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Title

Modelling the seasonality of Lyme disease risk and the potential impacts of a warming climate within the heterogeneous landscapes of Scotland

Short title

Lyme disease risk in a warming climate

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Abstract

Lyme disease is the most prevalent vector-borne disease in the temperate Northern Hemisphere. The abundance of infected nymphal ticks is commonly used as a Lyme disease risk indicator. Temperature can influence the dynamics of disease by shaping the activity and development of ticks and, hence, altering the contact pattern and pathogen transmission between ticks and their host animals. A mechanistic, agent-based model was developed to study the temperature-driven seasonality of *Ixodes ricinus* ticks and transmission of *Borrelia burgdorferi* sensu lato across mainland Scotland. Based on 12-year averaged temperature surfaces, our model predicted that Lyme disease risk currently peaks in autumn, approximately 6 weeks after the temperature peak. The risk was predicted to decrease with increasing altitude. Increases in temperature were predicted to prolong the duration of the tick questing season and expand the risk area to higher altitudinal and latitudinal regions. These predicted impacts on tick population ecology may be expected to lead to greater tick-host contacts under climate warming and, hence, greater risks of pathogen transmission. The model is useful in improving understanding of the spatial determinants and system mechanisms of Lyme disease pathogen transmission and its sensitivity to temperature changes.

Keywords

Agent-based model, *Borrelia burgdorferi* sensu lato, Climate warming, Environmental health hazard, *Ixodes ricinus*, Spatio-temporal dynamics

1 Introduction

Lyme disease (or Lyme borreliosis) is the most prevalent vector-borne disease in temperate regions of the Northern Hemisphere [1]. In the UK, the annual number of confirmed Lyme disease cases is over 1000 and still increasing in some areas each year [2]. The causative agents of Lyme disease belong to a species complex of spirochaete bacteria named *Borrelia burgdorferi* sensu lato (s.l.), which are transmitted principally by the tick *Ixodes ricinus* (castor bean, deer or sheep tick). In Scotland, *B. afzelii* (associated with rodents) is the most abundant genospecies, followed by *B. garinii* (associated with birds) and *B. burgdorferi* sensu stricto (s.s.) (associated with both rodents and birds) [3]. As no vaccine is available, the prevention of Lyme disease

relies heavily on improving understanding of the mechanisms of disease transmission and integrating multi-disciplinary knowledge and data to predict the patterns of disease risk in a changing environment.

The risk of Lyme disease is strongly related to the density of active infected ticks, which can be influenced by a wide range of biophysical factors related to host communities, climate, and landscape (see recent reviews [4-9]). Temperature, in particular, has gained much attention in eco-epidemiological studies of Lyme disease, in line with increasing concern about the effects of climate warming over the last few decades. Temperature affects the abundance of infected ticks in two main ways. First, it directly affects the behaviour (e.g., activity and diapause), interstadial development rate, fertility, and survival of ticks [10, 11]. Second, it influences the population and habitat suitability of host species. In addition, a warmer climate at higher altitudes may result in an increase in the population of important tick hosts such as roe deer, *Capreolus capreolus* [12]. Population dynamics of rodents (the transmission host) may also be influenced by temperature, as climate change shifts local faunal abundance and diversity [13].

Mechanistic models, that explicitly represent the key population groups and processes underpinning their interactions, are capable of providing unique insights in support of health-related decision making [14]. They have increasingly been applied to explain disease transmission system dynamics, understand observed disease patterns, test scenarios for potential future risk patterns and propose data and methodological improvements [15]. Existing mechanistic models for studying the effects of temperature on Lyme disease risk are increasing in number (e.g., [16-20]). However, existing models do not incorporate spatial heterogeneity or focus on issues related only to the dynamics of vector populations, ignoring key components, such as host/pathogen distribution and habitat suitability, which in reality are distributed unevenly and can change rapidly over time. To bridge these gaps, we developed a mechanistic model to investigate the spatio-temporal dynamics of tick-borne diseases by integrating a number of temperature-dependent functions for the temporal dynamics of tick populations into a recently developed spatial model for Lyme disease risk. The model considers the heterogeneity in tick population ecology, host movements and pathogen transmission across the landscape [21, 22]. The model was developed for Lyme disease risk assessment in mainland Scotland where the potential for disease exposure is high due to substantial public participation in nature-based activities.

The principal objective of this study was to use the outputs of the mechanistic model for the spatio-temporal pattern of infected tick abundance as a biophysical risk indicator (or “hazard”) of Lyme disease. The model was designed to take account of current scientific understanding of the system mechanisms so that it can serve as an explanatory tool for further research and educational purposes. A secondary objective was to predict the disease risk pattern and its seasonality for mainland Scotland. We did not attempt to make precise annual predictions, nor predictions of the distributional spread of the pathogen, but rather focus on the long-term (i.e., decadal) average approximation of the seasonality, which is appropriate for application to scenarios of long-term environmental change. To gain greater insight into the spatial determinants of disease risk pattern and its sensitivity to temperature changes, two modelling experiments were conducted: (i) an exploration of the relationships between the predicted disease risk patterns and environmental factors of local interest, i.e., annual average temperature (affects tick survival, development and activity); elevation (modifies the temperature, habitat distribution and deer movement); and deer density (influences tick reproduction); and (ii) prediction of changes in disease risk pattern under simple climate warming scenarios (i.e., regional increases of temperature by 1, 2 and 3°C throughout the year). Finally, we assessed the data and methodological barriers of adopting such a complex zoonotic disease model for regional-level real world applications.

2 Material and methods

A mechanistic, agent-based model was developed by integrating recent developments in simulating the temperature-driven temporal [16-20] and spatial [21, 22] dynamics of *I. ricinus* populations and *B. burgdorferi* s.l. transmission in mainland Scotland. Multi-sectoral data were used to prepare model inputs [23-30], modify model functions [23] and evaluate the model outputs [24] (see details and discussions in the electronic supplementary material). The model was used to predict the spatio-temporal pattern for the density of infected nymphs (DIN, as a Lyme disease risk indicator) based on 12-year (2000-2011) mean weekly temperature surfaces. The model was then applied to a number of simple temperature warming scenarios to explore the possible consequences of climate change on the DIN pattern. Finally, we further examined the

spatio-temporal patterns of simulation predictions by summarising the predicted DIN changes according to annual average temperature, elevation and deer density parameters to assess how the effects of these parameters may vary with a warming climate.

(a) Model overview

The conceptual framework for the Lyme disease risk model is presented in Figure 1. It is programmed using Repast Symphony (version 2.2) [31] in which the environment is represented as a two-dimensional, rectilinear grid with a cell size of 1 km² and a time step of one week. There are three interactive layers within the model where cells represent the population distributions of ticks and host animals and the configuration of the landscape. The mechanisms for the spatio-temporal developments and interactions of the model layers are represented as transition rules, which are grouped into three sets concerning tick population dynamics, pathogen transmission, and host population dynamics and movement patterns, respectively. The framework was designed to describe the general ecological processes of Lyme disease but the present model was parameterised for mainland Scotland. A summary of the model is provided in this section and detailed descriptions of the layers, parameters and transition rules are presented and discussed in the electronic supplementary material (supplemental model transition rules and parameters, see all parameter values in Table 2.1).

Tick population layer: Four life stages are modelled: “egg”; “larva”; “nymph”; and “adult”. In each post-egg life stage, ticks could be in questing, feeding or interstadial development phases. Total and infectious populations in all stages are simulated for each cell. When encountering hosts, questing ticks attach for blood meals, then drop and develop into the next life stages. Female adult ticks (assuming half of the emerged adult ticks are females) also need blood meals to produce eggs that hatch into larval ticks. Durations of feeding are assumed to be less than one week for larvae, and one week for nymphs and adults. We also assume that questing activity and interstadial development are sensitive to temperature, while feeding success is assumed to be dependent on the density of hosts [16-20].

Host population layer: Populations of three generalised host types are simulated for each cell: (i) transmission hosts that are capable of transmitting *B. burgdorferi* s.l. (e.g., rodents [32], birds [33] and lagomorphs [34]), (ii) deer (e.g., roe deer and red deer) and (iii) livestock (e.g., sheep and cattle). In the model, the overall number of transmission hosts varies with season, but that of deer and livestock is fixed. The spatial distributions of hosts can vary between time steps due to animal weekly and seasonal movements (i.e., home-ranging and dispersal), resulting in ticks being transported from one place to another. Due to limited data, only the generic *B. burgdorferi* s.l. was considered in the model, not the individual genospecies. As the density of common rodent species [35] is much greater than that of birds [30] in Scotland, the transmission host demography is assumed to be largely dependent on rodents. Hence, the populations of bird and lagomorph are included in the host layer, but their dynamics are not modelled explicitly. Therefore, considering the scale (the whole of mainland Scotland) and spatial resolution (1 km²), this model is more relevant for rodent-specialised *Borrelia* genospecies such as *B. afzelii* and *B. burgdorferi* s.s. than for the bird-specialised *B. garinii*. Moreover, the movement of transmission hosts is assumed negligible for a cell size of 1 km², as the home range sizes of rodents and birds are usually around 0.1-0.2 ha, and the dispersal distances are less than 1 km for rodents and at the continental or global level for birds [36, 37]. In the model, deer and livestock are assumed to be tick reproduction hosts which provide a large quantity of blood meals for tick development and reproduction but which do not support systemic *B. burgdorferi* s.l. transmission [38-41]. Sheep may support non-systemic pathogen transmission between co-feeding ticks [42]. However, such a transmission route is not included in the present model as there is debate on its significance in the maintenance of *B. burgdorferi* s.l. [43, 44]. The two reproduction host types (deer and livestock) use different land covers and perform different movement patterns. Home range sizes of both deer and sheep are assumed to change seasonally. The seasonal dispersal of deer (i.e., downhill migration during winter and uphill migration during summer [45]) is also modelled explicitly. While ticks in each post-egg life stage are assumed to be capable of feeding on all host types, in the model larvae preferred transmission hosts (rodents and birds), adults preferred reproduction hosts (deer and sheep) and nymphs were assumed to be generalists.

Landscape layer: The landscape is represented by four cell states: woodland; grassland; heathland; and non-vegetated/other areas. The model assumes that ticks can inhabit grassland and heathland, but that woodland is more suitable [5, 12]. Mortality rates of ticks, densities of hosts and movement patterns of hosts vary with the four land cover types. Transmission hosts can inhabit all woodland, heathland and grassland. Deer are considered to inhabit mainly woodland and heathland, and they can spend a proportion of their time in grassland for grazing. Conversely, livestock are assumed to be present mainly in grassland, but are also able to graze in heathland and woodland. All hosts can enter non-vegetated areas, but do not stay, hence, it is assumed that no ticks drop off in such areas. Elevation is used to simulate the seasonal uphill/downhill dispersal of deer and altitudinal changes in their home range.

At each successive time step, these transition rules are applied in sequence to update cell states simultaneously. Firstly, within each cell, the infectious and total populations of questing ticks at each life stage are updated by adding in the unfed ticks moulted from a previous life stage and removing those that die in the previous time step. At the same time, the infectious and total populations of transmission hosts are updated according to the seasonal carrying capacity and birth/mortality rates. Secondly, hosts encounter questing ticks in the same cell and pathogen transmission takes place. Finally, between-cell host movements are considered, i.e., all nymphs and adults attached to out-moving animals are transported and dropped off at the end of the time step. The transport of larvae, however, is considered negligible, as their feeding duration is assumed to be less than one week (around 3 days) and they are assumed to feed preferentially on small transmission hosts with small home ranges which do not move between cells.

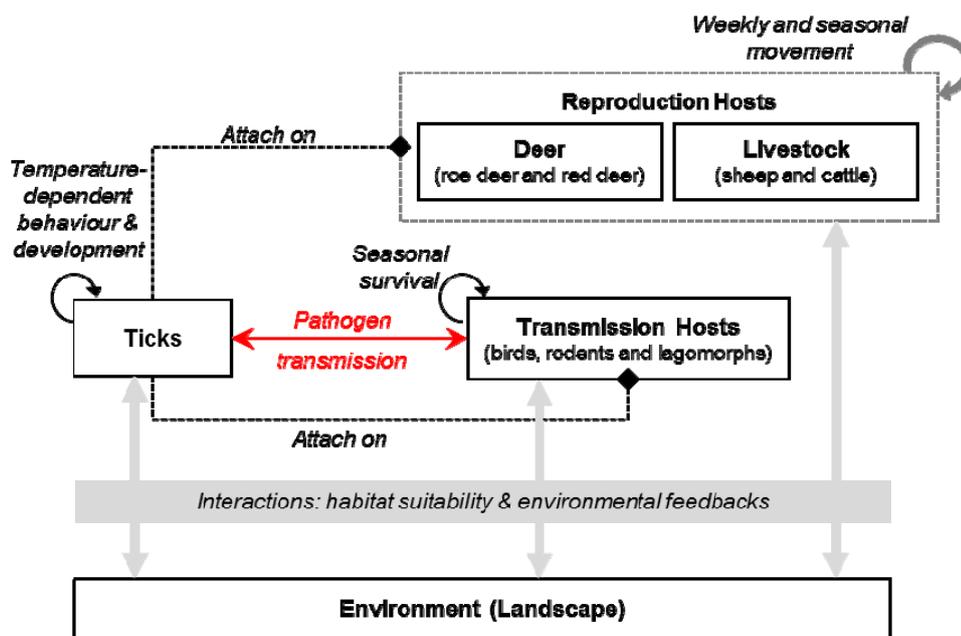


Figure 1 Model conceptual framework: Interactions between ticks, hosts, pathogens and landscape.

(b) Model inputs, outputs and initialisation

Input: Multi-sectoral datasets were processed and integrated, including empirical data on tick behaviour, *B. burgdorferi* s.l. infection and distribution [23, 24], earth observations on land cover and habitat types [25], long-term publically-accessible meteorological data [26], and host habitat suitability and distribution estimations based on census data, literature-based qualitative information and model predictions [27-30]. Data sources and preparation details are presented in the electronic supplementary material (supplemental data preparation details).

Output: The model can output an infected/uninfected tick density surface for all the different life stages (egg, larva, nymph and adult) at difference phases (questing, feeding or interstadial development). In the present study, only the density of questing infected nymphs (DIN) was output, as this is a widely-used Lyme disease risk indicator [4-9]. Nymphs are an order of magnitude more common than adult ticks. Nymphs are also

smaller than adult ticks and less likely to be spotted, allowing them to complete their blood meal and transmit *Borrelia* pathogens. Nymphs have been shown to be the stage causing most Lyme disease cases in people [46, 47]. Furthermore, we focused on simulations in woodlands, as field studies have shown that many more ticks have been observed in forests than open habitats[48].

Initialisation: All simulations were initialised with assumed initial densities of 2×10^5 and 5×10^4 per km^2 for the total and infected questing nymphs, respectively in woodland. All results were recorded after 2600 time steps (50 years) to ensure stabilised yearly cycles had been reached.

(c) Model evaluation

Two types of model evaluation were undertaken. The first qualitatively compared the shape of the overall tick/pathogen seasonality curve with empirical findings in Scotland or the UK from the literature. The second directly compared the spatial pattern of DIN with field observations based on: (i) species distribution data from the NBN (National Biodiversity Network) Gateway (<http://data.nbn.org.uk/>) to obtain a general sense of the degree of overall agreement and detect any under- or non-detected patterns; and (ii) the field study on the infection prevalence in nymphs (NIP) [24] to check the model's predictive power at 24 forest sites in mainland Scotland.

(d) Model simulation

The main objective of the simulation exercise was to predict the possible long-term disease risk pattern and its seasonality for mainland Scotland, as well as possible changes under climate warming scenarios. To gain an overview of disease risk pattern and seasonality, weekly surfaces of infected nymph density (a proxy of Lyme disease risk) were produced for mainland Scotland using a set of 12-year (2000-2011) average weekly temperature surfaces. Predicted disease risk pattern and its seasonality were compared between administrative regions. Then, the potential effects of climate warming scenarios were tested by applying increases of 1°C , 2°C and 3°C to the 12 year average temperature surfaces. Finally, by analysing the predicted DIN, we investigated the effects of some selected cell-level variables on disease risk, including: (i) annual average temperature (influences tick survival, development and activity); (ii) elevation (modifies the temperature, habitat distribution and deer movement); and (iii) deer density (affects tick reproduction). Temperature was selected due to climate change concerns [2, 7, 49], whilst deer densities were selected as these can be managed as part of disease risk controlling strategies [22, 50]. Elevation was hypothesised to be able to capture the intricacies of temperature, hosts and habitat better than the other two variables [51]. We first checked that the three variables were only weakly associated with one another (Spearman's correlation coefficients were -0.31 between (i) and (ii), 0.39 between (ii) and (iii), and -0.18 between (i) and (iii), and all significant at the 0.05 level), before summarising and plotting the predicted disease risk patterns against the three selected cell-level variables to determine the efficacy in predicting the effects of climate warming. To improve the visualisation of plots, we reduced the size of the predicted DIN data by averaging the cell-level predictions for each interval of 1(m) for elevation, $0.1(^\circ\text{C})$ for temperature and $0.1(\text{heads}/\text{km}^2)$ for deer density.

3 Results

(a) Model performance

Stabilised yearly cycles: Very similar stabilised yearly patterns in the density of infected nymphs (DIN) (less than 0.01% overall difference) were found after varying initial values by $\pm 90\%$. Hence, the model outcomes seem to be largely independent of differences in the initial tick densities. Model predictions on the seasonal patterns of questing tick populations and infection prevalence in different habitat types are provided and compared with field evidence found in the literature in the electronic supplementary material (section 4.1). Stabilised yearly cycles of infectious tick populations were achieved after 20-40 simulated years in all simulations in woodland habitats. Tick populations in other habitats also achieved stabilised cycles at lower levels, even though no ticks were assumed to be present at initialisation. The questing larval and nymphal ticks had similar predicted seasonal patterns with a peak in autumn (September-October). The questing adult

females had a relatively symmetrical predicted pattern with peak values in summer (June-July). The nymphal infection prevalence (NIP) and adult infection prevalence were predicted to be relatively stable over the course of the year. To assess the overall model performance, additional results on the predicted transmission host populations and feeding tick populations are also provided and discussed in the electronic supplementary material.

Spatial dynamics: Predictions and discussions on the spatial patterns of tick and NIP are provided in the electronic supplementary material (section 4.2). In general, model performance in predicting the spatial patterns was found to be satisfactory. Both the NBN (National Biodiversity Network) records and our model prediction suggest a wide distribution of ticks across mainland Scotland. Moreover, the model achieved “correct” predictions (if the field NIP values fell within the range of simulated NIP values) in 22 forest sites (out of 24) sampled the field study [24], with two underestimations in Inverness (The Highlands). The lack of further field evidence on DIN or NIP, as well as the lack of sampling-level conditions of habitat and transmission host, prevented us from making further comparisons.

Model sensitivity: Sensitivity analysis of all model parameters was undertaken and compared with the results of previous model sensitivity investigations from the original model, which we extended in this study. These were found to be identical for all parameters [21, 22]. In summary, the model had a relatively high sensitivity to tick mortality rate in the development phase from engorged larvae into questing nymphs, systemic transmission efficiencies, the mortality rate of questing nymphs, basal mortality rate of feeding larvae, transmission host feeding capacity for larvae, transmission host finding probabilities for larvae and nymphs, proportion of time-step spent in grassland for deer and the density of transmission hosts.

(b) Spatial pattern and seasonality of Lyme disease risk in Scotland

The simulated spatial pattern of DIN in woodland is shown in Figure 2A. The relative DIN, or the peak DIN (in week 37) as a percentage of the total DIN for all of Scotland, was used to analyse the capability of annual average temperature, elevation and deer density as simple indicators of high spatial disease risk. The relative DIN was predicted to decrease with increased elevation until it achieved a minimal value close to zero after 500m (visual inspection of Figure 2B; in accordance with empirical tick abundance data [51]). This was because, in the model, high altitude regions have (i) a colder environment which restricts tick development and questing activities (see [51]), and (ii) a large extent of non-woodland habitats with a low transmission host density (e.g. in montane and inland rock), which was predicted to limit the chances of pathogen transmission (c.f. adjacent habitat effects on pathogen transmission in Li et al. [21]). No consistent relationship was found between the predicted relative DIN and annual average temperature. However, where the annual average temperature was between 6 and 10°C, the DIN was predicted to be lower in warmer places (visual inspection of Figure 2C). Such places were predicted to be located in the central and southern parts of Scotland, and close to cities that had fewer deer, hence, the tick population was maintained at a low level. Otherwise (lower than 6°C or greater than 10°C), annual temperature did not predict the difference in DIN between cells, in which the effect of elevation was probably more dominant. Increasing deer density was predicted to be a good indicator of increasing disease risk in regions where deer density was between 15 and 22 heads/km² (visual inspection of Figure 2D). Alternatively, in places with deer density lower than 15 heads/km² or greater than 22 heads/km², the relative DIN was predicted to vary considerably. Some places had extremely high predicted DIN as they were suitable habitats for both deer and transmission hosts in low and medium altitude areas, whilst others had a predicted DIN of nearly zero as these cells were in high altitude areas, which are cooler and therefore have few ticks (after [51]) and fewer transmission hosts. The model predicted a similar seasonality of DIN for different Scottish regions, with some central and southern regions (Oban, Dumfries, Hamilton, Perth and Ayr) having a greater peak DIN value (Figure 3A). A relatively higher risk was predicted in autumn (weeks 37 – 40) than in other seasons, lagging 6 weeks behind the peak weekly temperature (week 31 – 33, see the electronic supplementary material, Figure 3.1F).

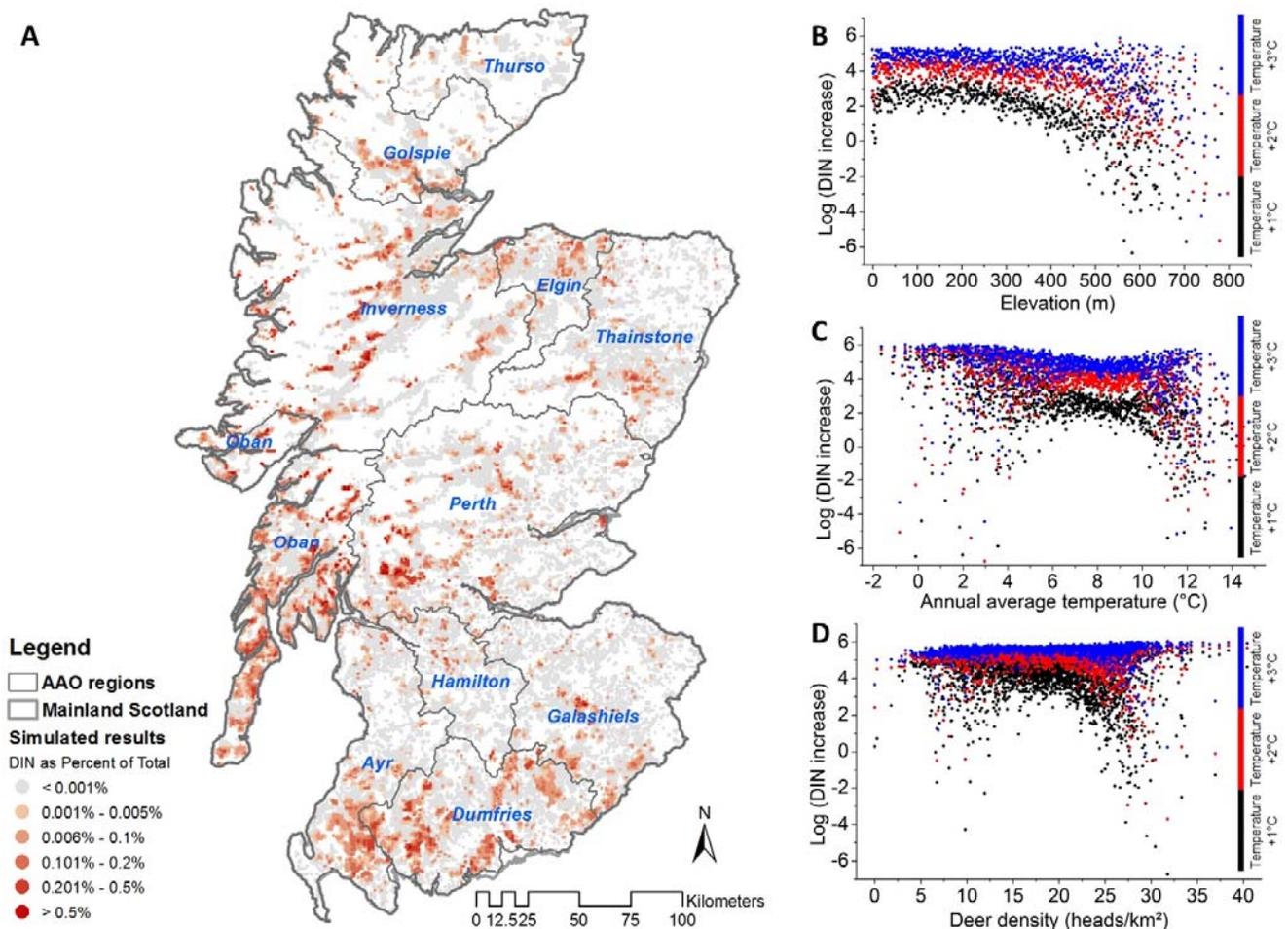


Figure 2 Simulated spatial dynamics of Lyme disease risk in mainland Scotland: (A) Predicted spatial pattern of relative peak DIN (density of nymphs per km² as percent of total), and; (B-D) Predicted influence of temperature increase on peak DIN on an increasing gradient of elevation (averaging interval of 1 m), annual average temperature (averaging interval of 0.1 °C) and deer density (averaging interval of 0.1 heads/ km²).

(c) Effects of climate warming on Lyme disease risk

Regional climate warming led to a predicted expansion of the disease risk to higher altitudinal (Figure 2B) and northern regions such as Thurso and Golspie (Figure 3). With a temperature increase of up to 3°C, late winter and early spring were simulated as being no longer free of disease risk (Figure 3). A warmer temperature was predicted to drive a greater proportion of ticks to resume development (from diapause) in spring and become more active over the winter. Thus, the duration of the interstadial development phase was predicted to be shortened and a greater tick population was predicted to survive before entering the questing phase. In addition, higher proportions of questing ticks were predicted to become active earlier in the spring and remain active later in the winter, resulting in a predicted prolonged duration of the tick questing season. Both could contribute to a greater frequency of tick-host contact and, hence, greater chance for pathogen transmission. By assuming that temperatures increased throughout the year, an upsurge in overall DIN was predicted for all regions (the electronic supplementary material, Figure 1.1). Compared with the baseline pattern (no temperature increase), temperature increases of 1°C, 2°C and 3°C resulted in the predicted peak value of DIN increasing by 2, 7 and 11 times, respectively, and the extent of the predicted endemic area enlarging by 2.68%, 3.66%, and 3.99%, respectively. The greatest increases in endemic area extent were predicted in Thainstone (3.96%, 6.24% and 7.80%), Hamilton (6.68%, 6.85% and 6.85%) and Ayr (5.12%, 5.56%, and 5.60%). The overall effect of the temperature increases was predicted to be weaker as elevation increased (Figure 2B). The predicted effect of climate warming scenarios was difficult to distinguish when plotted against annual average temperature (Figure 2C) and deer density (Figure 2D), because the two variables were both unable to explain the baseline DIN pattern (and the baseline DIN pattern was strongly correlated with the DIN increase in the

climate warming scenarios; a significant Pearson correlation coefficient of 0.67 was found between the predicted baseline DIN surface and the DIN surface under the temperature +1°C scenario).

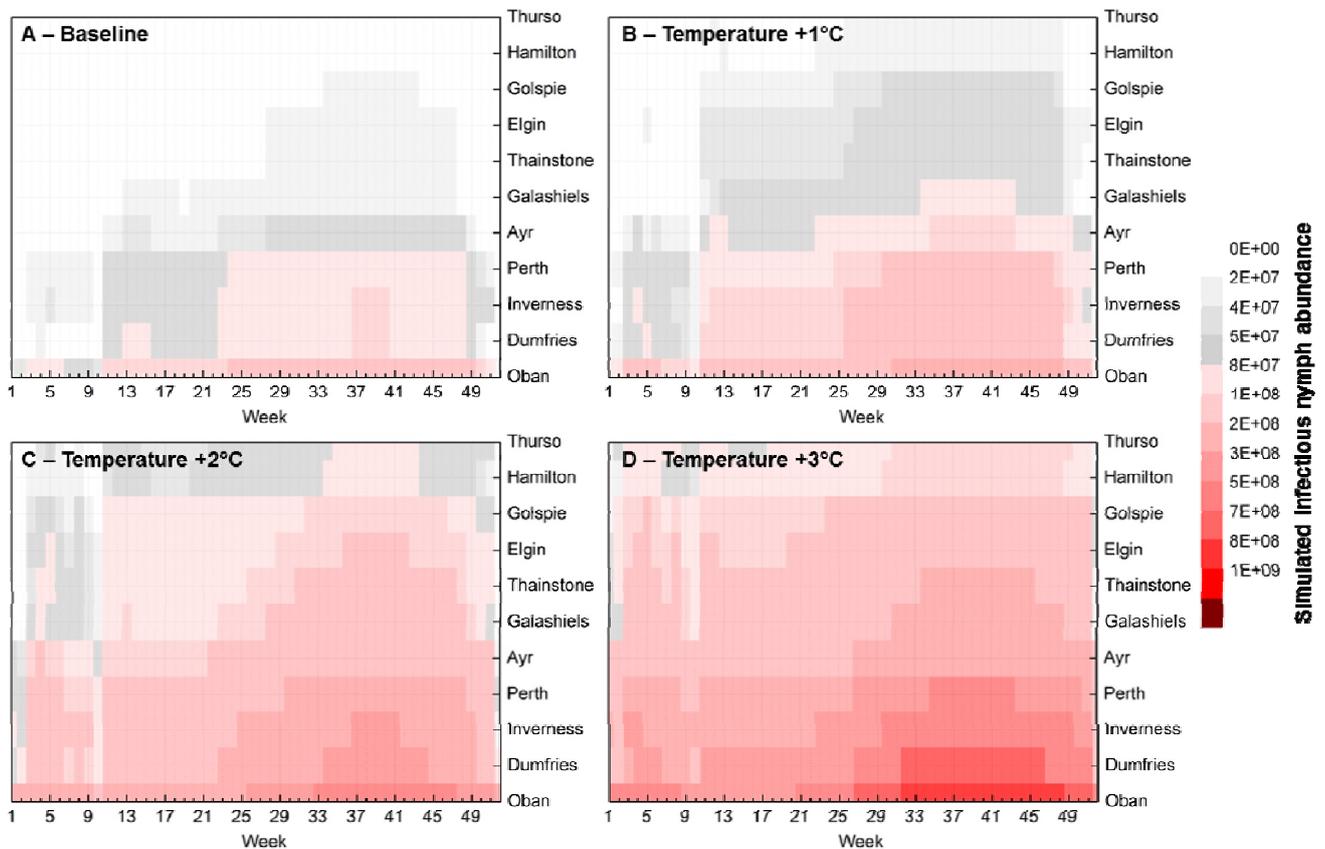


Figure 3 Predicted influence of temperature increase on the simulated seasonal variation of infected nymph abundance (summed DIN in woodland areas) in each AFRC (agriculture, food & rural communities) area office region.

4 Discussion

A mechanistic model was developed for mainland Scotland to predict the seasonal dynamics of the *Borrelia burgdorferi* s.l. infected nymphal *I. ricinus* ticks (or DIN, density of infected nymphs), a biophysical risk indicator of Lyme disease. The model integrates recent advances in simulating the temperature-driven temporal [16-20] and spatial [21, 22] dynamics of disease risk, with multi-disciplinary data based on the literature, empirical evidence, earth observation and model predictions. It was developed using an agent-based approach that consisted of three generalised grid layers (tick population, host population and landscape) and a range of transition rules describing their interactions under the influence of temperature. Considering the scale (the whole of mainland Scotland) and spatial resolution (1 km²) of this study, the model is more relevant for rodent-specialised *Borrelia* genospecies such as *B. afzelii* and *B. burgdorferi* s.s. than for the bird-specialised *B. garinii* or *B. valaisiana* because the densities of rodents are far greater than birds. However, recent empirical work in Scotland revealed that more than 40% of *Borrelia* is associated with birds, based on ticks collected across 25 woodland sites [3]. Further models specifically focussing on birds would be needed at a finer scale to gain a better picture of the *Borrelia* transmission network.

It should be noted that the focus of this study was on long-term risk and the predicted DIN pattern, i.e., the results were based on 12-year (2000-2011) mean weekly temperature surfaces. Model predictions may have been different if different temperature data had been used. Furthermore, we focused on the relative values of DIN rather than on absolute values, which are difficult to measure in the field due to the low sampling efficiency of the flagging method which varies widely depending on the vegetation type and due to variation in questing tick behaviour related to weather conditions at the time of sampling. The predicted risk patterns

suggest a spatial endemic foci in the Highlands (e.g., Oban and Inverness) and Tayside (e.g., Perth) and temporal foci in August and September, which are similar to the pattern of human incidence records [52, 53]. In line with a recent field survey [51] in which ticks were found to be strongly and negatively associated with elevation on nine Scottish hills, our model simulations predict a general decrease in DIN with increased altitude in Scotland up to 500m, above which the tick populations were close to zero. The ability of two other variables (annual mean temperature and deer density) to act as a proxy of disease risk was also analysed, but their explanatory capability may only be satisfactory within certain intervals: the DIN was predicted to be negatively associated with annual temperature between 6 – 10°C and positively with deer density between 15 – 22 head/km².

Climate warming has been found to accelerate tick phenology [49] and contribute to their geographical expansion [54]. Our model predicted similar overall conclusions from applying scenarios of regional warming to the Lyme disease model. First, the model predicted an overall rise in DIN across the year with a peak in autumn. Climate warming was predicted to contribute to a greater frequency of tick-host contact and therefore greater chance for pathogen transmission. The consequent predicted DIN increases were greater in low altitude regions of Scotland where DIN had already been established at a relatively high level. Second, the model predicted that climate warming could increase the extent of tick infested areas, albeit marginally (less than 4% increase under all three climate warming scenarios) as the distribution of ticks in mainland Scotland is currently widespread [24]. Newly emerged DIN cells were predicted to follow an altitudinal direction, as warming turned cold high altitude places into areas suitable for maintaining an adequate population of questing ticks for a long enough period of the year. Most of these regions were inhabited by deer, which help to sustain tick populations.

We have faced certain methodological and data challenges when applying such a complex modelling approach to a large area in the real world in line with those cited for complex socio-ecosystem modelling by Filatova et al. [55]. The most critical methodological challenge is how to represent the mechanisms of *B. burgdorferi* s.l. transmission as this involves multiple vector life stages, pathogen genospecies, host types and movement patterns. The potentially important mechanisms underpinning the interactions of system components are numerous and complex, but there is insufficient field evidence for their full quantification within our modelling framework. Hence, we focused on advancing the treatment of temperature effects within the model on tick population ecology and host population seasonality, whilst a number of simplifying assumptions were used for other parts of the system (e.g., generalising pathogen species and host populations) to avoid introducing too many uncertainties and computation burdens. Data challenges were numerous, but in general data were available for model input and evaluation. We integrated data from diverse sources with different levels of detail, but it was difficult to assess any biases in the model inputs, particularly for transmission host distributions, which have been identified as an important disease risk component in previous modelling studies [3]. Detailed field data on the seasonality of both tick and pathogen populations were not available across a wide range of locations to undertake a thorough evaluation of model output. It is also unfortunate that the model outputs remain highly sensitive to the parameters for which the empirical data are the least reliable (e.g. systemic transmission efficiencies, transmission host finding probabilities). This data-poor condition has been noted as a common bottleneck in the modelling of vectors and diseases [56]. Therefore, the evaluation and parameterisation experiments had to rely on the literature and discontinuous data from multiple sources. Further research is needed to fill these gaps either by improving data collection, or by advancing empirical model predictions.

The present study focused on the biophysical component of the disease transmission system. Disease risk (density of infected nymphal ticks) was derived from those processes underlying vector survival and pathogen circulation in wildlife populations and, hence, could be considered as the “hazard”. However, a high “hazard” does not always indicate a high human infection rate. Social factors shaping the pattern of land use for human outdoor activities, such as walking, forest rangers, hunting, hiking, scouting, orienteering and gardening [57-59], are likely to highly influence the disease pattern [53, 60]. Many of these outdoor activities are also likely to be influenced by climate change. Such activities expose humans to questing ticks and trigger pathogen spill-over to the human population. To date, combined hazard and exposure risk models remain rare for vector-borne diseases, and, to our knowledge, have not been developed for tick-borne diseases. Future integration of exposure assessment may benefit from recent advances in land use models, such as, agent-based

socio-demographical models for estimating the spatial pattern of human trips to forests [61]. Application of such models to more plausible scenarios of future climate and socio-economic change would also constitute a notable extension of existing research. The simple temperature sensitivity analysis undertaken in this study demonstrated the importance of climate warming for disease risk, but more complex scenarios (such as those from regional climate models, where the temperature change varies both spatially and temporally, and those from land use models, which include woodland expansion or contraction) are needed to better understand the pathways of disease risk and the uncertainties associated with these. Involving stakeholders in such future model and scenario development exercises (e.g. as undertaken in the CLIMSAVE project [62]), could significantly advance strategies for adaptive Lyme disease management under environmental change.

Data accessibility

The sources of datasets used in this modelling study have been presented in the electronic supplementary material (supplemental data preparation details).

Authors' contributions

S.L., P.A.H. and M.D.A.R. conceived and designed the study. L.G. contributed to the methods and data. S.L. performed the modelling experiments, interpreted the results and drafted the manuscript with contributions by all other authors. P.A.H., L.G. and M.D.A.R. edited the manuscript. All authors gave final approval for publication.

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Electronic supplementary materials for:

Modelling the seasonality of Lyme disease risk and the potential impacts of a warming climate within the heterogeneous landscapes of Scotland

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1 Supplemental Figures

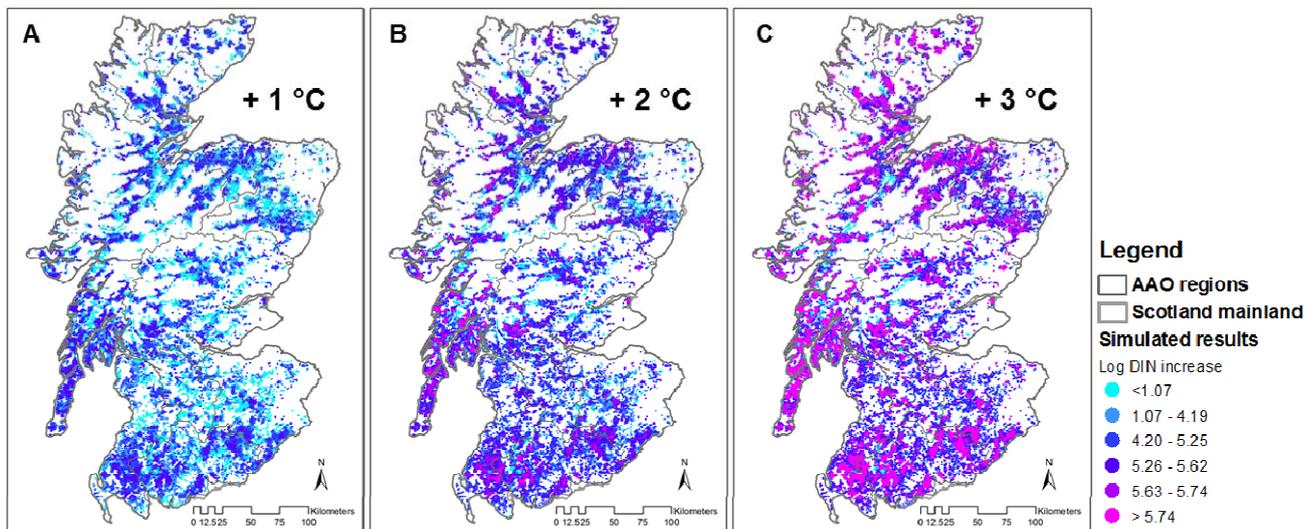


Figure 1.1 Influence of temperature increase on the spatial pattern of peak density of *Borrelia*-infected nymphs (DIN) in woodland habitats. Log DIN increase = Log (predicted DIN under temperature increases – baseline DIN).

2 Supplemental Transition Rules and Parameters

2.1 The spatial dynamics of Lyme disease risk

The transition rules on spatial disease risk were based on previous developments in the spatial dynamics of tick population and host movement patterns (Li et al. 2014) and the transmission of pathogens (Li et al. 2012a). Those that were integrated in this study are described briefly in this section. The parameterisation (Table 2.1) was based on field evidence extracted from literature, assumptions and whether they could contribute to a general realistic model performance in section 4.

Tick population dynamics: The functions for *Ixodes ricinus* population ecology were modified from Li et al. (2014). The life cycle of ticks was considered in four continuous stages: eggs, larvae, nymphs and adults. In each post-egg life stage, ticks can be in questing, feeding or interstadial development phases. Ticks in each post-egg life stage need to feed on host animals to develop into the next life stage. Female adults (assuming that half of the adult population is female) also need blood meals to lay eggs. Eggs then hatch into larval ticks. Feeding durations were assumed to be less than one week for larvae, and one week for nymphs and adults. In the model, at each time step, the questing tick population of a life stage was calculated by adding the ticks that moulted from a previous life stage, removing the ticks that died in the previous time step, and then removing the ticks that attached to hosts during the current time step. Thus, tick population dynamics were driven by three key sets of parameters, namely, interstadial developmental rates, mortality rates and feeding rates. Interstadial developmental rates (f_{dT}) describe the proportion of ticks in the interstadial development phase that would moult into the next life stage. They were set as constant in the previous study (Li et al. 2014), but were assumed to be temperature-dependent in the present study. Mortality rates were constant and were applied to ticks in all questing (m_{qT}) and interstadial development phases (m_{dT}). The mortality rates were assumed to be influenced by land cover types. As a result, scaling factors (Sf) were used to differentiate mortality rates in the different vegetated land cover types considered. Feeding rates, or the number of successful feeding ticks that engorge and drop off from a host, were determined using four steps: (i) the potential number of feeding ticks in a cell (fp) were estimated by multiplying the population of questing ticks by the proportion of questing ticks that may potentially attach to a host during a time step (f_{sqT} and f_{dqT} for transmission and reproduction hosts, respectively); (ii) the maximum feeding places on a host (fm) were estimated by multiplying the host density by the maximum tick attachments a host animal could offer (C_{TS} and C_{TD} for transmission and reproduction hosts, respectively); (iii) the potential feeding ticks in a cell (fp) was modified by the maximum feeding places on a host (fm) by assuming fp would not exceed mf (thus if $fp > fm$, then $fp = fm$) and; (iv) the final feeding rates were estimated by multiplying the modified fp by the density-dependent mortalities for feeding ticks at each life stage estimated by $m_{fT} + 0.049(\ln((1.01 + FT)/HD))$, where m_{fT} is the basal mortality rate, FT is the number of feeding ticks and HD is the host density. The previous study assumed all unfed ticks would be questing, while in the present study the proportion of questing ticks in all unfed ticks (f_{qT}) was assumed to be temperature-dependent (section 2.2).

Pathogen transmission: Among more than 10 named genospecies of *B. burgdorferi* s.l. worldwide (Kurtenbach et al. 2006), the bird-associated *B. garinii*, and rodent-associated *B. afzelii* and *B. burgdorferi sensu stricto* (s.s.) are most commonly found in Scotland (James et al. 2013). Systemic transmission (i.e., the pathogen is transmitted during the blood meal from an infected host to an uninfected tick or from an infected tick to an uninfected host) is the main transmission route commonly considered for the circulation of *B. burgdorferi* s.l. in tick and transmission host populations. The Susceptible-Infectious functions developed in Li et al. (2012a) were integrated for the systemic pathogen transmission (with host-to-tick and tick-to-host transmission efficiencies θ_{HT} and θ_{TH}). In this study, it was assumed that transmission hosts cannot clear their *Borrelia* infections and remain infected for life (Donahue et al. 1987, Gern et al. 1994). Future modelling efforts may test the effects of a θ_{HT} that declines rapidly over time following infection (Lindsay et al. 1997, Derdáková et al. 2004, Hanincová et al. 2008). Another previously reported route is transovarial transmission (i.e., the pathogen is passed on from infectious females to eggs) (Matser et al. 2009). However, recent empirical work (Richter et al. 2011) and a recent review (Rollend et al. 2013) suggest that this phenomenon does not occur in *B. burgdorferi* s.l. pathogens. According to these studies, the previous reports of transovarial

transmission were actually caused by the relapsing fever spirochete *Borrelia miyamotoi* or due to interrupted larva-host contacts. In this study, a very low proportion of larval ticks was assumed to experience interrupted host contacts which would lead to a low infection rate in questing larval ticks ($\theta_{LL} = 0.01$). Moreover, non-systemic pathogen can be transmitted between co-feeding ticks e.g., via sheep (Ogden et al. 1997). However, there is debate on the significance of non-systemic transmission for the maintenance of *B. burgdorferi* s.l. (Richter et al. 2002, Randolph and Gern 2003). More recently, a review generally concludes that non-systemic transmission makes only a minor contribution to the *Borrelia* prevalence in ticks (Voordouw 2015). Hence, non-systemic transmission was not included in the present model. Finally, transstadial transmission was assumed to be 100%, i.e., all larval and nymphal ticks that acquired spirochetes from an infected transmission host would develop into infected nymphs and adult ticks, respectively.

Host population dynamics and movement patterns: In the model, within-cell transmission host population dynamics were assumed to be time-dependent. The transitions rules (section 2.3) were based on periodic birth rates (b_s), mortality rates (m_s) and carrying capacity (K_s) to represent the cyclic population in transmission hosts, following recent rodent population models used in Hantavirus investigations (Sauvage et al. 2003, Sauvage et al. 2007, Amirpour Haredasht et al. 2011). Since there is no evidence that *B. burgdorferi* s.l. pathogens reduce the fitness of their transmission hosts (Hofmeister et al. 1999, Schwanz et al. 2010, Chambert et al. 2012, Norte et al. 2013, Voordouw et al. 2015), b_s and m_s were assumed independent of infection status. Total numbers of reproduction hosts were assumed constant and mostly affected by management practices. Transition rules for multi-phasic host movement patterns were developed in Li et al. (2014) and integrated into the present model (section 2.4). In the home-ranging phase, animals randomly move within their home range. Alternatively, in the displacement phase, animals tend to move over longer distances to travel to new habitats. In practice, home-ranging animals spend different proportions of time in different habitat types to establish home ranges, e.g., deer grazing on grassland ($pGrz_D$) or livestock grazing on heathland and woodland ($pGrz_L$). In the dispersive phase, proportions of the animal population are dispersive ($pDis$), leaving the original habitats for new habitats. This proportion can be set as either constant or density-dependent, according to the model purpose and field evidence. In the model, the host movement patterns were determined by a set of stochastic rules on carrying capacity of the cell's neighbourhood (K) and host's movement capacities (MC), whose details are provided in Li et al. (2014). Carrying capacity was used to indicate whether a cell could receive populations in a time step. Movement capacity was denoted by: (i) the maximum size of the home range in the home-ranging phase and (ii) the maximum travel distance per time step in the dispersive phase. This structure allows various host movement patterns to be tested under environment and management changes. In the present model, several updates were made to better represent field conditions: (i) the home-ranging and dispersal movements of transmission hosts were considered to be completed within each cell, given a cell size of 1 km² and a low movement capability for most transmission host species; (ii) deer were assumed to perform seasonal uphill/downhill dispersal; and (iii) deer and livestock were considered to experience seasonal home-ranging movements.

2.2 The influence of temperature on tick population dynamics

Temperature can shape tick population dynamics by influencing their behaviour and biological processes, for example the interstadial development speed, host-finding activity and diapause. Existing functions to quantify these effects can be found in a number of recent publications (Ogden et al. 2005, Hoch et al. 2010, Dobson et al. 2011a, Hancock et al. 2011, Wang et al. 2012). Those functions that are most commonly used were integrated into this model. Parameters related to the influence of temperature on tick population dynamics are listed in Table 2.1.

Interstadial development: Tick developmental stages include eggs developing into larvae, engorged larvae developing into nymphs, engorged nymphs developing into adults and engorged adults producing eggs. Following Hancock et al. (2011), the weekly development rates were estimated using temperature-dependent functions of the form: $f_{dT} = aT_t^2 + bT_t + c$, where T_t is the mean temperature of the week t , and a , b and c are constants. The value of f_{dT} represents the proportion of the total tick development that occurs in the week t . Following the assumption by Randolph et al. (2002), a threshold temperature T_0 , below which tick development stops, was introduced.

Questing activity: Tick questing behaviour has been found to be sensitive to microclimatic conditions, resulting in seasonal changes in the proportion of questing ticks in all unfed ticks (Gilbert et al. 2014). To account for such an influence, a temperature-dependent factor f_{qT} ($0.0 \leq f_{qT} \leq 1.0$) was introduced. Thus, for each cell, the unfed ticks in all life stages would be multiplied by f_{qT} to calculate the active questing tick populations. The f_{qT} equations were generated based on the data from a laboratory experiment by Gilbert et al. (2014) to quantify the temperature influence on the proportion of active ticks questing in *I. ricinus* collected from northeast Scotland: (i) $f_{qT} = -1.22T^2 + 36.04T - 149.92$ ($R^2 = 0.99$), when $T \leq 11$, and (ii) $f_{qT} = 17.77\ln(T) + 45.13$ ($R^2 = 0.77$), otherwise. As a result, a threshold temperature of approximately 5.24°C was determined, below which ticks were assumed inactive ($f_{qT}=0$).

Diapause: There is evidence that changes in seasonal host-seeking activity patterns can be associated with the effects of diapause (Gray 2008). In order to adapt to the seasonal variation of temperate climates, ticks regularly undergo diapause periods, during which their development rates are greatly reduced (Randolph et al. 2002, Dobson et al. 2011a). Following Hancock et al. (2011), it was assumed that a proportion, p_{TD} , of the questing larvae, nymphs and adults that obtain a blood meal between late July and December (between week 30 – 52) would delay the onset of development until the first week of the following year.

Ticks are also known to require a relatively humid microclimate. Laboratory experiments have demonstrated the importance of humidity (and vapour pressure deficits, usually being estimated as a function of temperature and humidity) to tick survival and questing activity (Gray 1998, Randolph 2004a). However, humidity was not included in our study because its effect remains unclear in the field. For example, contrasting results have been found which suggest the association between tick questing activity and humidity is insignificant (Brownstein et al. 2003, Gray et al. 2009), positive (Vail and Smith 1998) and negative (Ruiz-Fons and Gilbert 2010, Li et al. 2012b, Kiewra et al. 2014). Future empirical studies are needed to improve understanding of how other climatic factors might influence tick behaviour and development in the natural environment.

2.3 Seasonality of the transmission host population

In the present model, the transmission host populations were modelled on a weekly time step with demographic parameters, as the interaction between transmission hosts and ticks is key to disease transmission. In Scotland, both field vole and bank vole densities can range between 20 – 250 voles per ha (Lambin et al. 2000), which is much greater than the density range for common bird species, for example, 0.01 – 2 birds per ha for chaffinch, blackbird and blue tit (Balmer et al. 2013). Therefore, the transmission host demography was assumed to be largely related to rodents, and the dynamics of bird populations was assumed to have a negligible effect. A number of models on rodent population dynamics can be found in Hantavirus investigations (Sauvage et al. 2003, Sauvage et al. 2007, Amirpour Haredasht et al. 2011). The present work followed their approaches to consider a one-year periodic birth rate (b_{SM}), a three-year periodic carrying capacity (K_{SM}) and a combined mortality (m_{SM}) as a function of t (week):

$$b_{SM}(t) = 7.5|20\sin(2\pi(t/52 - 0.15))| + 20\sin(2\pi(t/52 - 0.15)) \quad (1)$$

$$K_{SM}(t) = 6(10 + (\cos(2\pi(t/52 + 0.35))/3)^2 - 20\sin(2\pi(t/52 + 0.35))) \quad (2)$$

$$m_{SM}(t) = (8 + 2/K_R(t))/52 \quad (3)$$

2.4 Host movement patterns

Home ranging: The home range size was found to be 0.1 – 0.2 ha for small mammals (Kikkawa 1964) and birds (Reed 1982). Given a cell size of 1 km², all home-ranging activities of transmission hosts were assumed to be within-cell. The cross-cell home-ranging movements were marginal and hence considered to be negligible. For reproduction hosts, the home range size for woodland and heathland deer was assumed to be 80-100 ha in winter and 40-60 ha in summer (Morellet et al. 2013), and for grassland livestock 10-33 ha in winter and 20-60 ha in other seasons (Lawrence and Wood-Gush 1988). In addition, the home range size of deer can be influenced by altitude. Thus, it was assumed in the model that each 200 m increase in altitude enlarges the home range size by 100 ha (Mysterud 1999).

Dispersal: The dispersal of transmission hosts was not included in the present study as small mammals usually have a dispersal distance of less than 1 km (Kikkawa 1964) and the seasonal migration of birds often takes place at the continental or global level. The seasonal dispersal of deer (i.e., downhill migration to low elevations during winter and uphill migration to high elevations during summer, 50% of the population) has been reported to start from the first week of April to the first week of June (week 15 to week 24, uphill) and from the first week of September to the third week of January (week 37 to week 3 of the following year, downhill), with a weekly-average maximum movement distance of 2 km (Mysterud 1999). To enable the representation of deer's seasonal dispersal in the model, an update to the dispersal rules was made by adding a new condition to the deer destination selection process: the altitude changes must be between 20 – 50m negative for the downhill migration and positive for the uphill migration. The dispersal of livestock was assumed to be anthropic and was not considered in the present study.

Table 2.1 Model Parameters

Parameter	Symbol	Value	Source
<i>Parameters related to tick population dynamics</i>			
Average no. eggs per adult	β	2000	Randolph and Craine (1995)
Mortality rates in woodland (week ⁻¹)			
Questing larvae, nymphs and adult ticks	m_{qT}	0.03, 0.03, 0.02	Daniel et al. (1976)
Developing from			
Engorged larvae into questing nymphs		0.03	
Engorged nymphs into questing adults	m_{dT}	0.01	Daniel et al. (1976) & Gray (1981)
Engorged adults into eggs		0.02	
Eggs into questing larvae		0.02	
Scaling factors for mortality rates of questing and developing ticks			
Woodlands (broadleaf and coniferous)	Sf	1, 1.05	Mount et al. (1997), Medlock et al. (2008) & Assumption
Grasslands (improved and semi-natural)		3, 1.25	
Heathlands (dwarf shrub/bog and montane)		1.2, 2	
Temperature-dependent proportion of questing ticks	f_{qT}	See text	Gilbert et al. (2014)
Basal feeding mortality rates (week ⁻¹)			
Larvae, nymphs and adults on transmission hosts	m_{fT}	0.65, 0.65, 0.55	Gray (1981) & Hancock et al. (2011)
Larvae, nymphs and adults on reproduction hosts		0.6, 0.6, 0.5	
Parameters in the temperature-dependent interstadial development rate functions	$f_{dT}(a, b, c, T_0)$	See text	Gardiner et al. (1981) & Randolph et al. (2002)
Eggs developing into larvae		-0.00001, 0.002, -0.019, 5	
Larvae developing into nymphs		0.00003, 0.00073, -0.007, 7	
Nymphs developing into adults		-0.000008, 0.0019, -0.016, 7	
Adults producing eggs		0.0001, 0.01, -0.062, 7	
Proportion of tick population undergo diapause periods	p_{TD}	0.8	Hancock et al. (2011)
Transmission host finding probability for questing larvae, nymphs and adults	f_{SqT}	0.03, 0.2, 0.01	Hancock et al. (2011) & Assumption
Deer or livestock host finding probability for questing larvae, nymphs and adults	f_{DqT}	0.001, 0.1, 0.3	Hancock et al. (2011) & Assumption
Host feeding capacity (week ⁻¹)			
Maximum larva, nymph, and adult attachments on one transmission host	C_{TS}	100, 6, 0.1	Oliver Jr (1989), Gray (2002), Cagnacci et al. (2012) & Assumption
Maximum larva, nymph, and adult attachments on one deer or livestock	C_{TD}	200, 200, 100	
<i>Parameters related to pathogen transmission</i>			
Transmission efficiency from transmission hosts to ticks	θ_{HT}	0.5	Randolph and Craine (1995)
Transmission efficiency from ticks to transmission hosts	θ_{TH}	0.8	Hartemink et al. (2008)
Transmission rate of questing larval ticks caused by interrupted host contacts	θ_{LL}	0.01	Hubalek and Halouzka (1998), Richter et al. (2011) & Assumption
<i>Parameters related to host population dynamics</i>			
Birth rate of transmission hosts (week ⁻¹)	b_S		Sauvage et al. (2003), Sauvage et al. (2007) & Amirpour Haredasht et al. (2011)
Mortality rate of transmission hosts (week ⁻¹)	m_S	See text	
Carrying capacity of transmission hosts (km ⁻²)	K_S		
Carrying capacity of deer (km ⁻²)	K_D	300	Putman and Watson (2010)
<i>Parameters related to host movement patterns</i>			
Movement capacity (km·week ⁻¹)			
Deer in home ranging phase	MC_{DHR}	0.5 (winter/spring); 0.3 (summer/autumn)	Putman (1988)
Livestock in home ranging phase	MC_{DHR}	0.2 (winter); 0.4 (other seasons)	Lawrence and Wood-Gush (1988) & Morellet et al. (2013)
Deer in dispersive phases	MC_{DDis}	2	Mysterud (1999)
Proportion of time step spent in grassland for deer (%)	p_{GrzD}	35	Putman (1986)
Proportion of time step spent in heathland and woodland for livestock (%)	p_{GrzL}	30	Steinheim et al. (2005)
Proportion of deer in seasonal dispersive phase (%)	p_{DisD}	5.0 (summer, uphill); 2.63 (winter, downhill)	Mysterud (1999)

3 Supplemental Data Preparation Details

3.1 Land cover map

Mapped land cover data for mainland Scotland (Figure 3.1A) were extracted from the Land Cover Map (LCM) 2007 dataset at a 1 km² spatial resolution, which was downloaded from the CEH Information Gateway (<http://eip.ceh.ac.uk/>). In the LCM2007 data, land cover is classified into 23 types (Morton et al. 2011). These types were regrouped into the “woodland – grassland – heathland – non-vegetated/other areas” landscape structure used in the model. The “woodland” class includes broadleaf (LCM type 1) and coniferous woodland habitats (LCM type 2). The “grassland” class includes improved grassland (LCM type 4) and semi-natural grassland habitats (LCM types 5-9). The “heathland” class includes dwarf shrub and bog (LCM types 10-12) and montane and inland rock habitats (LCM types 13 and 14). The rest of the LCM habitat types were grouped into a “non-vegetated/other areas” class. In addition, the SRTM data (Jarvis et al. 2008) were downloaded to generate an elevation surface (Figure 3.1B). Due to lack of data, all woodlands in LCM were assumed to be unfenced to allow access by tick host types.

3.2 Host distributions

As explained in the main text and previously (section 2 supplemental transition rules and parameters), hosts were organised into three generalised types, namely, transmission host, deer and livestock. In the model, species included in each host type were treated the same in terms of habitat and tick burden. Spatial population data for most transmission host species and deer were unavailable in an appropriate parameter format for the study region. Hence, habitat suitability maps were used to approximate host population distributions. Habitat suitability was given a value between 0-1 to indicate the capability of the cell to support the full carrying capacity (K_S and K_D , Supplemental model transition rules and parameters). Suitability values were specified from the literature and open habitat suitability data for transmission hosts and deer, from which initial population distributions of transmission hosts and deer were generated. For livestock, habitat suitability was not considered since they occur mostly on grassland habitats and their behaviour is largely controlled by humans. Regional livestock population data were available in Scotland and were mapped with parish-level data using simple spatial disaggregation methods.

Transmission host habitat suitability and population distribution: The suitability of each habitat type was calculated as its potential to support a maximum transmission host population. First, a number of key transmission host species were identified from the literature based on their reported abundance and tick burdens in Scotland (Table 3.1) (Tälleklint and Jaenson 1993, 1994, Gilbert et al. 2000, Matuschka et al. 2000, Jaenson et al. 2009, James et al. 2011, James et al. 2014, Millins et al. 2015). Secondly, by reviewing an open source database (the “Species Fact Sheet” by the Mammal Society) and the literature (Harris 1995, Battersby 2005), data were recorded for each selected species on: (i) the upper level population density (WUD) in preferable habitat; and (ii) a qualitative level of presence in all habitats ranging from frequent to rare. Thirdly, a weighted sum of WUD per km² was calculated for each habitat type weighted by the presence level. As a result, broadleaf woodland had the largest WUD while montane/rock habitats had the lowest. Finally, a habitat’s suitability was estimated by dividing its WUD by the largest WUD value found in all habitat types (i.e., the WUD of broadleaf woodland). In model simulations, an initial population density was assigned to each habitat type by multiplying its suitability by an assumed transmission host density in broadleaf woodland (6000 hosts per km²).

Table 3.1 Presence of transmission hosts and their abundance in different habitats

Transmission host species	Upper level density (km ⁻²)	Level of presence in habitat (2=frequent; 1=regular; 0=rare)					
		Broadleaf woodland	Coniferous woodland	Improved grassland	Semi-natural grassland	Dwarf shrub heath & bog	Montane & rock habitats
Birds							
Common Blackbird (<i>Turdus merula</i>)	400	2	1	1	1	1	0
Great Tit (<i>Parus major</i>)	140	2	1	1	1	1	0
Chaffinch (<i>Fringilla coelebs</i>)	200	2	1	1	1	1	0
Rodents							
Field vole (<i>Microtus agrestis</i>)	30000	1	1	1	2	1	0
Bank vole (<i>Myodes glareolus</i>)	40000	2	2	1	1	1	0
Wood Mouse (<i>Apodemus sylvaticus</i>)	20000	2	2	1	2	2	1
Lagomorphs							
Mountain hare (<i>Lepus timidus</i>)	100	0	1	1	1	2	2
Rabbit* (<i>Oryctolagus cuniculus</i>)	1000	1	1	2	2	2	1
Weighted sum of upper level density		152480	151840	92840	142840	112940	21200
Habitat suitability		1	0.996	0.609	0.937	0.741	0.139
Initial density (km⁻²)		6000	5975	3653	5621	4445	835

* Considered as alternative transmission hosts that may also contribute to tick reproduction. The exclusion of rabbits was found not to influence the main results found in the present study.

Deer habitat suitability and population distribution: The roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) suitability maps at 1 km² from the EDENEXT project (Alexander et al. 2014, Wint et al. 2014) were used to generate a generalised suitability map for Scottish deer. A simple weighting scheme was applied according to the ratio of the two deer species' populations. Based on the SPICE briefing report (Edwards and Kenyon 2013), the estimated recent populations for red deer and roe deer were between 360,000-400,000 and 200,000-350,000, respectively, in the whole Scottish region. Hence, the general deer habitat suitability was calculated as 0.6 * red deer habitat suitability + 0.4 * roe deer habitat suitability, and was scaled to [0,1] and mapped on to the woodland and heathland habitat types for mainland Scotland. By assuming a total deer population of 600,000 in mainland Scotland, an estimated deer population distribution was generated using a simple estimation: deer population of a cell = total population * cell suitability / summed suitability across all cells (Figure 3.1C).

Livestock distribution: Grazing livestock were assumed to mostly occur on grassland and hence are exposed to tick bites. Sheep and cattle are the most abundant livestock species in Scotland with a population of 7.5 and 1.9 million in 2007, respectively (out of 10.05 million total livestock population) (Volkova 2008). The sheep and livestock population data in 2010 at AFRC (agriculture, food & rural communities) area offices (AAO) and parish levels were acquired from the Rural and Environment Science and Analytical Services of the Scottish Government. The density of total sheep and sheep on grassland was calculated for each parish. Due to confidentiality reasons, some parish-level data were undisclosed. For those parishes, the AAO-level density was calculated and used instead. Finally, population per grassland cell was estimated (Figure 3.1D). Due to data constraints, the model assumed all livestock were not treated with acaricides.

3.3 Temperature data

Gridded daily temperature data covering the whole of the UK between 2000 and 2011 were downloaded from the UK Met Office (UKCP09: Daily data sets, 5 km² resolution) (Jenkins et al. 2009). To prepare the model inputs, these daily temperature data were firstly analysed to generate weekly mean temperature surfaces for each of the 12 years between 2000 and 2011. Then, for each week in a year, the mean temperature surfaces were averaged across the 12 years, resulting in 52 grids as model inputs. The spatial patterns of averaged weekly temperature and seasonal pattern of temperature in mainland Scotland are presented in Figures 3.1E and 3.1F. A simple elevation-based downscaling of temperature was applied to approximate the temperature variations for each week at the 1 km resolution (Sheridan et al. 2010), by $dT = -dH * 0.0098^{\circ}Cm^{-1}$, with dH being the difference between the elevations averaged at 5 km and 1 km resolutions.

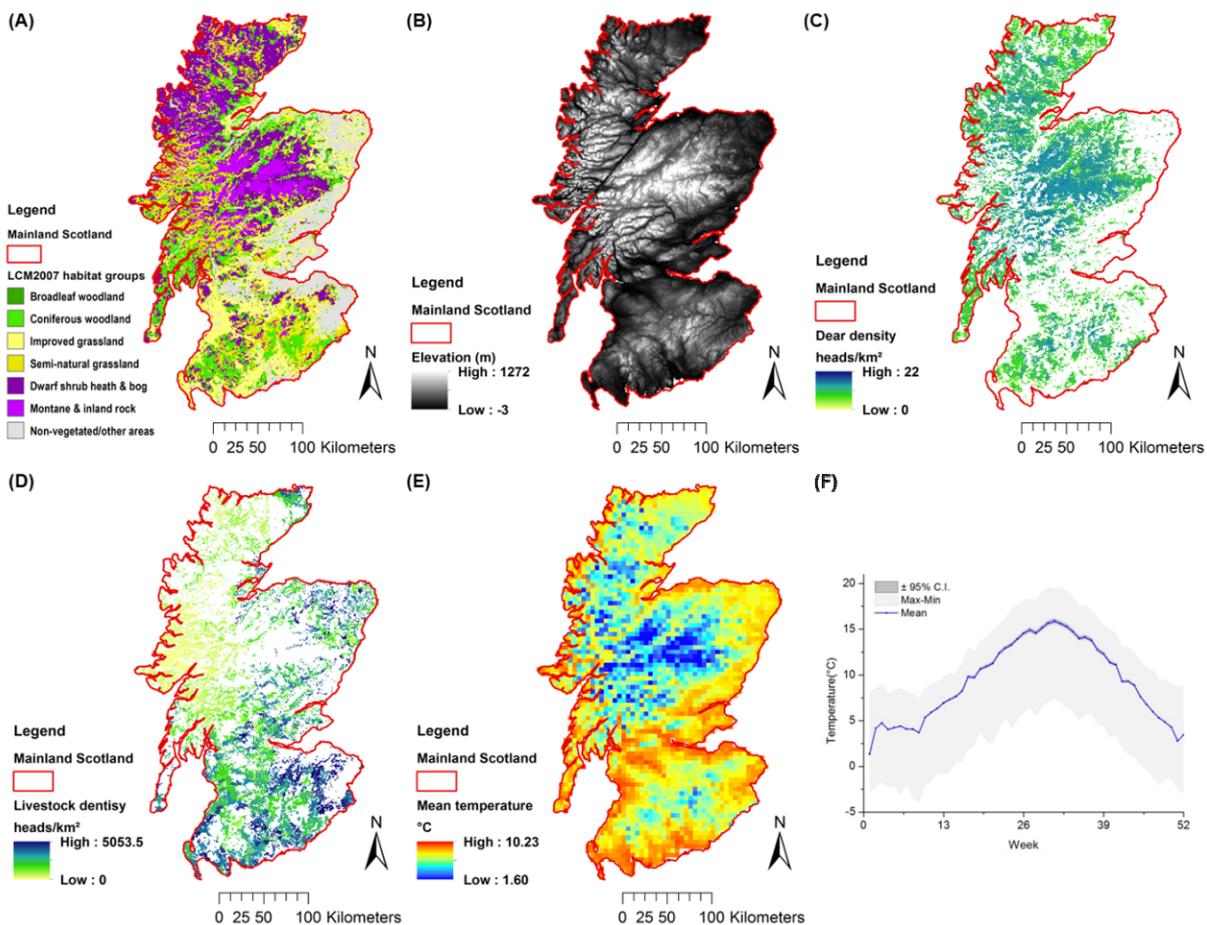


Figure 3.1 An overview of data preparation for mainland Scotland as model input: (A) land cover/habitat type; (B) elevation maps based on open earth observation data; (C) distribution of deer estimated based on assumptions and model predictions; (D) livestock distribution disaggregated from census data; and (E) and (F) temperature data retrieved from the national meteorological office.

4 Supplemental Model Evaluation Results

4.1 Comparison with existing empirical findings on seasonality

Limited field evidence exists in the literature on tick and pathogen population seasonality across the different regions of Scotland, making a comparison of predicted values against empirical data difficult. Simulated questing immature ticks (larvae and nymphs) had similar seasonal patterns with a peak in autumn (September-October, see Figure 4.1A-C). In the literature, patterns of questing immature ticks were found to be different between regions and dependent on the temperature profiles in, and prior to, the sampling years. For example, in 1999 and 2000, an autumn peak of larvae was found in Wales, whilst in England (Exmoor and Dorset) larvae peaked in the summer (Randolph et al. 2002, Randolph 2004b). In the same studies, nymphs were found to peak in summer in Dorset, but in spring in Exmoor and Wales. In addition, the sampling method may influence field observations of seasonality. For example, a study in Exmoor between 2008 and 2010 found a spring peak of larvae using blanket-drag sampling, but a summer-autumn peak using heel flags (Dobson et al. 2011b). Field studies for recent immature tick seasonality in Scotland were rare in number. A recent dynamic *I. ricinus* population model based on long-term average temperature in Braemar, northeast Scotland predicted a similar seasonal emergence of questing nymph between August and October (Hancock et al. 2011). Gilbert et al. (2014) used tick behaviour vs temperature to predict a single mid-summer peak in activity for questing nymphs in upland northeast Scotland. Our model predicted that questing adult ticks (females) had a relatively symmetrical, seasonal pattern with relatively high values between weeks 25 and 29 (June-July). This result was in agreement with a recent study in Scotland, in which seasonality of female ticks feeding on deer was found to be symmetrical and peaked in June/July (Gilbert et al., unpublished). The peak value of the weekly mean densities of active questing ticks were approximately 150 larvae, 15 nymphs and 2.5 adult females per 100m² in broadleaf woodland. In peak seasons, the maximum densities of active questing ticks in each cell were approximately 10 times higher, e.g. 1500 larvae, 150 nymphs and 25 adult females per 100m² (not shown), which were slightly lower than the maximum densities of 1500 larval ticks, 700 nymphal ticks, and 40 adult females per 100 m² estimated in a field study in England (Dorset) (Randolph 2004b), as might be expected in a colder climate. In all habitat types, the weekly mean values of simulated cell-level nymphal infection prevalence (NIP) and adult infection prevalence were predicted to be relatively stable over the course of the year (see Figure 4.1D-E). Furthermore, in Scotland, the proportion of infection in all nymphs sampled in spring and summer was found to be similar, despite nymphs being statistically more likely to be infected in late than early summer (James et al. 2013). As the NIP was relatively stable, the seasonal pattern of the density of infected nymphs (DIN: the product of NIP and density of nymphs) was largely driven by the density of nymphs (DON).

Additional simulated seasonal patterns are provided to help the readers gain a better overview of the model's features and performance. In Figure 4.2, seasonality of total and infectious populations of transmission hosts is provided. The population density and infection prevalence were higher in woodlands and semi-natural grassland, where habitat suitability was higher (Table 3.1). In the three-year life cycle, transmission host population peaked in each summer (weeks 31, 83 and 135, when the infection prevalence was the lowest in each year) and was relatively higher in the third year. Over the course of the transmission season, the figure shows a clear decrease in the proportion of infected transmission hosts, as reproduction adds new susceptible individuals to the population. Figure 4.3 presents the seasonality of feeding larval, nymphal and adult female ticks on different host types and Figures 4.4-4.6 provides information on where these feeding ticks were encountered. The predicted average feeding ticks were 1.94 larvae, 0.15 nymphs and 0.0008 adults on transmission hosts in peak season, which are lower than the average values (6, 0.2, 0.001) used in Hartemink et al. (2008). In general, the model performed correctly as designed (see section 2 supplemental transition rules and parameters): (i) transmission hosts fed more larvae and nymphs in all habitat types, (ii) deer fed more adults in woodlands, (iii) livestock fed more adults in grasslands, and (iv) montane heathland had a low level of questing ticks.

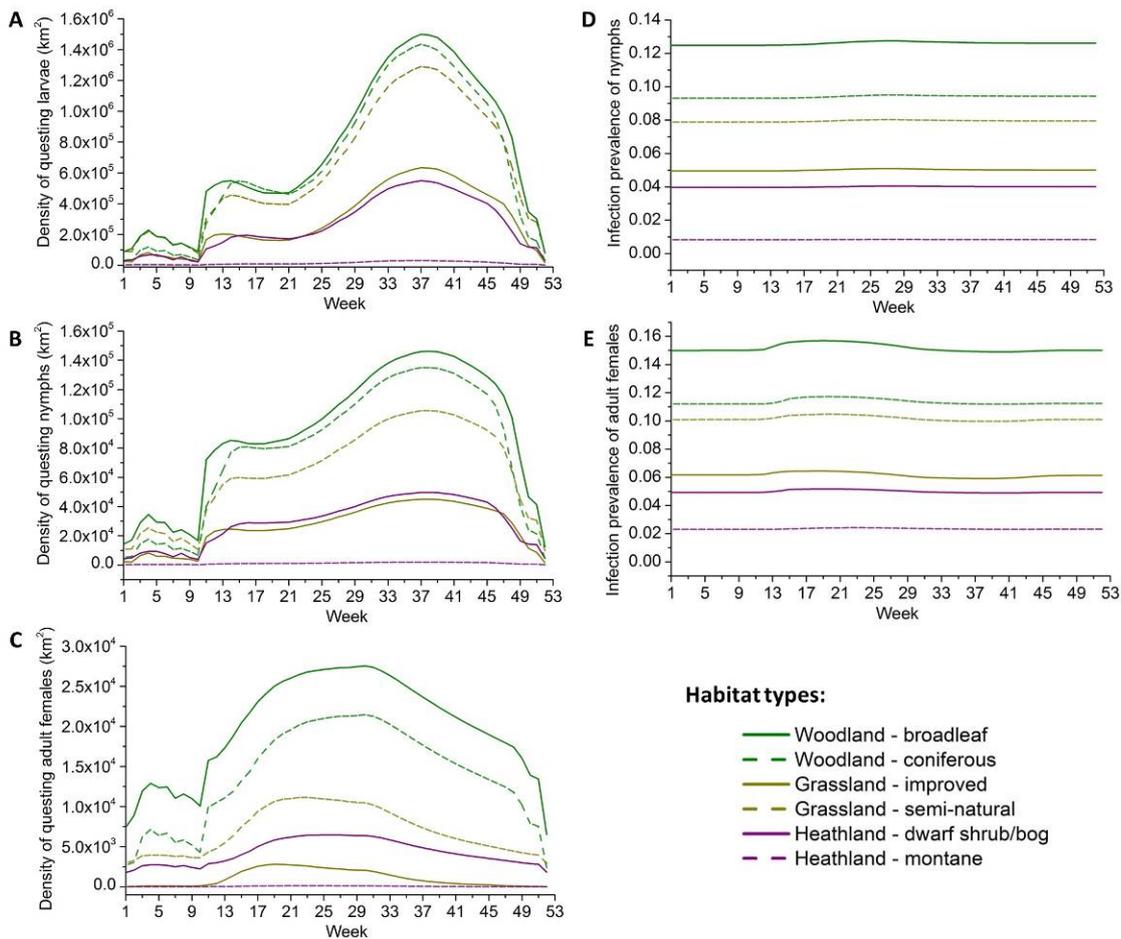


Figure 4.1 Simulated seasonality of *Ixodes ricinus* tick populations and infection prevalence in different habitat types: predicted mean density of questing larva (A), nymph (B) and adult female (C) densities (km^{-2}) and predicted mean *Borrelia burgdorferi sensu lato* infection prevalence in nymphs (D) and adults (E).

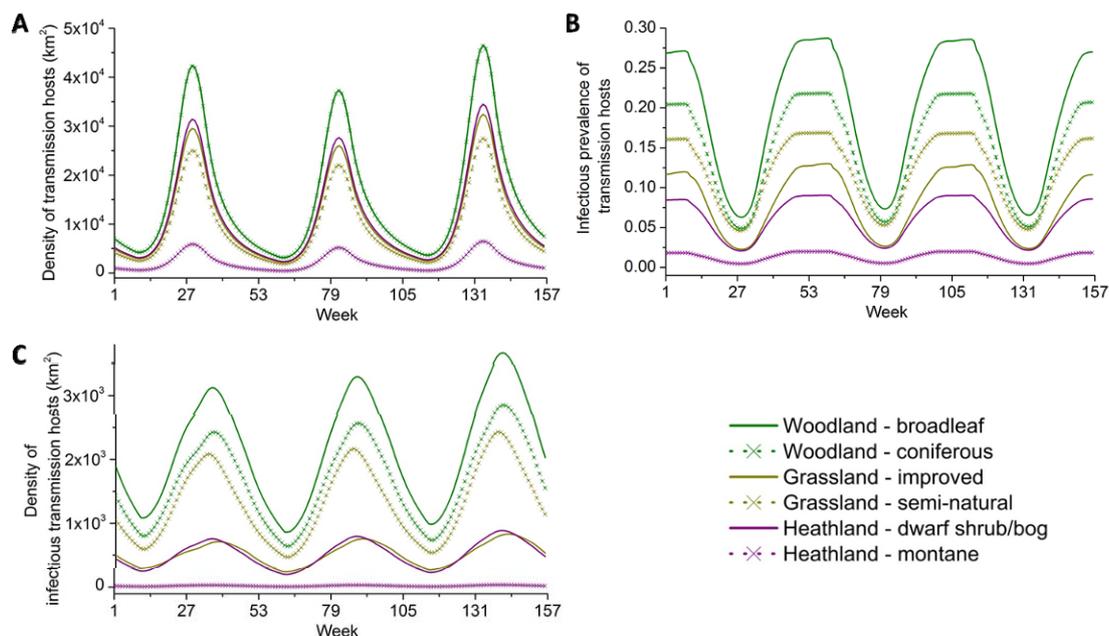


Figure 4.2 Simulated three-year life cycle of transmission host population density (A), *Borrelia burgdorferi sensu lato* infection prevalence (B) and infectious population density (C) in different habitat types.

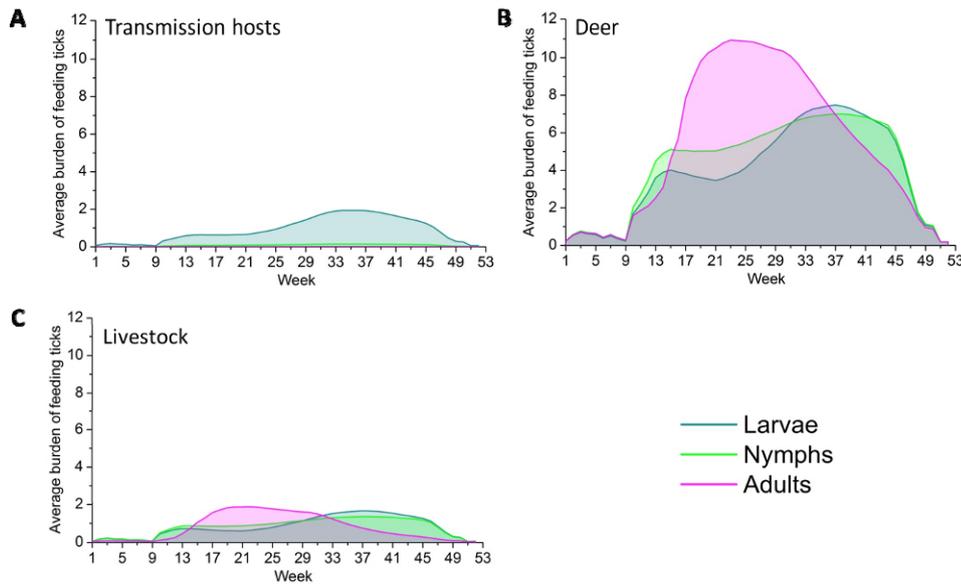


Figure 4.3 Simulated mean number of feeding ticks surviving on transmission hosts (A), deer (B) and livestock (C).

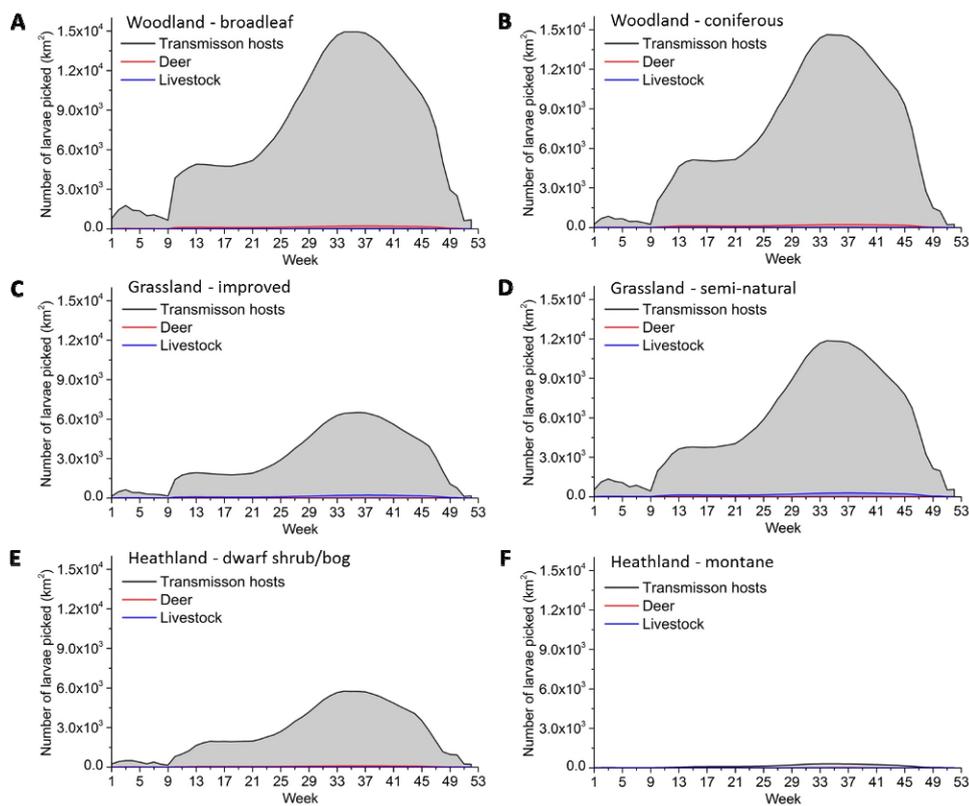


Figure 4.4 Simulated mean number of feeding larval ticks in different habitat types from which they are picked up: woodland (A-B), grassland (C-D), and heathland (E-F).

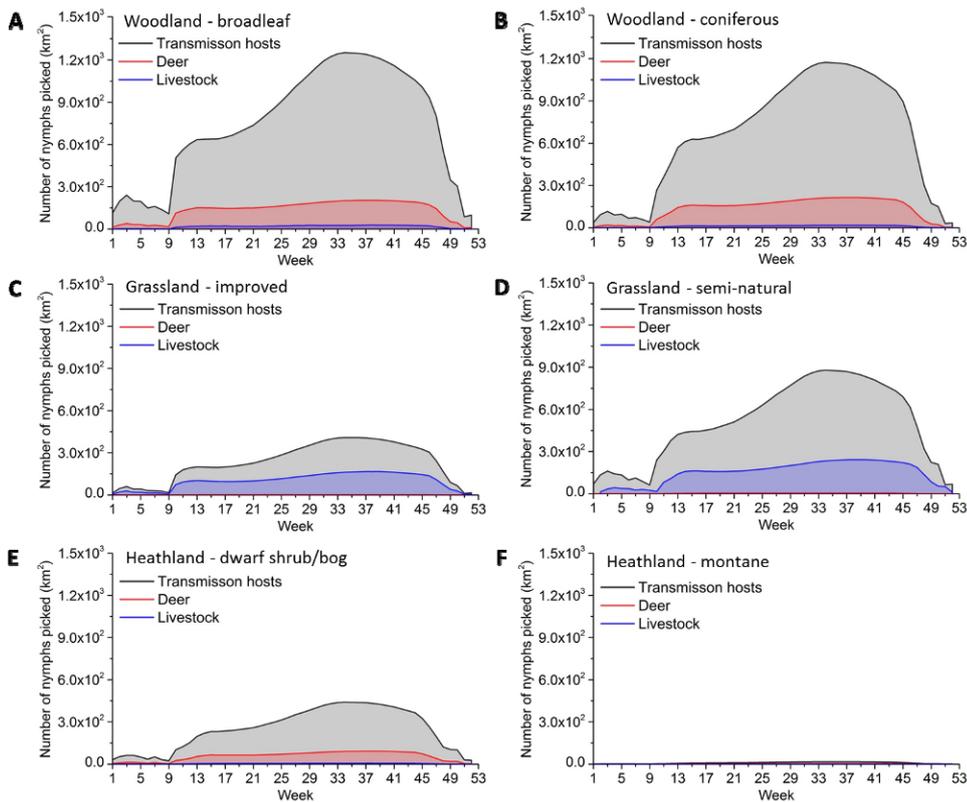


Figure 4.5 Simulated mean number of feeding nymphal ticks in different habitat types from which they are picked up: woodland (A-B), grassland (C-D), and heathland (E-F).

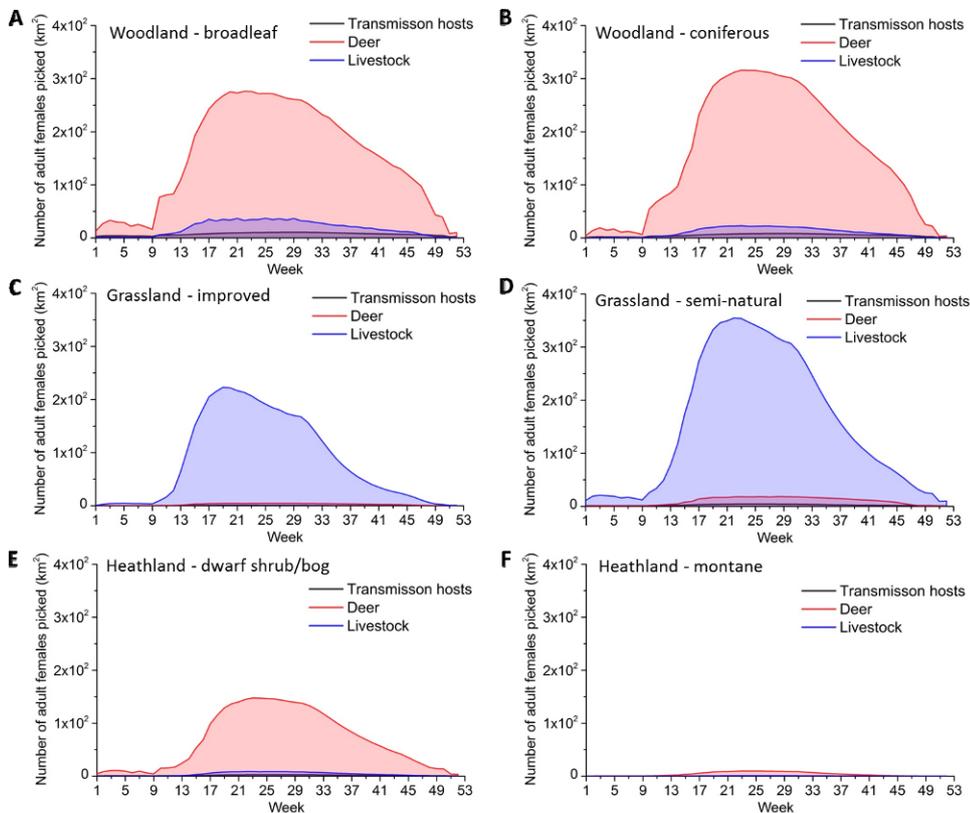


Figure 4.6 Simulated mean number of feeding adult female ticks in different habitat types from which they are picked up: woodland (A-B), grassland (C-D), and heathland (E-F).

4.2 Comparison with field observations of spatial dynamics

The NBN (National Biodiversity Network) dataset (<http://data.nbn.org.uk/>) on the *I. ricinus* tick distribution in Great Britain contains presence records from various individual data providers, e.g. the Biological Records Centre Field datasets (last update 2008), Highland Biological Recording Group (last update 2014). The use of such presence data for evaluation was limited. However, a visual comparison between the record locations and the simulated tick distribution was useful in obtaining a general sense of overall agreement and detecting any under- or non-detected patterns. From the NBN Gateway, in total 420 records of *I. ricinus* presence were retrieved for mainland Scotland (Figure 4.7). Both the NBN records and our model prediction suggest a wide distribution of ticks in mainland Scotland.

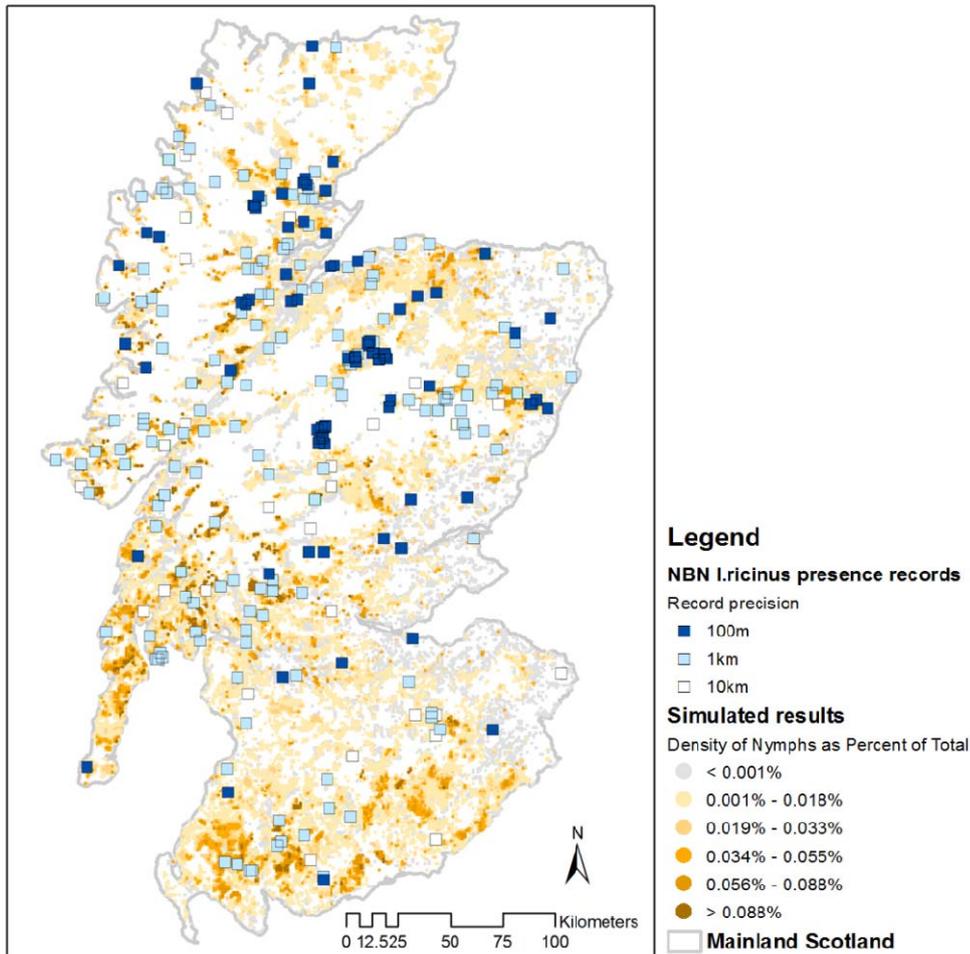


Figure 4.7 Comparison of the simulated distribution of nymphs with the *I. ricinus* distribution data from the NBN (National Biodiversity Network) Gateway.

We used the James et al. (2013) data on nymphal infection prevalence (NIP) for comparison of field observations with model predictions. The James et al. (2013) field data at 24 forest sites in mainland Scotland (out of 25) were extracted for model evaluation. At each forest site, ticks were sampled from different locations, a 5 km buffer area was created for the centroid of each forest site to ensure complete coverage of the sampling area. For each buffer area, model predictions were summarised for their range of NIP. A correct prediction of NIP was suggested if the field NIP value fell within the simulated range. A comparison of the James et al. (James et al. 2013) data with the model predictions is shown in Figure 4.8. Simulated NIP values for each woodland cell were recorded in week 38 (of the model's time) as an approximation of the average value of NIP between April-October, as only marginal changes ($\pm 0.2\%$) are predicted during this period. The average value of the simulated mean NIP in the 5-km buffer region was 5.11% (range 0.01% - 19.8%), which was very similar to the empirical mean NIP of 5.6% (range 0.8–13.9%) found in James et al. (2013). For all the 24 sampling sites, the rate of correct prediction (if the field NIP value fell within the range of simulated

NIP) was 91.7% (Figure 4.9), with two underestimations in Inverness (The Highlands). It is unfeasible to make further comparison based on the James et al. (2013) data, due to the loss of fine-level habitat detail by using a 1 km² grid, missing transmission host population data, or biases related to tick sampling practices (e.g. weather conditions and sampling size). Field evidence on ticks and pathogens was limited for other regions of Scotland – only recent field work in forests in Britain reported that a forest in Dumfries (the Mabie Forest) had relatively high tick abundance and *B. burgdorferi* s.l. infection prevalence among 17 forests in central Britain (Bettridge et al. 2013). Similarly, our model predicted high DINs for some woodland cells in Dumfries (main text, Figure 2).

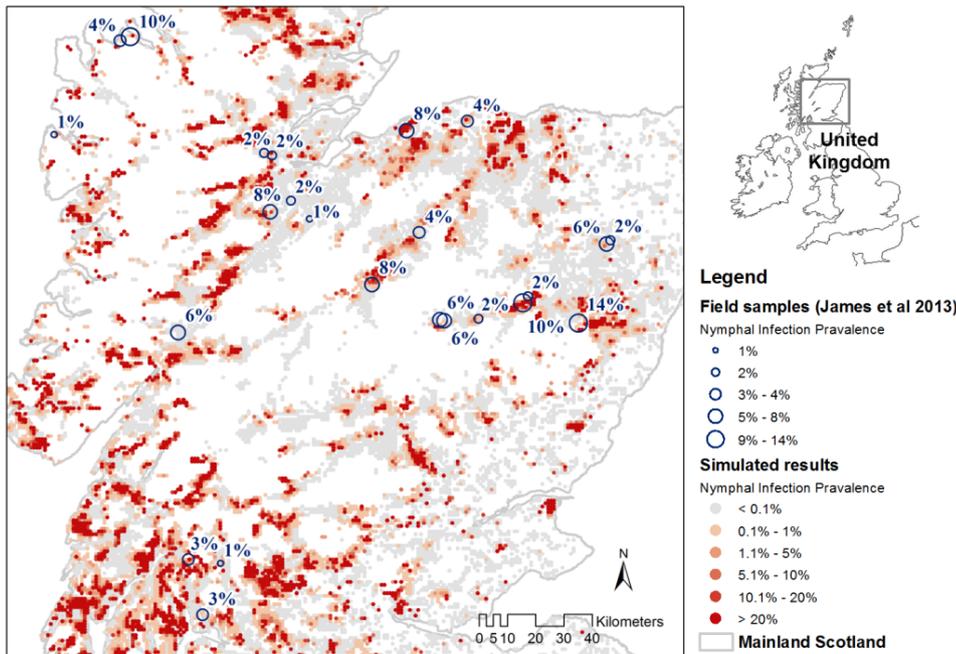


Figure 4.8 Visual comparison of simulated nymphal infection prevalence with field observations in James et al. (2013).

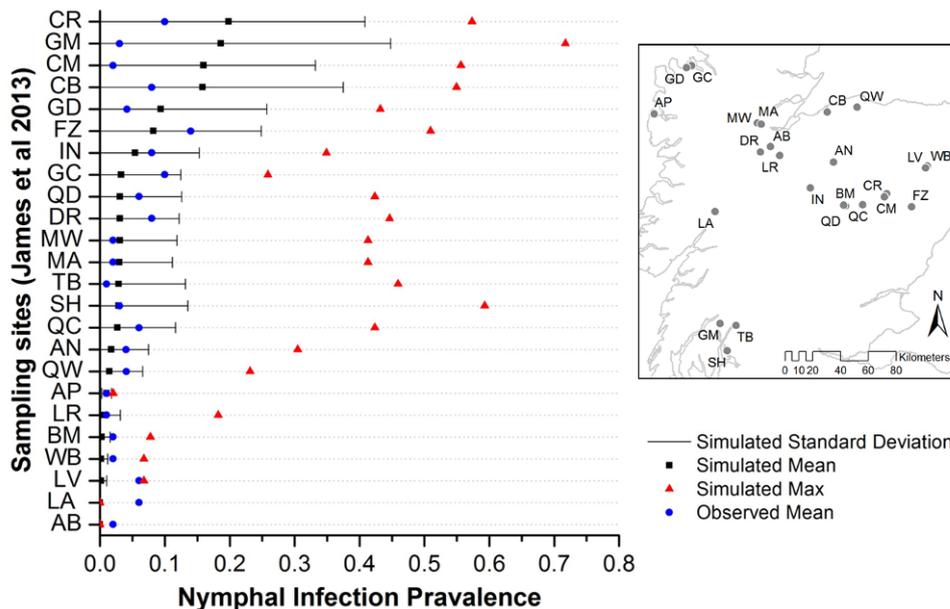


Figure 4.9 Site-level comparison of simulated ranges of nymphal infection prevalence with field observations in James et al. (2013).

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