log-likelihood values			
$\emptyset_{N_q}$	Overdispersion for nymph in a negative binomial distribution	Uniform (0, 10)	The observed tick density was assumed to exhibit overdispersion, attributed to unknown heterogeneity in the data, such as unaccounted demography processes and sampling bias.
$\emptyset_{A_q}$	Overdispersion for adults in a negative binomial distribution	Uniform (0, 10)	