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The effect of historic climate change on the population dynamics of *Ixodes ricinus*

Dominic P. Brass[1], Steven M. White[1], Sarah J. Burthe[2], Stefanie M. Schäfer[1] and Bethan V. Purse[1]

[1]UK Centre for Ecology & Hydrology, Wallingford, UK
[2]UK Centre for Ecology & Hydrology, Edinburgh, UK

DPB, 0000-0002-4900-9124; SMW, 0000-0002-3192-9969; SJB, 0000-0001-8871-3432; SMS, 0000-0002-8748-7725; BVP, 0000-0001-5140-2710

The distribution and intensity of tick-borne disease (TBD) transmission events across Europe are increasing in response to changes in climate, land use and host populations. Understanding how changing environmental factors drive seasonal tick population dynamics is critical for predicting the public health impacts of TBDs. Here, we develop an environmentally driven system of stage-structured delay-differential equations to predict the population dynamics of *Ixodes ricinus*, the primary vector of human TBDs in Europe. We validate the model against data from 77 tick populations in 20 European countries, finding that 55% of the variation observed in the population dynamics of nymphs can be attributed to the effects of climatic variation. Over the last 40 years, we predict a climate change-induced increase in tick abundance and seasonal activity in northern Europe, and commensurate decreases across southern Europe, which should be accounted for in national health policy and climate change adaptation plans.

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Author for correspondence:
Dominic P. Brass
e-mail: dombra@ceh.ac.uk

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1. Introduction

This century has seen rapid changes in the incidence of tick-borne diseases (TBDs) in Europe, with a widespread increase in the incidence of Lyme borreliosis and tick-borne encephalitis (TBE) in endemic regions as well as the emergence of new TBE virus (TBEV) foci [24,84,87]. TBEV can cause neurological damage and death in unvaccinated people, while Lyme disease can cause severe debilitation if left untreated [31,72]. Across Europe, TBDs place a substantial burden on public health, and each year there are an average of 128 888 reported human cases of Lyme borreliosis, and 3000 reported cases of TBE [9,37]. Understanding the mechanisms underpinning changes in disease incidence is necessary to design effective interventions and risk management strategies [20,79]. However, tick life cycles are complex and sensitive to variation in both biotic and abiotic environments, making it challenging to produce robust predictions of TBD risk across broad geographical scales. Temperature, humidity, land cover and host activity are all critical in driving the timing and intensity of tick activity and therefore in determining regional and seasonal variations in tick exposure hazard [50].

Ixodes ricinus, the primary vector of human TBDs in Europe, has a broad environmental niche, and active populations are found from southern Spain to below the Arctic Circle in Norway (36–66° latitude) [25,39]. Across this environmental gradient, inter-regional variation in tick population dynamics is observed, underpinning the occurrence of human infection for both Lyme borreliosis and TBE [44,66]. Ticks are ectotherms with complex life cycles spanning multiple years, and many of their life-history traits are highly sensitive to

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variation in the abiotic environmental conditions [58]. For example, the time required for an engorged larva to complete development and become a nymph varies from one month at 25°C to four months at 14°C [11]. Similarly, the vapour pressure deficit, a measure of the drying power of air, determines the amount of time that ticks can spend actively seeking hosts before needing to cease activity and rehydrate. Bouts of questing have been observed to last for a few hours at high vapour pressure deficits to multiple days when the vapour pressure deficit is low [30,61]. Biotic factors are also important in determining TBD hazard owing to the inter-relationship between the requirements of hosts, parasites and pathogens. *Ixodes ricinus* has three active developmental stages, larvae, nymphs and adults, each of which require a blood-meal to either progress to the next life-stage or to develop eggs. *Ixodes ricinus* has been observed to parasitize a broad range of vertebrate host species. These host species include small mammals (such as bank voles) and birds that can develop infections with TBEV and *Borrelia* and are competent reservoirs of pathogens, and large mammals, such as deer and livestock, that play a key role in feeding tick populations, but within which pathogens do not replicate, and are therefore referred to as reproductive hosts [42,49]. For the majority of tick-borne pathogens, humans are dead-end hosts and are infected in spill-over events. To understand the risk of human TBD, we therefore need to understand the endemic transmission cycles driven by interactions between climate, ticks and non-human hosts that determine the period and intensity of tick exposure risk [73].

Mechanistic models are powerful predictive tools that can provide insights into how species with complex life cycles will respond to environmental change at the population level [26]. Previous mechanistic models for *Ixodid* ticks have addressed a range of questions, such as determining the effects of tick phenology on disease dynamics and predicting how decadal variation in land use and wildlife populations alters patterns of tick exposure risk across Europe [19,47,48]. However, owing to the complexity of tick life cycles, previous models often make simplifying assumptions about tick life-history processes, are poorly validated against field observations or are back-fitted to a limited number of field studies to establish climate-life history relationships. Consequently, these models lack the necessary biological details for accurate, broad-scale predictions of abundance and seasonality, which would ensure they are robust to novel combinations of environmental conditions. Here, we derive a detailed model for *Ixodes ricinus*, using environmentally driven stage-structured delay differential equations (DDEs) to better represent the tick developmental cycle [33]. DDEs show excellent predictive ability in other vector-borne disease systems, predicting mosquito-borne disease transmission dynamics accurately at continental scales [7,26], but have yet to be applied to ticks. We extensively validate our model against field data from 77 tick populations across 20 European countries, finding that 55% of the variation in tick population dynamics observed in field populations can be attributed to effects of climatic variation on tick life history. Extrapolating the validated model across *I. ricinus*' environmental niche, we determine how the intensity and seasonality of tick exposure risk have changed over the last 40 years in Europe, and explore the sensitivity of tick dynamics to plausible variation in host density. We highlight the potential of the framework for informing short- and long-term decision making.

2. Methods

2.1. Overview of tick biology

Ixodes ricinus has a life cycle with four distinct developmental stages: eggs, larvae, nymphs and adults (figure 1) [69]. To transition between non-egg stages, the tick must successfully find and feed upon a host to acquire the nutrients necessary to develop to the next stage [13]. To find a host to feed on, *Ixodes ricinus* exhibits a host-seeking behaviour known as questing, during which it ascends nearby vegetation and waits for a host to brush past. After attachment, the tick begins to feed, a process that can take several days [16]. Once replete, the tick detaches and begins the process of developing to the next developmental stage (moulting) if immature, or developing and subsequently laying eggs if an adult female. Once development is complete, ticks remain dormant for a short period while their cuticle hardens and then begin questing again. This cycle of questing, resting, feeding and moulting repeats as the tick progresses through the larval, nymphal and adult developmental stages, ending when engorged females develop, produce eggs and then die (figure 1).

To allow *Ixodes ricinus* populations to persist through periods of unfavourable climatic conditions, the species has a range of diapause and quiescence responses (figure 1) regulated by photoperiod, temperature and humidity that pause either development or host-seeking activity until the return of favourable environmental conditions [5]. Eggs express either a non-diapausing or diapausing phenotype in accordance with the female's previous experience of photoperiod while questing [17]. Diapausing eggs are cold-resistant and remain dormant until a critical temperature threshold is reached, after which they hatch into larvae. The proportion of time that ticks spend questing is dependent on the temperature and saturation deficit, with the ability of ticks to maintain hydrostatic balance determining the duration of bouts of questing and the time taken to rehydrate after questing and subsequently resume host-seeking activity [61,83]. During the questing period, conditions of decreasing photoperiod concurrent with low temperatures can trigger behavioural diapause during which questing activity is reduced. Behavioural diapause is terminated when photoperiod lengthens, and temperature begins to rise, leading to increased host-seeking activity [5]. The same conditions of decreasing photoperiod and low temperatures can induce morphological diapause in freshly engorged ticks, halting development until photoperiod lengthens and temperature rises.

Hosts pick up *Ixodes ricinus* as they move through the vegetation upon which ticks are actively questing, meaning that the number of ticks that successfully find a host is dependent on both the density and activity of host species. *Ixodes ricinus* has been observed to parasitize a broad range of host species, which are generally categorized as either small hosts, such as bank voles that are competent reservoirs of disease (transmission hosts) or large hosts, such as roe deer, that provide the majority of the blood meals

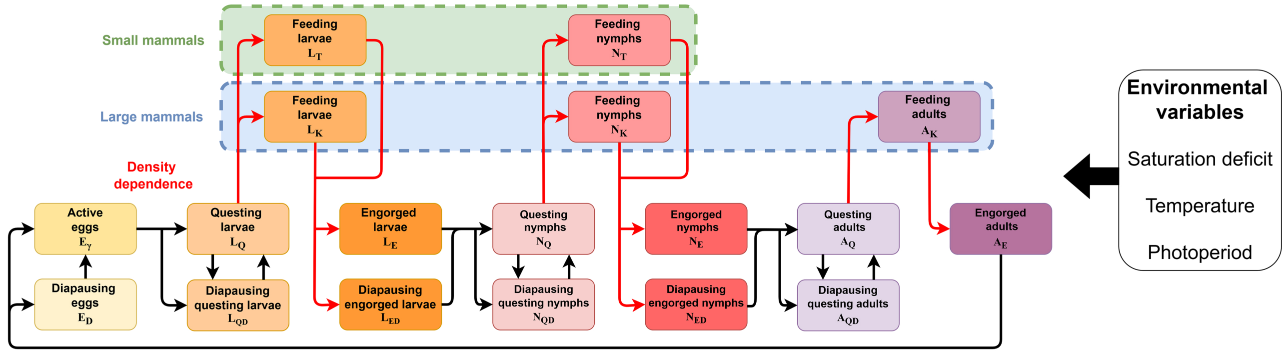

Figure 1. A schematic of the model used to represent the population dynamics of *Ixodes ricinus*. We use a stage-structured modelling approach with four distinct developmental stages, eggs, larvae, nymphs and adults with stage transitions occurring either owing to the completion of development, finding a host for a bloodmeal, becoming engorged or entering a state of diapause. Temperature, photoperiod and saturation deficit are environmental variables used throughout the model to alter the life-history traits expressed by ticks, increasing or decreasing the growth, mortality and activity rates of ticks. Red arrows indicate the stage transitions that are density-dependent, either owing to the effect of tick density on questing success or the effect of the host immune response on surviving on-host feeding. These density-dependent stage transitions are important as they define points in the tick life cycle in which the population is regulated by host immunity and availability.

tick populations require, but within which *Borrelia* spp. and TBEV do not replicate (reproductive hosts). Adult female ticks have been found to exhibit a preference for larger mammalian hosts, such as deer or livestock, which are also often observed feeding high densities of other developmental stages, with the consequence that these hosts are thought to play a key role in amplifying tick populations [23]. While feeding on hosts, ticks experience mortality through a combination of host grooming behaviours and immune responses, the intensity of which is mediated by the host's experience of current and historic tick infestations [18]. These two processes, questing success and feeding success, are the primary sources of density dependence in the tick life cycle we have identified, and are therefore critical in determining tick population size.

2.2. Model overview and summary of delay differential equation approach

To model the complex *Ixodes ricinus* life cycle (figure 1, overview provided in §2.1), we derive a novel system of stage-structured DDEs with environmentally variable delays [55], with each state equation describing the rate of change of individuals as they move into (recruitment rates) and out of (maturation and death rates) stages of their life cycle. The recruitment, maturation and mortality terms that are the constituent elements of the state equations are in turn composed of functions, called reaction norms, describing the life-history traits of ticks under different environmental conditions. Reaction norms are parametrized using data from laboratory experiments describing the response of the life history of *Ixodes ricinus* to constant environments, and were identified using a snowballing literature search procedure. For the one trait for which no suitable studies were identified (the proportion of ticks that survive after feeding on large hosts), we utilize data from another three-host *Ixodid* tick, *Rhipicephalus appendiculatus*. To predict the population dynamics of *Ixodes ricinus* at a given time and location, we use high-resolution environmental data from the ERA5-land reanalysis dataset as inputs to the DDE model [54]. This results in developmental-stage specific predictions of tick population dynamics which we then use to understand how environmental variation alters spatio-temporal tick exposure risk. We independently validate our predictions of tick population dynamics using observations from field populations of *Ixodes ricinus* across the species' European range. A brief description of the DDE approach is provided below and a full description of model equations, our validation procedure for comparing scaled model predictions to field observations, and inclusion criteria for field studies are detailed in S1 in the supplementary material.

The stage-structured DDE approach [55] consists of an inter-linked system of state equations, each of which describes the rate of change of individuals as they move into and out of particular stages of their life cycle. We describe the rate of change of individuals in developmental-stage X_i at time t, $\frac{dX_i(t)}{dt}$, as the sum of the rate at which individuals enter into developmental-stage at time t, denoted $R_{X_i}(t)$, minus the rate at which individuals leave the stage through means other than death $M_{X_i}(t)$ and the rate at which individuals leave the developmental-stage through death $\delta_{X_i}(t)X_i(t)$, where $\delta_{X_i}(t)$ is the mortality rate of individuals in developmental-stage X_i at time t. We therefore describe the rate of change of individuals in developmental-stage X_i through the following equation:

$$\frac{dX_i(t)}{dt} = R_{X_i}(t) - M_{X_i}(t) - \delta_{X_i}(t)X_i(t).$$

By allowing us to explicitly include variable delay terms, this framework enables us to account for the different times required for different biological processes to complete. For example, the time between an egg being produced and hatching varies according to the egg's experience of the historical temperature. In a classical stage-structured ordinary differential equation model, this would be represented by a temperature-dependent rate, causing individuals to constantly hatch, potentially at times that are not biologically justifiable. By comparison, a DDE allows us to refer to the state of the system at previous time points, ensuring that hatching occurs only after embryogenesis has completed.

Accurately accounting for variable developmental delays requires us to define two ancillary state equations to describe the rate at which the stage duration varies and the rate at which the proportion of individuals that survives through the stage varies over the same period [55]. We define $\tau_{X_i}(t)$ to be the duration of stage X at time t, $g_{X_i}(t)$ to be the growth rate of an individual in developmental-stage X_i at time t and $S_{X_i}(t)$ to be the proportion of individuals maturing at time t that survived through the developmental-stage from recruitment into developmental-stage i to maturation into developmental-stage $i+1$. Then, the rate at which these two quantities change at time t can be described by the following equations:

$$\frac{d\tau_{X_i}(t)}{dt} = 1 - \frac{g_{X_i}(t)}{g_{X_i}(t-\tau_{X_i}(t))}$$

$$\text{and} \quad \frac{dS_{X_i}(t)}{dt} = S_{X_i}(t)\left(\frac{g_{X_i}(t)\delta_{X_i}(t-\tau_{X_i}(t))}{g_{X_i}(t-\tau_{X_i}(t))} - \delta_{X_i}(t)\right).$$

If developmental-stage i has a developmental delay, we can therefore use these two quantities to describe the rate at which individuals mature out of developmental-stage i and into developmental-stage $i+1$ at time t as follows: $M_{X_i}(t) = \frac{g_{X_i}(t)}{g_{X_i}(t-\tau_{X_i}(t))} R_{X_i}(t - \tau_{X_i}(t)) S_{X_i}(t)$. In this way, we use the growth and death rates to iteratively define recruitment and maturation terms in terms of historic recruitment in previous life stages.

The full set of equations, the forms of reaction norms, history functions, initial conditions and more detailed explanations of how tick life history is mathematically represented are provided in S1 in the supplementary material. All equations were solved in the R programming language version 4.5.0 using the package PBSddesolve version 1.13.4 [14,65].

3. Results

3.1. Model validation

We independently validate our predictions of tick population dynamics using those observed in field populations of *Ixodes ricinus* across the species' European range. In each validation, we use the same host scenario and initial conditions for the tick population, modifying only the environmental data to be spatially and temporally specific (see supplementary information for further details). The model performs well across the European environmental gradient and predicts the start, end and peak of tick activity in field populations from Finland to Portugal, and our predictions align well with both historical and present-day tick dynamics. Examples of model predictions for a single year are shown in figure 2, and we report in full all corresponding multi-year outputs and validation metrics in the supplementary validation document. Across the 77 European locations considered, we explain an average of 55.0% (s.d. 25.7%) of all variation observed in the density of questing nymphs, 40.3% (s.d. 25.8%) of variation in the density of questing larvae and 41.5% (s.d. 40.2%) of variation in the density of questing adults despite assuming fixed host densities across all of Europe. Given the broad range of sampling procedures, uncertainty surrounding host dynamics and densities at each location and experimental stochasticity, we suggest that this demonstrates our approach can accurately predict field-observed larval, nymphal and adult tick dynamics. We compare the DDE model's performance to three simpler models of tick seasonal activity, one that consists solely of the questing activity functions (supplementary material, eqns (51), (61), (71) for larvae, nymphs and adults) that describe the abiotic environmental suitability for tick questing activity, another that additionally assumes a simple sinusoidal variation in tick abundance, peaking in late spring, which is then multiplied by the same questing activity functions and a standard baseline model that assumes for each time point that the observed abundance is the same as the abundance observed at the previous time point. All simpler models perform substantially worse than the full model ($R^2 = 0.22$ for the simple activity model, $R^2 = 0.33$ for the activity model with sinusoidal dynamics and $R^2 = -1.4$ for the baseline model), indicating that tick population dynamical processes influence seasonal tick activity in a way that is not simply explained by phenomenological descriptions of tick dynamics.

To evaluate the effect of the relative density of different host types on metrics of tick exposure risk, we simulate the system under a range of published estimates of transmission and reproductive host densities, and again account for variability in climate conditions, representative of different climate zones [10,46,63]. We consider tick populations located in Austria, the UK, Spain, Finland, France and Italy, representing a range of climates, and vary the density of transmission hosts between 1 and 20 000 individuals per km^2, and the density of reproduction hosts between 1 and 200 individuals per km^2. In general, we observe that as host densities increase, so does the density of questing nymphs and the duration of the tick activity period (defined to be the number of days for which the density of questing nymphs exceeds one individual per 100 m^2 per year) and that this increase occurs at different rates in different climates (see fig. S10 for questing period and S2 in the supplementary material for changes in other metrics). In general, under the same host densities, regions with climates that are either dry (La Rioja, Spain) or cold (Seili, Finland), support fewer days of questing than regions with wetter, more temperate climates (Rambouillet, France). We find that within locations, although our predictions of tick density change over the host density gradient, the patterns of tick population dynamics remain largely the same, with the exception of boundary regions where low densities of eitherhost type prevent the

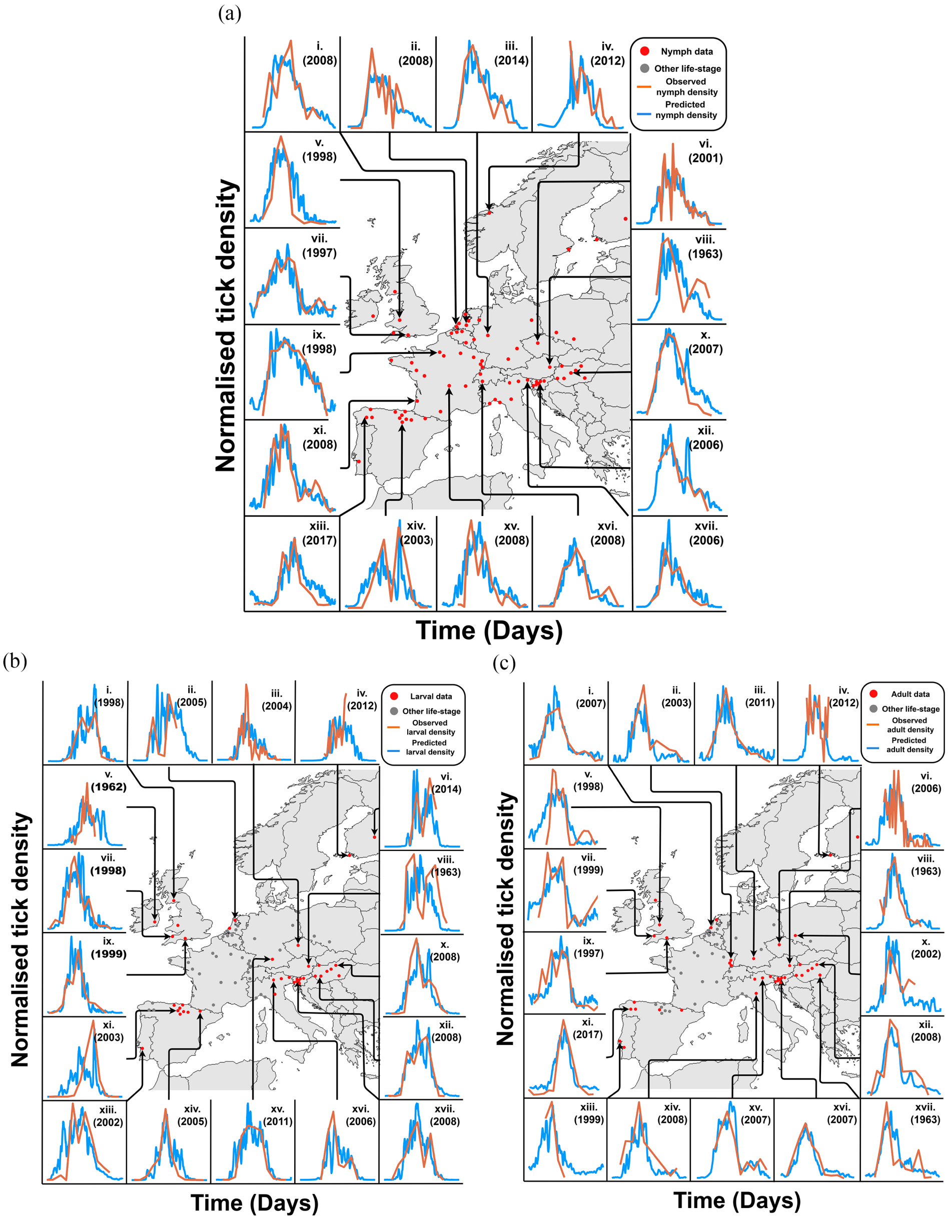

Figure 2. Validations of the model's scaled predictions against field data. Full details of our comparison procedures are provided in supplementary material, S1 and details pertaining to each prediction are supplied in the supplementary validation document. For each location, the x-axis is time starting on the first day of January and ending on the last day of December of the year indicated. The y-axis shows the scaled density of questing ticks. Blue lines show the model's scaled predictions of the dynamics of the tick population at the corresponding location, and the orange lines show normalized field observations of tick density from that same location. (a) Comparisons of the density of questing nymphs **i.** [12], **ii.** [12], **iii.** [56], **iv.** [64], **v.** [68], **vi.** [15], **vii.** [68], **viii.** [62], **ix.** [85], **x.** [22], **xi.** [12], **xii.** [43], **xiii.** [71], **xiv.** [1], **xv.** [12], **xvi.** [60], **xvii.** [81] . (b) Comparisons of the density of questing larvae **i.** [86], **ii.** [78], **iii.** [15], **iv.** [76], **v.** [29], **vi.** [13], **vii.** [68], **viii.** [62], **ix.** [68], **x.** [22], **xi.** [1], **xii.** [22], **xiii.** [3], **xiv.** [1], **xv.** [75], **xvi.** [81], **xvii.** [43]. (c) Comparisons of the density of questing adults **i.** [82], **ii.** [27], **iii.** [75], **iv.** [76], **v.** [68], **vi.** [15], **vii.** [68], **viii.** [62], **ix.** [68], **x.** [8], **xi.** [71], **xii.** [22], **xiii.** [2], **xiv.** [81], **xv.** [81], **xvi.** [43], **xvii.** [22].

establishment of tick populations (supplementary material, S2). This suggests that the assumption that host densities are constant is unlikely to have substantially altered the comparison of model predictions to field observations within years.

3.2. Tick exposure risk between 1980–2024

To explore how the suitability of the European climate for *Ixodes ricinus* populations has changed, we simulate the model from 1980 to 2024 over Europe. At each location, we output annual summaries of metrics of tick exposure risk to people, specifically the total density of questing nymphs (total density of questing nymphs per year) and the duration of the period of high-intensity questing activity (number of days with at least one questing nymph per 100 m^2 per year). We consider a host scenario that assumes transmission and reproductive host densities at the upper end of what has been observed in the field to reflect the dynamics of populations of ticks in the most suitable habitats. In later analyses, we consider the medium host density scenario used for the

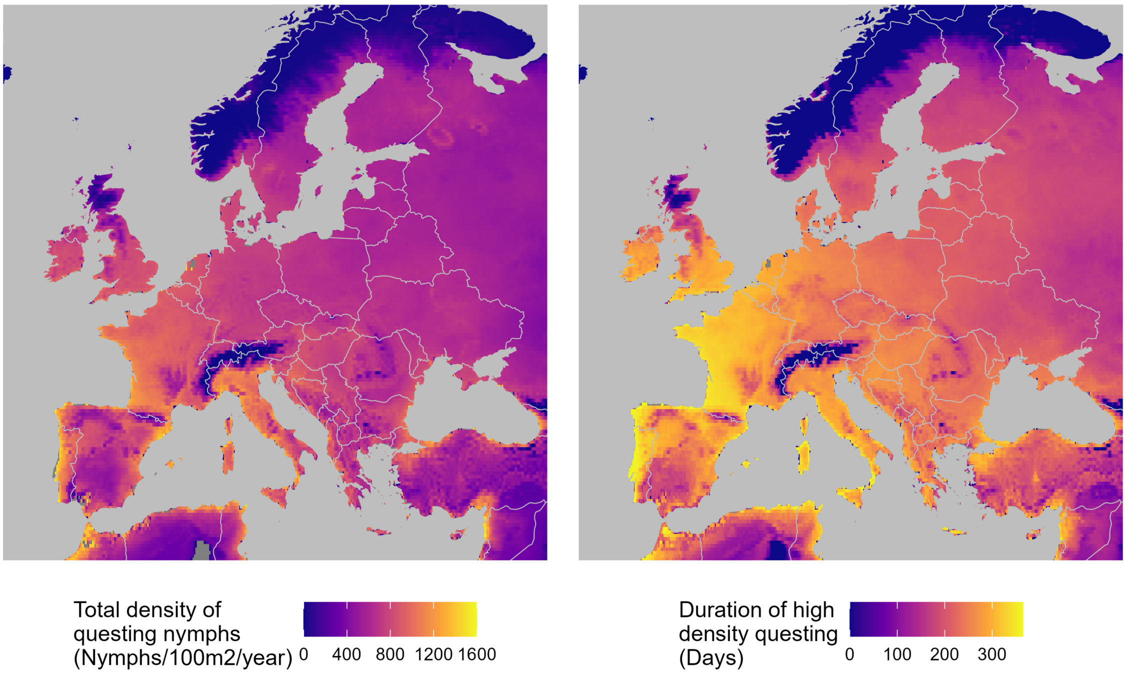

Figure 3. Predictions of annual questing nymph density and the number of days suitable for high density questing across Europe in 2024 under the high host density scenario. The total density of questing nymphs is defined to be the sum of the density of questing nymphs per 100m^2 yr^{-1}. The duration of high density questing is defined to be the number of days per year where the density of questing nymphs is predicted to be greater than 1 nymph per 100m^2.

model validations and a low host density scenario to determine how changes in host communities impact metrics of tick exposure risk. Host scenarios were chosen by referencing host densities observed in the field, using extreme densities for the high and low host scenarios (supplementary material, S1) [10,46]. The effects of varying host densities on population dynamics across climates are further explored in S2 in the supplementary material. Owing to our necessary assumptions about host density, the following predictions are measures of the relative environmental suitability for *Ixodes ricinus* under the assumption that a host community of the specified size is present at the location. To see the effect that the use of high-resolution estimates of host densities has on the predictions of tick suitability, see S3 in the supplementary material. There, we simulate the model for the UK using high-resolution estimates of the relative abundance of deer [51,63]. Köppen climate classes are used to group locations to summarize differences in metrics of tick exposure risk (see S4 in the supplementary material for a glossary of zone classifications and maps of their locations) [4].

Under the high host density scenario in 2024, the suitability of the European climate for *Ixodes ricinus* was high, with only 13% of the total area predicted to be unsuitable for tick populations under current-day conditions (figure 3; see S5 in the supplementary material for medium and low host density scenarios). We predict that locations as northerly as 66° latitude can support limited periods of questing activity, aligning well with the current known distribution of *Ixodes ricinus* [21]. Areas predicted to be unsuitable for tick activity are either too dry (e.g. desert regions of southern Spain) or too cold, either owing to altitude (e.g. the Alps) or latitude (e.g. northern Scandinavia). Throughout the year, western Europe is more suitable than eastern Europe for high densities of *Ixodes ricinus* at equivalent latitudes. On average, regions with temperate climates with warm summers support the highest density of questing ticks and longest duration of activity (Köppen classes Csb and Cfb, for example, regions of northern and southern France, respectively), with both regions able to support eight months of activity on average. The least suitable climatic zones for tick populations are located at latitudes above 59° (Köppen classes Polar, tundra (ET) and cold, no dry season, cold summer (DSc), for example, northern Norway) which are suitable for 0–1 month of activity on average. After this, the least suitable climates for tick populations are either arid (Köppen classes BWh and BWk, for example, regions of southern Spain) or cold (Köppen classes Dsa, Dsb, for example, parts of eastern Turkey) climates concentrated in southern Europe and northern Africa supporting 2–4 months of tick activity. This suggests that *Ixodes ricinus* is climatically limited at its northern and southern range limit, and its distribution is therefore sensitive to climate change-induced niche shifts at the continental scale.

To determine how the seasonal duration of tick activity has changed between 1980 and 2024, we perform a generalized least-squares trend model for each grid cell in each season (with year as a predictor), accounting for temporal auto-correlation and retaining models significant at the 95% level. The coefficients (slopes of the trend) estimated by the generalized least-squares method are used to determine the net change in the metric between 1980 and 2024. We define spring to be March–May, summer to be June–August, autumn to be September–November and winter to be December–February. We exclude the climate classes cold, dry summer, cold summer (Dsc) and temperate, no dry season, cold summer (Cfc) from further analysis owing to the low number of pixels in Europe with these classifications.

In both 1980 and 2024, we predict high suitability for nymphal questing in spring and summer, less suitability in the autumn and limited suitability in the winter (figure 4). Year-round activity is limited by the ability to quest through winter, which occurs mostly

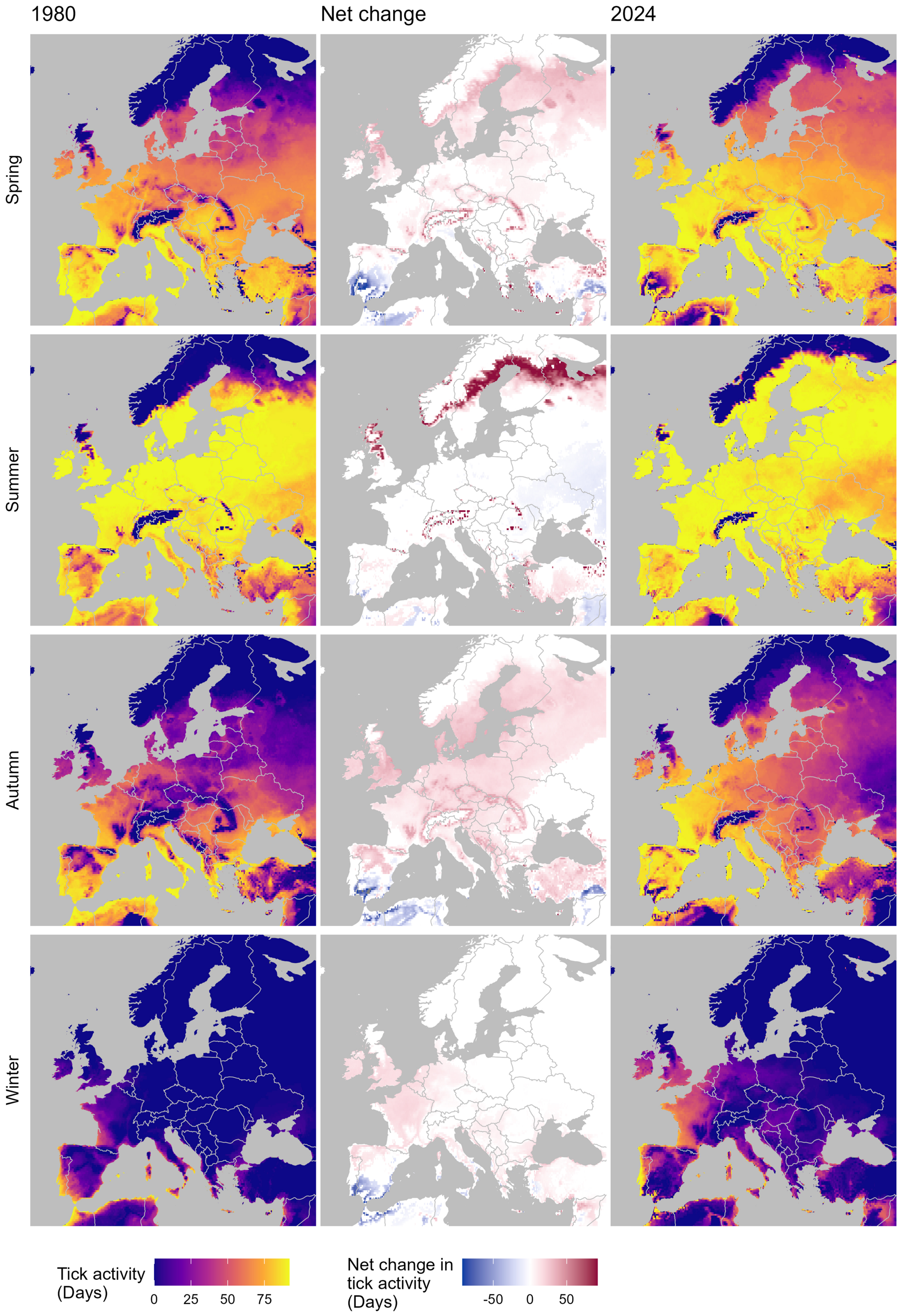

Figure 4. Predictions of the number of days suitable for high density nymphal questing (number of days with more than 1 nymph per 100 m^2) per season across Europe between 1980 and 2024 under the high host density scenario. Graphs in the 1980 or 2024 are predictions for the corresponding year in the season indicated at the start of the row. Net change shows the change between these two time points and is calculated by statistically fitting a linear model per pixel accounting for temporal autocorrelation and multiplying the gradient of the fitted slope by the total duration of the period in years. Only models significant at $p = 0.05$ are retained and all others are found to have no evidence for change.

in south-western Europe, though some coastal south-eastern regions and isolated northern regions support year-round activity (for example, the Western Isles of Scotland, albeit at low levels). Between 1980 and 2024, we predict increases in metrics of tick exposure risk across much of northern Europe, with decreases limited to arid areas of southern Europe, the Middle East and northern Africa. Between 1980 and 2024, we predict a 4% increase in the total area over which there is at least one month of tick activity, and a 10% increase in the density of questing nymphs. Climate-induced changes in tick activity are exacerbated by increases in host density. Between the medium host density scenario in 1980 and the high host density scenario in 2024, we predict a 21% increase in the total area with at least one month of tick activity. Across the overall region, there has been an extension of questing activity in spring and autumn, with 40% of the region experiencing increased spring activity and 54% of the region experiencing increased autumn activity (high host scenario). Although increases in summer tick activity are predicted over a smaller geographical area (20% of the region), these occur in regions that were unsuitable in the 1980s and are of a larger magnitude (an average increase of 34 additional days of questing in the summer compared to 16 and 18 days in the spring and autumn, respectively).

The predicted changes in tick activity are driven by underlying changes in climatic conditions, which are not evenly distributed through space and time. To understand how tick population abundance has changed over the region through time, we compare the average annual density of questing nymphs predicted for each year between 1980 and 2024 (figure 5*a*), and the average density of questing nymphs per month for each climate zone between 1980 and 1984 and 2018 and 2024 (figure 5*b*). The annual density of questing nymphs has changed substantially between 1980 and 2024, with increases in suitability in many cold and temperate climate classes, and decreases in arid climates and climates with hot summers. In the regions with the most rapid increases in suitability for tick populations (Köppen classes Dfc and Cfb, for example, north Sweden and the UK), increases in tick density are generally distributed evenly throughout the year. By comparison, regions with tick populations that are either rising more slowly (Köppen class Dfb, for example, Poland) or are decreasing (Köppen class Dfa, for example, southern Romania) generally have lower suitability for tick activity during the summer period in the 2020s than in the 1980s, which is then offset to varying degrees by an increasing suitability for tick activity in the autumn. In climate classes where the suitability for tick activity is increasing, the predicted change is often extreme, with the median tick density in the early 1980s being one standard deviation below the median density in the later period (for example, Cfb).

4. Discussion

Over the last 40 years, Europe has experienced a shift in TBD prevalence, but our ability to understand the mechanisms underpinning these changes is hindered by the complexity of multi-host TBD systems [57,67]. By developing an extensively validated mathematical model, accounting for relevant environmentally driven development delays for different tick developmental stages, we show how the biotic and abiotic environment jointly shape tick population dynamics and predict significant climate change-driven increases in *Ixodes ricinus* abundance and seasonal host exposure to ticks since the 1980s. Consistent with observational studies, in northern Europe, we predict broad-scale increases in the population density of *Ixodes ricinus* populations and an extension in the distribution and the seasonal duration of tick activity that will probably have increased exposure of people and animal hosts to ticks [28,39,40]. In newly suitable areas at the northern range limit, we predict that tick activity is predominately unimodal and limited to the summer. In the south of Europe and in northern Africa, hotter, drier summers have led to an overall reduction in population density and tick activity. These shifts in seasonal abundance and questing have significant implications for public health interventions that are targeted seasonally (e.g. annual public awareness campaigns [41]) and for animal health (e.g. managing seasonal livestock grazing to minimize tick-borne pathogen risks) [70,80]. The accuracy of our model in independent validation across a continental climate gradient highlights that stage-structured DDEs are powerful tools for predicting population dynamics, even for systems with substantial life-history complexity, such as is present in the life cycle of *Ixodid* ticks. The ability of model predictions to anticipate field dynamics using only climate reanalysis data as external inputs demonstrates the importance of considering developmental delays and mechanisms of density dependence when predicting population dynamics and inferring the effects of climatic and host variation on vector populations.

Despite the high predictive ability demonstrated by the model, gaps in our understanding of tick and host ecology still hamper our ability to fully address some questions of critical relevance. The simplified host scenarios considered here demonstrate the substantial impacts of host density on tick exposure risk and highlight the importance of considering host and climate factors jointly when attributing observed changes in tick populations and TBD transmission to climate change [57,67]. However, many of the parameters we use to describe the interactions between deer and ticks are borrowed from tick–cattle systems, owing to a lack of experimental data on ticks feeding on deer [18,38]. This parameter is critical because it is one of the ways in which host and tick densities interact, and therefore in determining the number of ticks we predict that each host can support. Further, deer abundance has increased significantly across Europe during the same 40-year period during which we predict that environmental suitability for ticks has increased [32,77]. This increase in deer abundance has been implicated by prior studies as a driver of increases in tick populations [19] and TBD transmission [45]. Incorporating observed changes in host density into our framework (as opposed to scenarios) would provide more specific predictions of how TBD risk is changing, but requires spatio-temporal predictions of how deer populations are changing on a continental scale. Unless existing gaps in host density estimates and species-specific life-history parameters are addressed, mathematical models will be able to predict general trends in tick-hazard but remain unable to accurately predict the magnitude of absolute changes in tick abundance and seasonal exposure. This ability to link host densities to changes in absolute tick abundance is critical for understanding how deer management plans impact the transmission of TBDs, given planned large-scale woodland expansion under biodiversity and climate change mitigation policies [45,53,59]. Nevertheless,

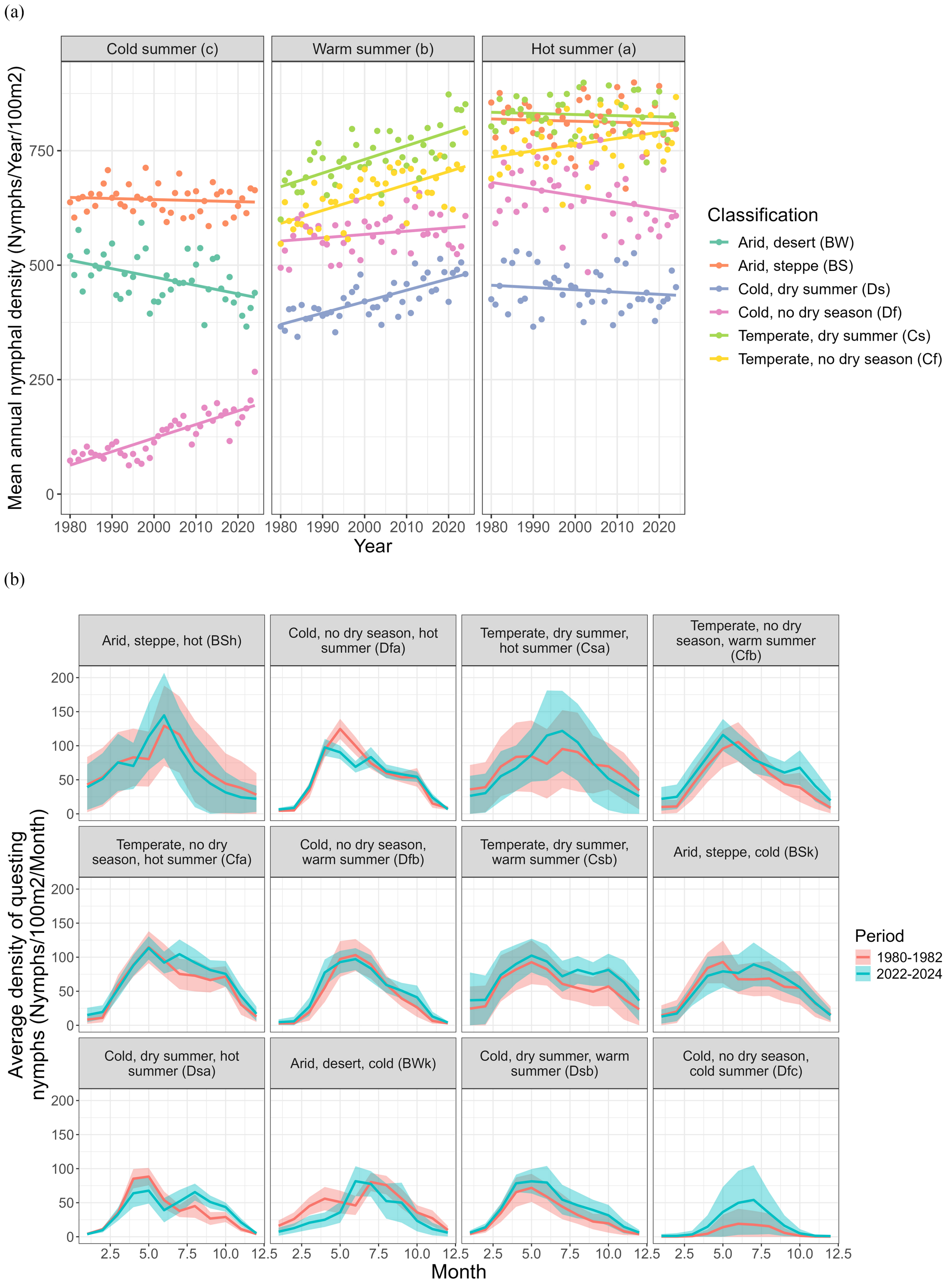

Figure 5. The mean change in the density of questing ticks across groups grouped by Köppen Climate class between 1980 and 2024. We use the Köppen classification defined by Beck *et al.* [4], and maps showing the classification corresponding to each point in Europe can be found in S4 in the supplementary material. (a) The change in mean annual questing nymph density between 1980 and 2024 grouped by Köppen Climate class. Each line indicates the mean of all locations within the classification, and the shaded region indicates the standard deviation. Arid climates tertiary classifications are grouped with the corresponding summer temperature classification. (b) The average density of questing nymphs per year for each Köppen Climate class is summarized by month for the periods 1980–1982 (red lines) and 2022–2024 (blue lines).

despite these data gaps, our model provides a valuable framework for understanding how the current trend of increasing deer populations will interact with climate change and can be updated as further empirical data on host density and host immune responses are available.

Having demonstrated that our model framework accurately predicts the population dynamics of *Ixodes ricinus*, we are confident that this same framework would extend to other medically important tick species. For other three-host ticks in the genus

Ixodes, this extension is straightforward, but requires a complete reparametrization of the reaction norms with empirical data and subsequent validation across the species range. This is a substantial undertaking and requires a large body of data from laboratory and field experiments for the tick species of interest. Key vectors for which such data already exist include *I. scapularis* and *I. persulcatus*, the primary vectors of *Borrelia* spp. in North America and Asia, respectively. Adaptation of the framework to two-host ticks, such as *Hyalomma marginatum*, the primary vector of Crimean-Congo Haemorrhagic Fever Virus in Europe requires additional minor modifications to the model structure to represent key differences in life cycle and host-seeking behaviour. Research efforts to downscale these models to local scales to inform risk and interventions should focus on intersecting impacts of microclimate variability on tick populations, and integrating empirical and modelled data on animal host and human resource use and movements across the landscape, to produce more specific and locally actionable estimates of disease transmission risk [34,47,48]. Downscaled spatial versions of the model will also be vital for assessing the effects of extreme events, such as drought, flooding and wildfires, on tick populations [6,74,88].

Model outputs are robust enough to be used by public health and animal health decision makers at national and sub-national levels in Europe to map the geographically variable seasonal and peak risk periods for human exposure to nymphal ticks, and to better target seasonal tick, deer and livestock surveillance and awareness-raising activities for key at-risk groups [36]. Model outputs could provide a complementary data source for understanding and tracking short-term changes in tick distribution and seasonal tick exposure risk, alongside current surveillance systems in ticks, people and animals [41]. For national adaptation planning, these models provide a preliminary indication of whether climate zones and countries are becoming more or less suitable for *Ixodes ricinus* ticks over decadal time scales, and therefore, how human tick exposure risk is changing through space and time. To better predict the consequences of current and future climate and host changes for disease transmission for horizon scanning and risk management, these tick population models should be integrated into disease transmission models for TBEV and *Borrelia burgdoferi* s.l. that account for the variable transmission routes and host associations of these pathogens [35,52]. By providing a robust picture of tick dynamics in source and sink locations for TBD transmission, this model framework will also be valuable for disentangling the seasonally varying roles of natural and human-mediated processes of introduction (e.g. transport of infected ticks on migratory birds, livestock and pests and infected wildlife/livestock movements) in fostering disease spread and maintenance from landscape to regional scales, and consequent mitigation opportunities.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All code and data associated with this manuscript are freely available at [89].

Supplementary material is available online [90].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.B.: conceptualization, formal analysis, methodology, software, validation, writing—original draft, writing—review and editing; S.M.W.: conceptualization, methodology, supervision, writing—review and editing; S.B.: investigation, writing—review and editing; S.S.: investigation, writing—review and editing; B.V.P.: conceptualization, funding acquisition, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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