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Exploring temperature effects on tick population dynamics: What are agent-based models saying?

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Abstract

Agent-based models can be applied to infer the effects of climate change on complex ecological systems such as addressing the behaviour of the vector-host system under temperature change and assess its effects on vector activity and density. Ticks are important vectors of pathogens that cause the spread of many tick-borne diseases. The tick population dynamics depend on several biotic and abiotic factors, such as temperature and host density. Such complexity of dependence and non-linear interactions makes it challenging to predict the dynamics and density of ticks under a changing climate. The objective of this study is to evaluate the reconstructed temperature signals using an agent-based model, where we only consider temperature to be the limiting abiotic factor influencing the development of ticks to infer patterns of tick population dynamics. We parametrized the model using the blacklegged tick Ixodes scapularis data and we simulated tick population dynamics for ten years in five scenarios in which we modified the input temperature signals. We found that tick responses to changing spring-autumn and constant trends vary considerably. Higher interseason duration leads to more stable but lower overall populations, whereas, conversely, very low interseason duration results in substantial population growth. Extending the duration of the warm season led to a population explosion, while an increase in the cold season resulted in a low population abundance and decreasing trends. These results highlight the importance of season duration variability and potential non-linearity in the tick population’s response to environmental change.

Author summary

Ticks play a crucial role as vectors for various pathogens, and a range of biotic and abiotic factors influence their population dynamics. Understanding how vectors

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transmit pathogens requires a deep exploration of their population dynamics. However, assessing the impact of climate change on these dynamics remains a complex challenge. One potential approach to addressing this is modeling, which can help predict the effects of shifting abiotic factors, such as temperature. In our study, we focused specifically on temperature as a key limiting factor. We aimed to determine which aspects of temperature—such as fluctuations, long-term trends, or the duration of temperatures above or below the annual mean—have the most significant impact on tick population dynamics.

Introduction

Climate and environmental changes significantly impact the ecology of macroparasites in general, as well as ticks and tick-borne diseases specifically. These changes disrupt ecosystem balance not only at the regional level, but also on a global scale (*e.g.* [1–4]). Compelling evidence indicates that global changes, direct or indirect, affect ticks' ecology and, consequently, the diseases they transmit [5]. Landscape and climate alterations may shift the spatial distribution of vectors, expanding their geographic range and exposing new regions to vector-borne diseases [6–9], potentially leading to the emergence and establishment of new diseases [10].

Climatic factors such as temperature and precipitation can influence tick abundance and activity, altering their life cycle duration and potentially accelerating reproduction rates. This, in turn, can lead to increased frequency and intensity of disease transmission cycles [8] and extended transmission seasons [5]. Therefore, assessing and monitoring the potential effects of temperature changes on tick populations and the transmission and prevalence of tick-borne diseases is crucial. Temperature fluctuations undoubtedly influence the complexities of tick life cycles and transmission seasonality, and the accelerating pace of these changes has prompted the development of studies and tools to understand the intricate dynamics of tick-host systems and their response to changing conditions. Ticks are highly sensitive to temperature changes, particularly warmer temperatures, which can accelerate the development of immature stages, such as larvae [11]. This acceleration can lead to more rapid population growth [11,12] and influence their survival rates [13,14], as well as their vectorial competence and capacity [15–17]. On the other hand, temperature changes may also affect the dynamics of tick populations and the distribution and abundance of their hosts [18,19].

Moreover, climate change is likely to impact the evolutionary trajectories of all components of the tick–host-pathogen system [20]. Navigating this complexity, modeling is a relevant tool for characterizing and detecting emergent phenomena that may be hidden within the interactions of the tick-host system [21]. An improved mechanistic understanding of tick life cycles, population processes, host dynamics, and pathogens is essential to validate and support these models.

As we delve into the intricate world of vector-host ecology, a fundamental and multifaceted question arises. The question is how temperature intricately shapes the dynamics of vector populations, particularly those of ticks. This question reveals a maze of interrelated factors where the interplay between temperature features and temperature-dependent development emerges as a crucial determinant of tick life cycle seasonality and temporal distribution. Among the complexities, essential questions arise: To what extent does temperature variation influence the overall dynamics of tick populations? Is it the duration of warm or cold seasons that most affect tick populations, or could it be the mild seasons that mark the transition between them? Furthermore, which temperature feature exerts the most significant impact on tick dynamics? Is it the temperature trend, the frequency or duration of extreme temperatures, or the temporal temperature distribution throughout the year? These questions highlight the intricate relationships between temperature and tick ecology, underscoring the need for nuanced understanding and comprehensive analysis.

To address these questions and determine the global role of temperature in shaping tick population dynamics, we used a multi-agent model to explore the emergence of various interactions within a vector-host system under different reconstructed temperature scenarios. These scenarios were designed to highlight variations in amplitude and temporal patterns, allowing us to discern which changes most significantly impact the population dynamics of a given tick population. Current models of tick population dynamics (*e.g.* [20,22]) often incorporate the life cycle, physiology, and behavior of these macro-parasites in a simplified way. Physiological processes such as diapause and mortality are essential for describing the life cycle of ticks. These processes are themselves conditioned by environmental factors such as temperature, which directly influence the behavior and survival of individuals. Furthermore, the coupling between tick development and the spatial movements of hosts offers an additional approach and an advantage for exploring interactions within the 'vector-host-pathogen' system. Agent-based models have already been used to explore various aspects of the dynamics of the tick-host-pathogen system. These include the exploration of associations between hosts and ticks; the identification of the conditions necessary for the invasion of a tick species and a tick-borne pathogen; and the analysis of host dispersal as a function of environmental context and habitat fragmentation, which influence the heterogeneity of loads of infected ticks. In addition, modeling of the combined effects of habitat and hosts on tick invasions was also addressed [23]. Agent-based modeling is a modelling approach that focuses on the actions and interactions of autonomous agents in order to understand and analyse complex systems. Agents can represent individuals, groups or entities within the system. Each agent has its own set of characteristics, behaviours and decision-making rules, allowing for a wide variety of interactions [24]. Thus, our model differs from existing models in that it aims to be generic and adaptable to different vector systems. Unlike other approaches that focus on specific conditions, our model seeks to test the impact of a single abiotic climatic parameter, such as temperature, that regulates the vector population. In addition, we consider host availability as the main biotic factor influencing vector population dynamics. Finally, the biological processes we incorporate are common to a wide range of vectors, allowing our model to be applied to a variety of species and ecological contexts while retaining a certain simplicity and generic scope.

The paper is organized as follows: Section Materials and methods describe background knowledge of the vector's life cycle, model implementation, and simulated scenarios. Then, in section Results, we present our simulation results by analyzing the parameter variations and comparing the behaviors of tick population dynamics against the different scenarios comparisons. Finally, in section Discussion, we discuss our results and pinpoint some limits and perspectives of our work.

Materials and methods

Ecological background of tick life cycle

Hard ticks have four developmental stages: an egg and three obligatory active hematophagous ectoparasitic stages characterized by only larva and nymph stage before reaching the adult life stage. Each life stage is characterized by discontinuous feeding with a single blood meal required to progress into the next stage of life. After the incubation period, characterized by embryo development, eggs hatch into larvae. As soon as the integuments harden, the larva begins to seek a host [25]. Ixodid ticks can survive extended periods without feeding and consume large amounts of blood within a few days after attaching to their vertebrate hosts. Two host-finding strategies are described in the literature [26,27]: a passive strategy known as "*questing*", in which ticks wait for a host to come into contact with them, and an active search strategy, where ticks actively seek hosts. Different species of ticks adopt these strategies in various ways.

The blood meal on the host for the larvae lasts three to six days before they detach and fall to the ground. Metamorphosis or molting is temperature-dependent and completed in up to three to fourth months [28,29], resulting in the nymph stage. If environmental conditions are unfavorable for host-seeking, feeding, or molting, the tick enters a phase of dormancy known as behavioral diapause. This torpid stage responds to adverse environmental conditions, particularly low temperatures [30]. Tick life cycles are characterized by the tropism of the host of both the immature and adult stages. The life cycles of ditropic and telotropic ticks [31], which involve different hosts for the adult and immature stages, are more complex and widespread among tick species compared to monotropic cycles, where the adult stages feed on the same type of host as the immatures. Furthermore, the complexity of tick life cycles is further increased by the number of parasitic phases, ranging from a single host for the entire life cycle to two or three hosts where the immature and adult stages feed on different individuals [31].

Model description

The model used in this paper is based on the framework presented in [32], where the model description has followed an "Overview, Design and Details" paradigm for the description of agent-based models [33]. In brief,two agents are considered, respectively, *vector* and *Host* agents. The *Host* agent is subdivided into two sub-agents; *Rodent* and *Large Host* that inherit attributes and processes from the *Host*. The Host agent in the model represents organisms interacting with vector agents (ticks). *Large Host* , as larger livestock for example, graze in the environment and return to a fixed location, while Rodents, smaller hosts, exhibit distinct movement patterns. This differentiation between two types of hosts, is to represent the preference of ticks juvenile life stages (i.e. larva) for small animals [34], while mature life stages (i.e. adult) are more attracted to larger animals. Also, this choice to differentiate between two hosts is an implicit representation of host species variety, and the names assigned to the different types of Host do not represent a unique species of hosts, for example, rodents do not represent one specific species but can represent a panoply of rodent species and also all types of small hosts as lezards. The host population is assumed to be constant and temperature-independent throughout the simulation. The model explicitly represents all life stages of ticks—egg, larva, nymph, and adult—where development is temperature-dependent. Second, it incorporates host movement patterns, simulating random and herd movement behaviors for *Large Host* and random movement for *Rodent* agent to explore how these affect vector population dynamics. Third, the model is set in a hypothetical square environment (1 km x 1 km) featuring a fixed location where *Large Host* agents return after grazing, with temperature as the primary climatic factor influencing tick life cycles. Fourth, the model simulates vector-host interactions through blood meals, with stationary ticks waiting for hosts to approach before feeding. Submodels handle processes like movement, attachment, detachment, and tick life cycle transitions. Additionally, the model aims to capture emergent properties, such as ticks' abundance and stage distribution, arising from the interplay of temperature, host availability, and the behaviors of both vectors and hosts. We assume that *Large Host* agents perform a herd movement. The *vector* agent represents the hard tick with its different life stages. For this study, we used telotropic life cycle involving two hosts. In our model, *rodent* agents host the immature stages, while *Large Host* agents host the adult stage. This type of life cycle is observed in various tick species in several genera, including *Hyalomma, Rhipicephalus*, *Dermacentor*, *Ixodes*, and *Haemaphysalis* [35]. We also assume that hosts (both rodents and *Large Host*) can have a carrying capacity for the vectors.

We recall that the ecological processes included in this model reproduce the interaction between the *vector* (tick agent) and the *Host* (rodent and *Large Host*) agents in a hypothetical environment. Temperature is the only abiotic parameter influencing the development of the vector agent. Humidity, while implicitly considered non-limiting, is excluded as a regulating factor not out of simplicity or perceived insignificance but to focus the study on evaluating the sole influence of temperature in regulating and reconstituting the life cycle of ticks. At each life stage (larva, nymph, and adult), the tick attaches to a host, takes a blood meal, detaches, and then transitions to the next stage via molting. While our model does not explicitly assign three distinct host types, it assumes that each life stage requires a new host, and these hosts are always distinct individuals. The model is implemented to accommodate the agents' actions and behaviors with different temporal and spatial scales. The model consists of sub-models representing ecological processes and agent behavior. The execution of these sub-models varies depending on the associated time step. Two distinct time steps govern the processes: one for agent behavior and actions, and another for ecological and physiological processes. Ecological processes, such as host mobility (*e.g.* herd movement *versus* random movement) [32] and vector-host interactions (*e.g.* blood meal; attach and detach processes), are executed hourly. Physiological processes for the vector agent, including tick fecundity and mortality, are executed daily. The process scheduling follows a logical sequence aligned with the various stages of the tick's life cycle (refer to Fig 1).

Seasonality plays a crucial role in the dynamics of tick populations, influencing both tick development and the life histories of hosts and vectors [36–38]. We evaluated the model under various temperature scenarios to examine its sensitivity to temperature variations in tick population dynamics. We assume that temperature is the sole climatic factor that affects the development of the vector agent. Our objective is to evaluate the impact of interannual temperature fluctuations on the development and dynamics of the tick population. To this end, we used real temperature datasets from 1990-2000 [39] to reconstruct temperature signals.

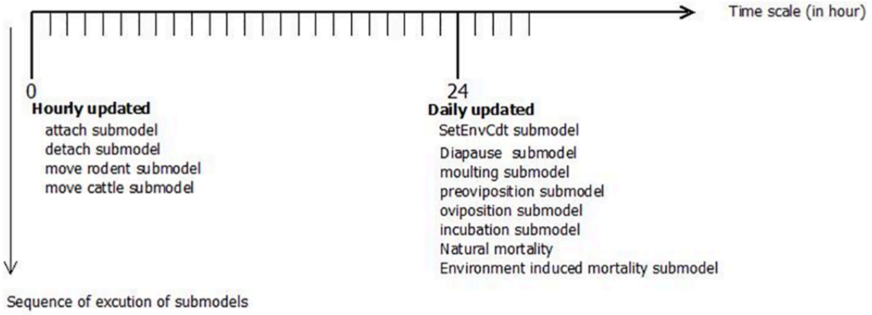

Fig 1. Timesteps and scheduling of model processes. Two timesteps are considered for *vector* and the *Host* agents processes and the environment update.

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Number of optimal simulation replications

The simulations were run under GAMA 1.9.1 [40]. Since our model has a solid stochastic component, we determine the optimal number of replications per parameter set by running 100 replications of a parameter set with different seed values. We used a standard variation of mean population abundance as a measure output of the simulation (refer to Fig 2). On that basis, we decided to run our simulations for $n = 30$ replications.

Empirical validation

To validate the model, we used a pattern-oriented modeling approach [41], comparing the proportions of questing larvae, nymphs, and adults from field datasets of the tick species *Ixodes scapularis* [11,20,42] with our simulation outputs. We ensured that the geographical regions where the observed data were collected matched the temperature dataset used. The climate data utilized in this model are derived from the Climatic Research Unit (CRU) TS Time Series datasets 4.04 [39]. This dataset provides monthly temperature estimates spanning the period from 1990 to 2000, with a spatial resolution of 0.5° × 0.5° grids for the Wisconsin region. Daily temperature estimates were generated by fitting the data points to a third-order polynomial function, ensuring a smooth interpolation of the temporal patterns.

Our model accurately replicates the seasonal patterns of tick species. Larvae emerge from early summer to early autumn in simulated and real data. However, the two datasets have a discrepancy in nymph emergence timing. Adult emergence shows two peaks in both datasets: the first in early spring, the second in late summer to early autumn in the simulated data, and early autumn in the real data (see Fig 3). This approach enables us to identify shifts that

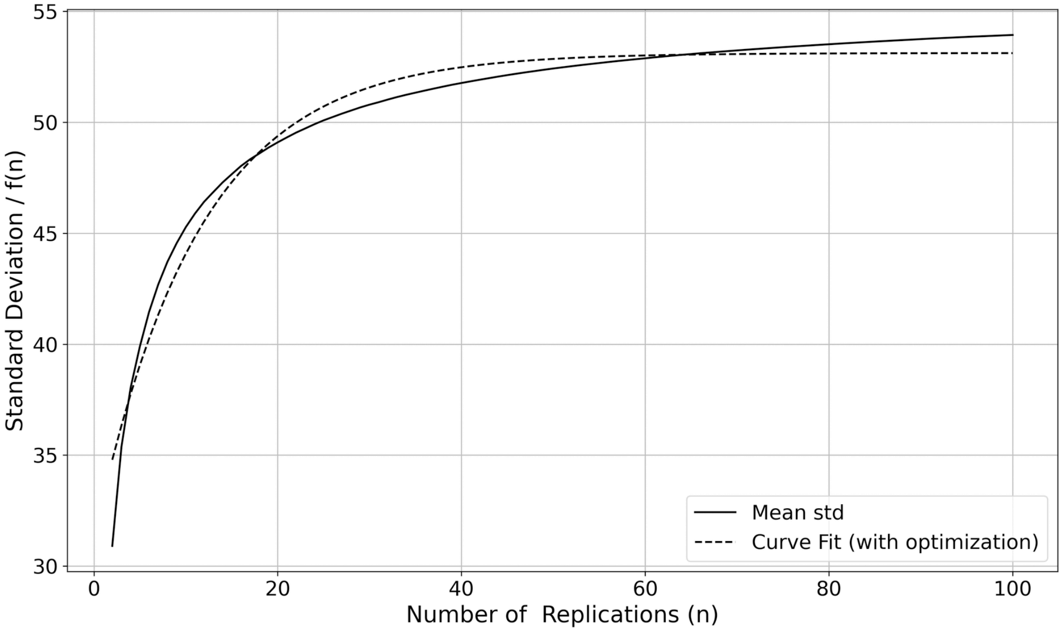

Fig 2. The standard deviation of the mean total population abundance was calculated at each time step. At each step, we randomly selected n replications, forming "n-uplets" with n ranging from 2 to 100. For each set of combinations, 5000 samples were randomly chosen, and the mean and standard deviation of all "n-uplets" were calculated. The resulting curve was fitted to the function $f(n) = \varsigma\,[1 - \varkappa \exp(-n/n_0)]$ to identify the optimal number of replications, defined as when the ratio $\frac{f(n)}{\varsigma}$ reaches or exceeds 0.95.

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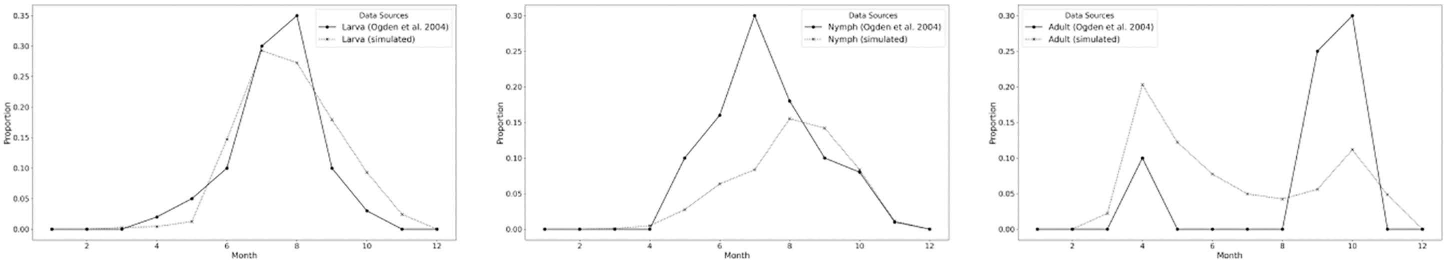

a: Questing larva proportion

b: Questing nymph proportion

c: Active adult proportion

Fig 3. Comparison between model outputs and empirical monthly population proportion as described by [11].

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may contribute to the observed discrepancies in model outputs, such as the timing of emergence, and assess how these changes influence the alignment of simulated and real data across different scenarios.

Parameters calibration

We parameterized the model to align with the ecology and biology of *Ixodes scapularis*. To ensure robustness, we selected the most commonly reported values for this species under laboratory conditions, as these are generally considered the most controlled and reliable. The same rationale guided the selection of all other parameter values, avoiding extreme or outlier data. All parameter definitions and values are reported in Table A and Table B in S1 Appendix. Since diapause is a complex physiological process influenced not only by temperature but also by genetic factors [43], calibrated parameters include fecundity and the diapause temperature thresholds for the larva, nymph, and adult stages, as detailed in Table 1 (refer also to Table B in S1 Appendix).

Sensitivity analysis used the finite differences approach in the "one-at-a-time" method [44]. The simulations were run by adjusting one model input at a time from the base values to the sensitivity values. Specifically, we shifted the threshold temperature parameter by half a unit and the fecundity parameter by one unit (see Table 1). The RMSE (Root Mean Square Error) was used as our sensitivity indicator [45]. We then compared the RMSE distributions using the Kolmogorov-Smirnov (KS) test [45] to evaluate the statistical significance of differences between the parameter values at a 95% confidence level. We tested the null hypothesis H_0 for all parameters: The RMSEs obtained for one pair of parameter values have the same distribution as those obtained for another pair of parameter values. In Table 2, we note that only the RMSE for the threshold diapause temperature in the adult stage shows a similar distribution across the sensitivity values. The RMSEs between different parameter value pairs significantly differ for all other parameters.

Scenarios description

Using signal decomposition [45], we broke down the original temperature signal from real datasets (1990-2000) [39], $T_{S0}(t)$, into three distinct components: the trend component

Table 1. Overview of the definition of the model parameters and the model outputs studied. The full list of model parameters and values is in Table A and Table B in S1 Appendix.

Parameter	Description	Symbol	fixed/Varying	Unit
Input Parameters				
fecundity	fecundity per one adult vector agent	FECUNDITY (FEC)	fixed $\in \{4, 5, 6\}$	Individual of *vector* agent
Threshold temperature	Larva Diapause Threshold Temperature	THRESHOLD_T_L (TTL)	fixed $\in \{1.5, 2, 2.5\}$	°C
	Nymph Diapause Threshold Temperature	THRESHOLD_T_N (TTN)	fixed $\in \{3.5, 4, 4.5\}$	°C
	Adult Diapause Threshold Temperature	THRESHOLD_T_A (TTA)	fixed $\in \{3.5, 4, 4.5\}$	°C
Temperature T_{S1}	Input Temperature	CurrentTemp	Varying $\in \mathbb{R}$	°C
Temperature T_{S2}	Input Temperature	CurrentTemp	Varying $\in \mathbb{R}$	°C
Temperature T_{S3}	Input Temperature	CurrentTemp	Varying $\in \mathbb{R}$	°C
Temperature T_{S4}	Input Temperature	CurrentTemp	Varying $\in \mathbb{R}$	°C
Temperature T_{S5}	Input Temperature	CurrentTemp	Varying $\in \mathbb{R}$	°C
Outputs				
Daily total population	The total daily number of *vector* agents	$N(t)$	$\mathbb{N}$	Individual of *vector* agent
Daily population per-stage	The total daily number of *vector* agents per stage, respectively, egg, larva, nymph, and adult	$N_{stage}(t)$	$\mathbb{N}$	Individual of *vector* agent

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Table 2. Kolmogorov-Smirnov (KS) test for the different parameter value pairs at a 95% confidence level. We tested the null hypothesis H_0 for all parameters: The RMSEs obtained for one pair of parameter values have the same distribution as those obtained for another pair of parameter values.

Parameter Pair	P_{value}	H_0 Conclusion
FEC=5 vs FEC=4 and FEC=5 vs FEC=6	9.22×10^{-38}	Reject H_0
TTN=4 vs TTN=3.5 and TTN=4 vs TTN=4.5	9.42×10^{-4}	Reject H_0
TTL=2 vs TTL=1.5 and TTL=2 vs TTL=2.5	1.26×10^{-49}	Reject H_0
TTA=4 vs TTA=3.5 and TTA=4 vs TTA=4.5	0.739	Accept H_0

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$Tr_{S0}(t)$, the seasonal component $S_0(t)$, and the residual component $R_0(t)$ (refer to Fig 4)

$$T_{S0}(t) = Tr_{S0}(t) + S_0(t) + R_0(t) \tag{1}$$

The scenarios were developed by comparing variations in four features of the input temperature signal: (1) noise, (2) trend, (3) curvature near extreme values, and (4) the duration of the warm and cold seasons (refer to Fig 5).

First, we examine the effect of noise elimination, followed by the impact of using a fluctuating trend versus a constant trend in the input temperature signal after noise removal. We compared the original trend with the constant trend without applying a scaling factor. Next, we assessed how varying amplitude influences the model output by introducing scaling factors to the temperature signal, forming *scenarios 1 (S1)* and *2 (S2)* for the constant and varying trends. Temperature extremes are between −9°C and 23°C for the case of S1, $k = 1$ as well as for S2.

Furthermore, we investigated the influence of modifying the temperature distribution near extreme values by adjusting the curvature of the signal. This analysis, represented by *scenarios 3 (S3)* and *4 (S4)* considers both variable and constant trends. Finally, in *scenario 5 (S5)*, we

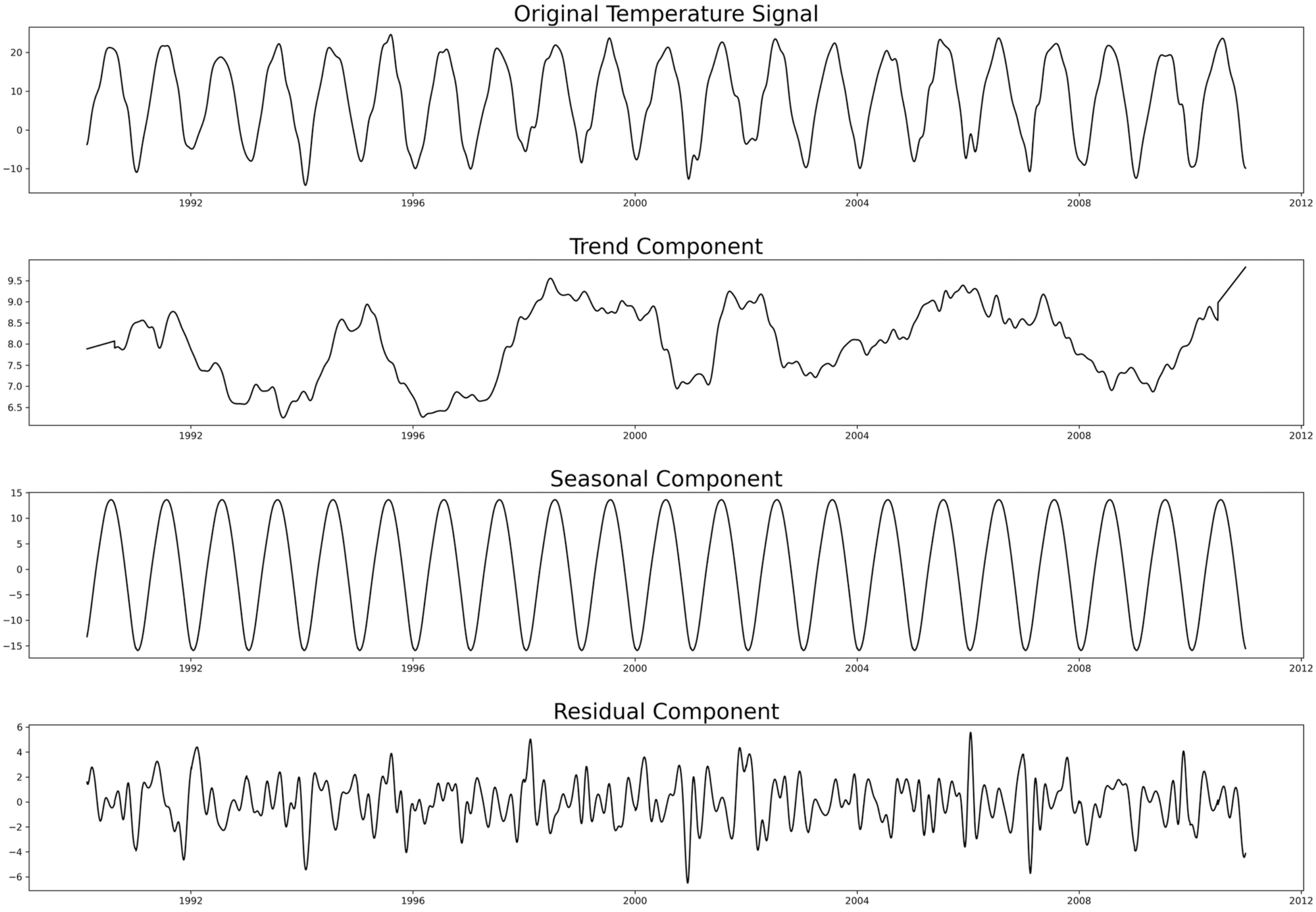

Fig 4. Additive decomposition of the original temperature signal, $T_{S0}(t)$, from real temperature datasets (1990-2000) [39], into three distinct components: the trend component $Tr_{S0}(t)$ (top), the seasonal component $S_0(t)$ (middle), and the residual component $R_0(t)$ (bottom).

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explored changes in the duration of warm and cold seasons where extreme temperatures are between −9°C and 23°C. The original temperature signal case is referred to as *scenario 0 (S0)* where temperature extremes are between −14°C and 24°C.

Some scenarios exhibit a pronounced temperature distribution at the extremes (*e.g.* S3 and S4), indicating a prevalence of very warm or very cold temperatures (Temperatures reach, respectively, −10°C and 35°C). In contrast, others showcase a more homogeneous distribution across the temperature range. This comparison highlights the diverse effects that adjustments in temperature parameters can have on the overall temperature distribution, emphasizing the importance of considering such variations in understanding the dynamics of the tick population.

Variable trend: *Scenario S1.* In the first scenario, we focus solely on the deterministic aspects of temperature signals, assuming $R_1(t) = 0$. We derive the temperature input according to Eq 2, where $T_{S1}(t)$ is defined as the sum of the trend component $Tr_{S0}(t)$ and the seasonal component $S_0(t)$. Here, $Tr_{S0}(t)$ represents the trend of the actual temperature signal

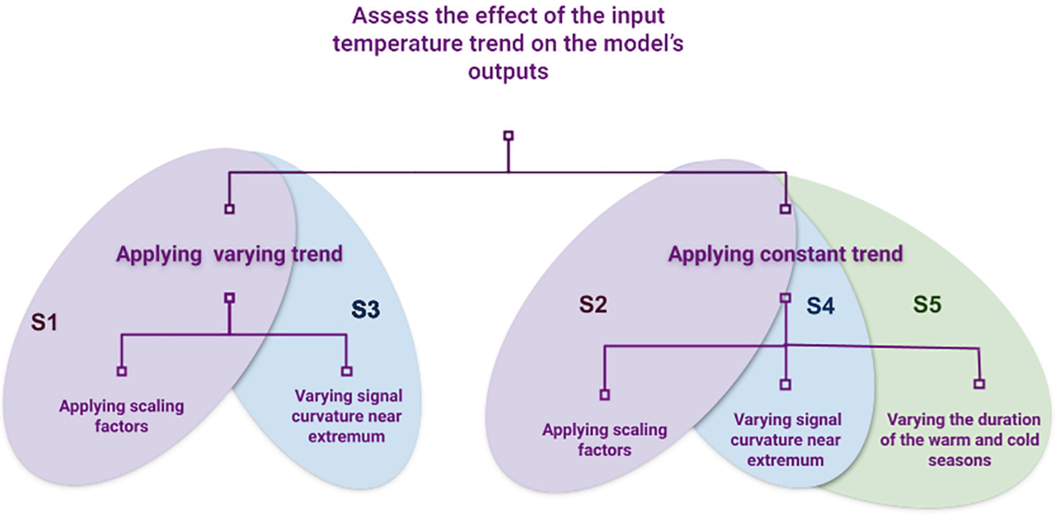

Fig 5. Schematic diagram for the input temperature signal features and scenario labeling. We compare and evaluate three levels while removing temperature signal noise: the effect of a constant trend, curvature at extreme values, and variations in warm season duration.

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T_{S0}, while $S_0(t)$ denotes its seasonality.

$$T_{S1}(t) = Tr_{S0}(t) + S_0(t) \tag{2}$$

Next, we introduce a scaling factor k as a function to modify the mean magnitude of $T_{S0}(t)$ and explore the effects of varying magnitudes. The resulting signal, denoted as $T_{S1_k}(t)$ (see Sect B.1 in S1 Appendix for details), allows us to adjust the amplitude, with values ranging from 0.8 to 1.2, providing information on the effect of amplitude variations on the resulting signal (refer to Fig 6).

Constant trend: *Scenario S2.* In the second scenario, we adopt a different approach, perceiving the temperature signal as a sum of the mean trend of real temperature and its actual seasonality, defined by the Eq 3:

$$T_{S2}(t) = \mathbb{E}[Tr_{S0}(t)] + S_0(t) \tag{3}$$

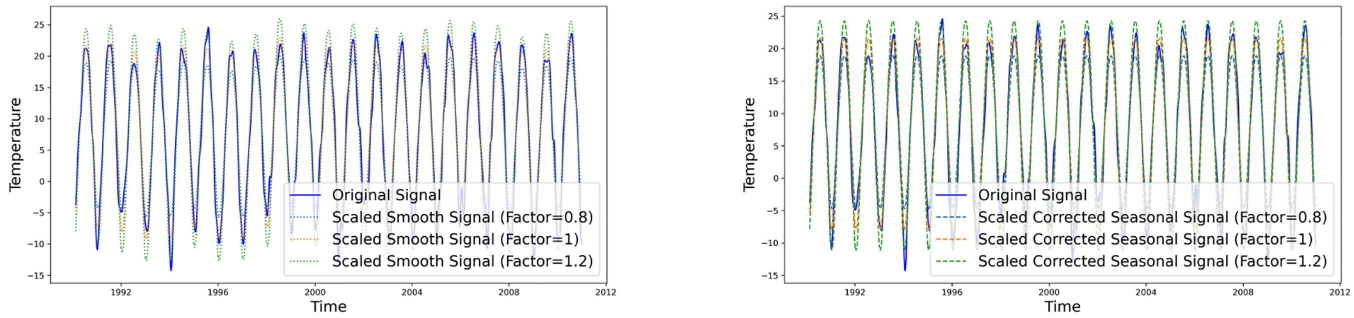
Here, $\mathbb{E}[Tr_{S0}(t)]$ represents the mean of the trend component $Tr_{S0}(t)$, while $S_0(t)$ remains the seasonality of the original temperature signal. Similarly to the previous scenario, we investigate the effects of varying amplitudes by applying the same scaling factor k as in Scenario S1 (see Sects B.1 and B.2 in S1 Appendix for more details).

Controlled curvature near extreme values: *Scenarios S3 and S4.* In this scenario, we introduced variations in the curvature of the signal $T_{S0}(t)$ using a correction function, y (see Sect B.3 in S1 Appendix for details). The resulting signal is a smoothed, curvature-controlled signal denoted as $T_{S3}(t)$:

$$T_{S3}(t) = Tr_{S0}(t) + y \tag{4}$$

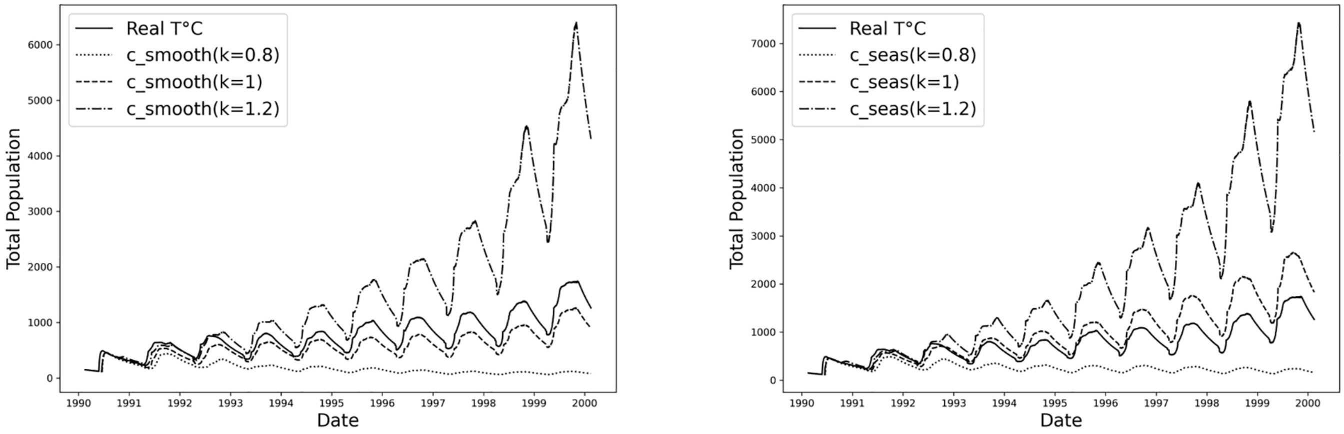
The corrected, seasonally controlled curvature signal, $T_{S4}(t)$, follows a similar procedure as $T_{S3}(t)$:

$$T_{S4}(t) = \mathbb{E}[Tr_{S0}(t)] + y \tag{5}$$



a: Original and smoothed temperature signal$T_{S1}(t)$ for the different values of the scaling factor.

b: Original and constant temperature trend signal,$T_{S2}(t)$, for the different values of the scaling factor.



c: The proportion of the total population abundance for the first scenario S1.The figure highlights the importance of the scaling factor.

d: The proportion of the total population abundance in the first scenario, S2, highlights the importance of the scaling factor.

Fig 6. Temperature signals $T_{S1}(t)$ and $T_{S2}(t)$ and their respective model outputs. The role of the scaling factor is to increase or decrease the amplitude while keeping the smoothed signal to evaluate the effect of smoothing on the population growth independently of the amplitudes. We notice the importance of the scaling factor that can affect the total population abundance by changing the temperature amplitude.

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However, instead of using the trend component $Tr_{S0}(t)$, it employs the mean of the original signal trend $\mathbb{E}[T_{S0}(t)]$. This ensures that $T_{S4}(t)$ maintains controlled curvature while incorporating the mean trend of the original signal.

For both S3 and S4, constructing the y signal (see Sect B.3 in S1 Appendix for details) introduces a parameter α that controls the curvature signal. Lower α values result in a broader curvature, leading to longer periods of extreme temperatures (winter and summer) and shorter durations of intermediate seasons (autumn and spring). Conversely, higher α values produce longer transitions between extremes, resulting in shorter winters and summers and extended autumn and spring periods. As α approaches 0, the signal asymptotically resembles a square wave, with near-instantaneous transitions between extreme temperatures.

Controlled balance of the warm-cold seasons: *Scenario S5.* In this scenario, we introduced variations in the duration of both warm and cold seasons within the temperature signal. We define warm-season days as those with temperatures above the annual mean of the seasonal component, while temperatures below this mean identify cold-season days.

Thus, we modified the signal $T_{S2}(t)$ by increasing or decreasing the duration of the warm season by ε. When $\varepsilon < 0$, the cold season becomes longer than the warm season; when $\varepsilon > 0$, the warm season surpasses the cold one.

This scenario, S5, can provide insight into how the length of warm and cold seasons influences overall temperature dynamics and, consequently, the ecological processes that depend on temperature variation throughout the year.

Results

The analysis of scenarios focuses on three main objectives: comparing the effect of removing noise while maintaining the original temperature trend, using a constant trend, and evaluating the effects of scaling factors for both scenarios (Scenarios S1 and S2). Additionally, we study the impact of variations in temperature distributions near extreme values, which otherwise reflects the variation of interseason duration (Scenario S2 and S4). Finally, we examine temperature and temporal distribution by modifying the duration of warm and cold seasons (Scenario S5). For scenario S3, since its reconstruction comes from S1 and S4, and its results are logically inherent from S4, we present its outcomes in Sect B.3 in S1 Appendix. The outputs analyzed include the total population abundance and the per-stage population over ten years.

Effect of noise suppression

Eliminating temperature noise (Scenario S1) while maintaining the original trend primarily affects the yearly amplitudes of total population abundance. When the scaling factor $k = 1$ (see Fig 6), the total population abundance consistently remains below that of Scenario S0. This discrepancy may be due to the reduced amplitudes in the smoothed temperature signal T_{S1} compared to the original temperature signal $T_{S0}(t)$ (refer to Fig 6).

With a scaling factor of $k = 1.2$, the population shows a substantial increase compared to $k = 1$, with abundance nearly 300% higher in the last year of the simulation. This increase in the amplitude of the mean temperature signal and the extreme points results in a population explosion. On the contrary, with $k = 0.8$, the population decreases over the years, approaching near-extinction levels. Reducing the maximum temperature values for both warm and cold temperatures prevents the population from stabilizing; lowering extreme temperatures and elevating all temperatures to the mean fails to sustain a stable population.

In contrast, when the temperature trend is removed (Scenario S2), the total population abundance for $k = 1$ is higher than in Scenario S1. Maintaining a stable trend in the temperature signal allows for higher population abundance even when daily temperature fluctuations are eliminated.

Adjusting the scaling factor k similarly affects the total abundance of the population. For low scaling factors, such as $k = 0.8$, the population shows a decreasing trend over time, corresponding to lower temperatures compared to other scaling factors and the original signal. Conversely, a high scaling factor, such as $k = 1.2$, results in an increasing population trend, reflecting elevated temperatures, as depicted in Fig 6.

Regarding the per-stage distribution, it is surprising that, across all life stages, for the case of $k = 1.2$, all scenarios (S1 and S2) exhibit the same relative peaks as those of S0. We observe a significant peak in the egg stage, which is delayed by one month compared to S0 when $k = 0.8$.

Furthermore, when $k = 1$, S1 and S2 experience peaks alternately delayed by one month relative to S0. For the larva stage, similar to the egg stage, in the case of $k = 0.8$, the peaks for both S1 and S2 are delayed by one month compared to S0. Interestingly, the situation differs for $k = 1$ and $k = 1.2$: S0 exhibits a two-month larval peak in the former, with the S1 and S2 peaks overlapping the second peak of S0. In the latter case, the peaks of S1 and S2 coincide with the first peak of S0. For the nymph stage, like the larva and egg stages, the peak is delayed by one month for both S1 and S2 when $k = 0.8$, and they exhibit alternate peaks relative to the egg stage when $k = 1$. Interestingly, the adult population shows similar behavior for S1 and S2, but differs significantly from S0 for $k = 0.8$, where the adult peak experiences a six-month phase shift. However, for $k = 1$, the adult population behaves very similarly to S0 (refer to Fig 7).

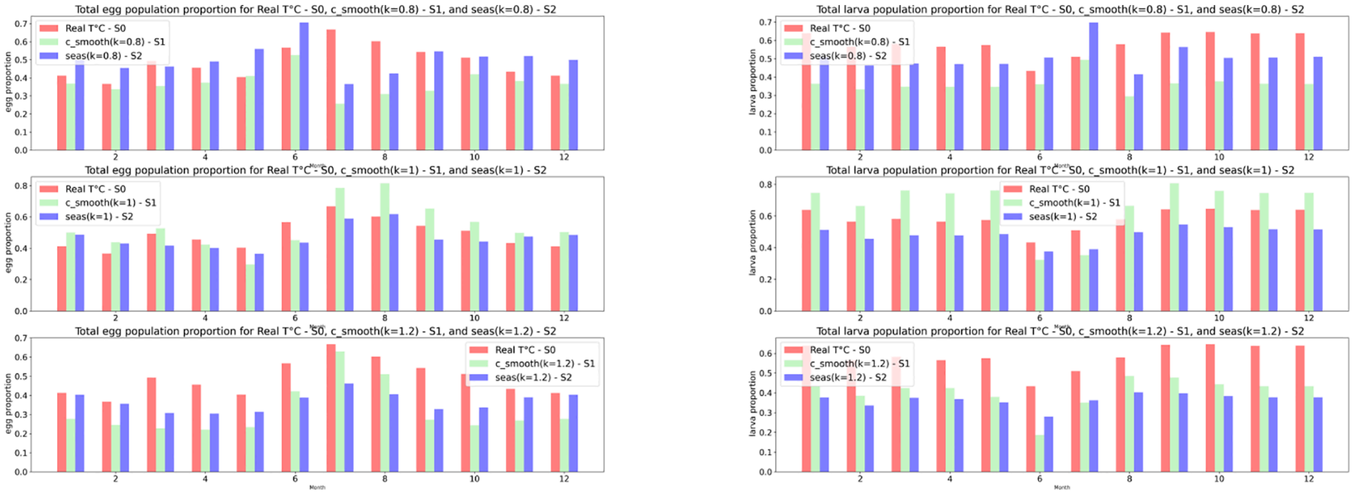
Effect of the variation of inter-seasonality

The interseason duration variation permits analyzing the length of the shoulder seasons, making it possible to distinguish the effect of the length of autumn and spring on population dynamics.

For high values of α, in the case of $\alpha = 5$, representing a long duration of autumn and spring seasons, the population is steady during all simulation years and relatively low, representing nearly 30% of the final year total population of scenario S0. When α is very low ($\alpha = 0.005$), the population is growing, representing a growth of almost 75 % in the last year of simulation of that of S0. Nevertheless, the annual peaks are sharp, similar to those of S2 when k = 1, and slightly larger. The population most similar to that of S0 is the one where the α case equals 0.5. For the egg stage, S4 experiences a delay of 1 month compared to S2 for α values of 0.1 and 0.5. When α is 5, a delay of 2 months is observed. A phase lag of almost six months is noted for very low α values close to zero (0.005). In the larval stage, S4 also displays two peaks similar to S0, with the first peak coinciding with the second peak of S0 when α is 0.1. For $\alpha = 0.005$, there is a single peak. When α is 5 or 0.5, S4 shows a single peak occurring one month after the second peak of S0. For the nymph stage, all α values except 0.005 show a single peak one month later than S0. For $\alpha = 0.005$, the nymphs exhibit two peaks, with the first occurring one month after S0. In the adult stage, S4's behavior is almost identical to S0, except when α equals 5. In this case, the population exhibits a second peak with a six-month shift with S0 and the first peak of S4 (refer to Figs 8 and 9).

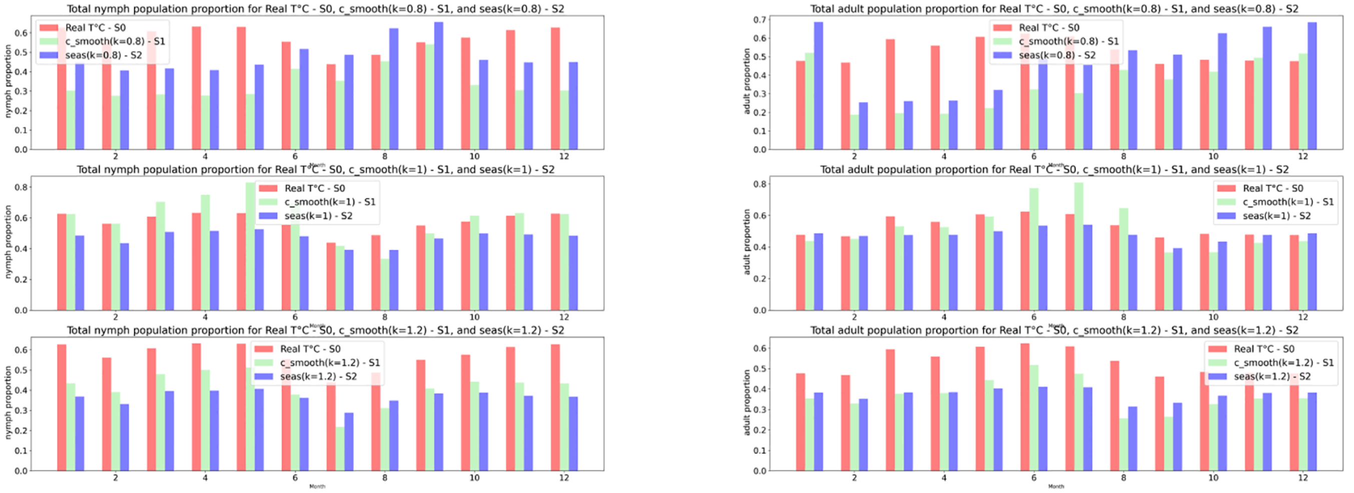
Effect of the duration of warm and cold seasons

In Scenario S5, we examined the effects of varying duration of the warm and cold seasons on tick population dynamics. We denote by ε the difference in duration between the warm and cold seasons; higher ε leads to longer warm and shorter cold seasons and vice versa. Increasing the ε increases the abundance, leading to an explosion in population abundance when $\varepsilon = 50$. Conversely, when the duration of the warm season was reduced ($\varepsilon = -10, -20, -30, -50$ days), we observed a decrease in population abundance, accompanied by a decreasing trend. Although there was a slight increase in abundance during the final years of simulation in scenarios with smaller negative ε values, overall, the population trend remained downward. Since the duration of the warm and cold seasons depends on the value ε, the models's outputs are more or less different. In the case of positive ε, the population knows an increasing trend, and in contrast to negative values of ε, the population knows a decreasing trend. For the equal duration of warm/cold season, the population ($\varepsilon = 0$), we observed a stable population with a rising trend. A slight increase in the cold season ($\varepsilon = -10$ days) did not significantly alter this trend. However, extending the cold season ($\varepsilon = -20, -30, -50$ days) led to an abrupt population explosion, surpassing the individuals compared to the initial population abundance.



a: Total egg population per month (in proportion) for scenarios S0,S1 and S2 for all scaling factors

b: Total larva population per month (in proportion) for scenarios S0, S1 and S2 for all scaling factors



c: Total nymph population per month (in proportion) for scenarios S0, S1 and S2 for all scaling factors

d: Total adult population per month (in proportion) for scenarios S0, S1 and S2 for all scaling factors

Fig 7. The per-stage monthly total population proportion for scenarios S1 and S2.

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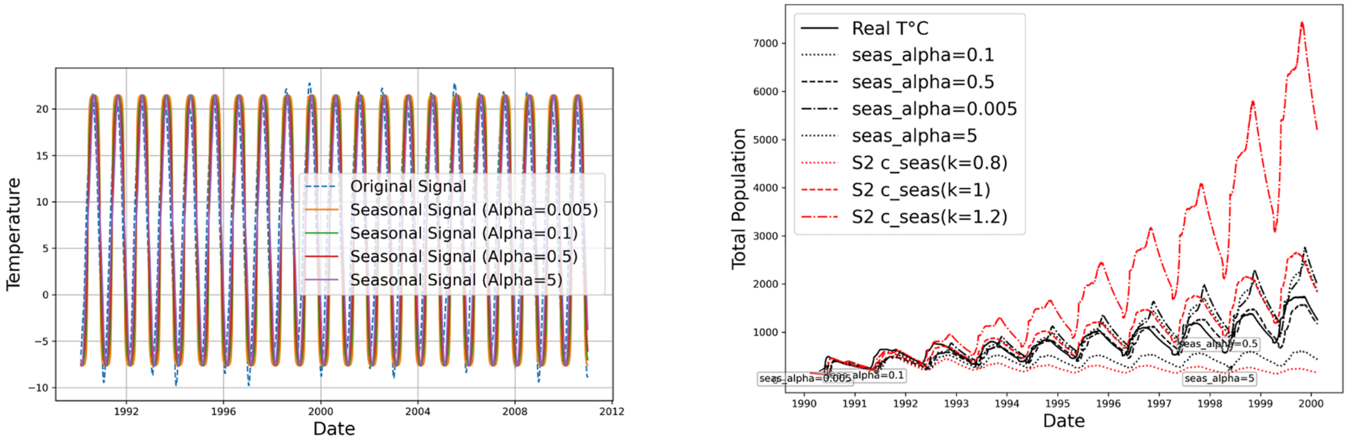
Conversely, increasing the duration of the warm season (case of $\varepsilon = 20, 30, 50$ days) resulted in a declining population abundance and decreasing trends (refer to Figs 10, 11, and 12).



a: Temperature signal $T_{S4}(t)$ relative to the fourth scenario S4.

b: Total population abundance for the fourth scenario S4 and the different values of *alpha versus* the total population abundance for, both Scenario 0 and scenario S2 for $k = 1$.

Fig 8. Reconstructed temperature signal, $T_{S4}(t)$ for the controlled curvature, respectively for the scenarios S0, S2$_{k=1}$ and S4 for the different values of α.

https://doi.org/10.1371/journal.pcsy.0000065.g008

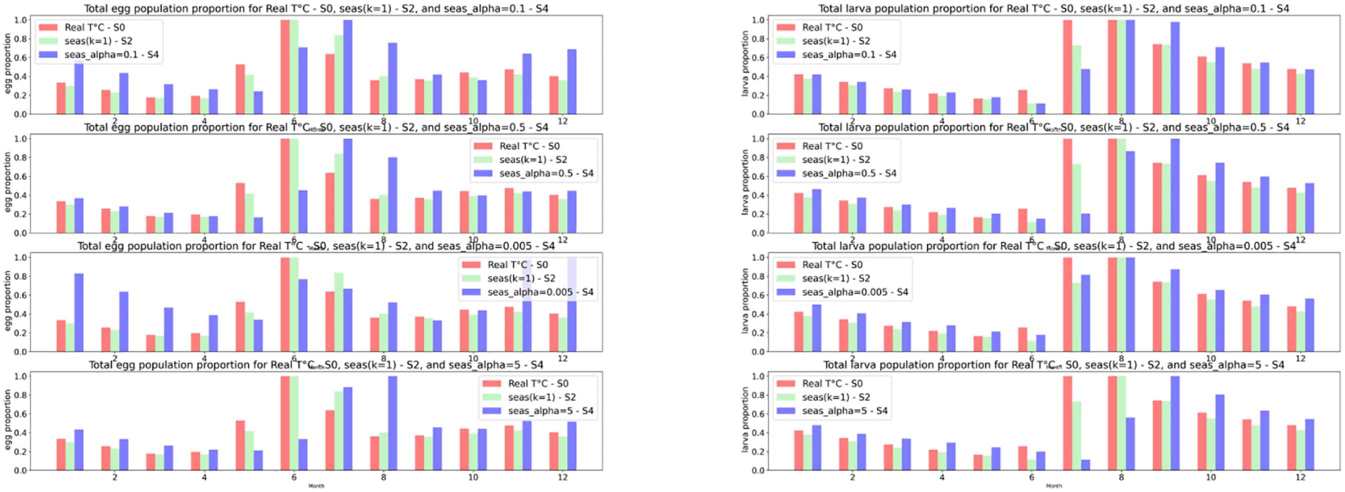
Discussion

We developed a structured agent-based model to simulate natural tick-host systems, focusing on temperature-dependent processes and population dynamics over ten years. Our primary objective was to identify key temperature signals influencing population dynamics and developmental stages. We used reconstructed temperature data from 1990-2000 to assess the impacts of extreme fluctuations, trends, and seasonality on tick abundance. Although our model was calibrated using empirical data for the species *Ixodes scapularis* in North America, and its quantitative results are thus specific to this species and context, the analytical framework is designed to offer broader insights into temperature-driven dynamics in tick populations.

Model purpose

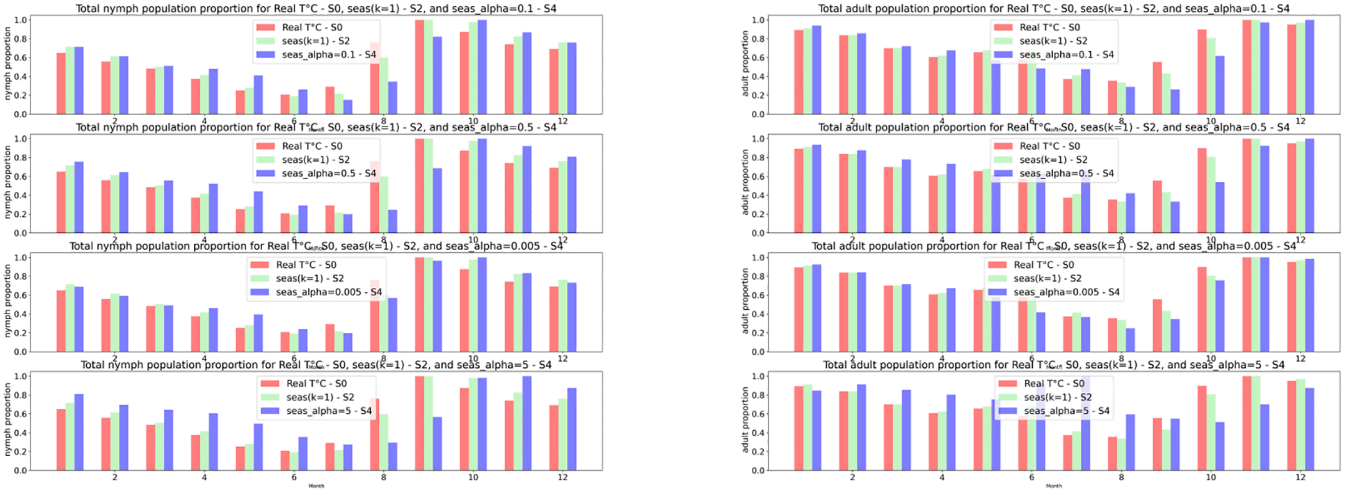
Our work serves a dual purpose. First, we aimed to replicate the observed system behavior, representing its functionning as a network of interactions. Second, we sought to develop a methodological framework to address ecological challenges more effectively, aiming to contextualize vector-host systems comprehensively. This effort aims to create a flexible methodology and propose a unifying framework to elucidate a broad spectrum of vector species. This pursuit is guided by the notion that theory takes shape when mechanistic explanations for regularities or patterns emerge from fundamental principles and are grounded in minimal assumptions [46,47].

Generally, the proposed models fall into two categories: models representing inter-annual dynamics, where life stages are represented by a single value (*e.g.*, egg, larva, nymph, or adult density), and where the model is represented in a matrix form [48]. The second category includes models representing intra-annual dynamics, focusing on transitioning from one stage to another with little or no consideration of demography [49,50]. Inter-annual models are typically compartmental models, where the compartments represent tick life stages [51].



a: Total egg population per month (in proportion) for scenarios S0, $S2_{k=1}$ and S4 for all α values.

b: Total larva population per month (in proportion) for scenarios S0, $S2_{k=1}$ and S4 for all α values.



c: Total nymph population per month (in proportion) for scenarios S0, $S2_{k=1}$ and S4 for all α values.

d: Total adult population per month (in proportion) for scenarios S0, $S2_{k=1}$ and S4 for all α values.

Fig 9. The per-stage population distribution for the different values of α for scenarios S0, $S2_{k=1}$, and S4 and the original temperature scenario S0.

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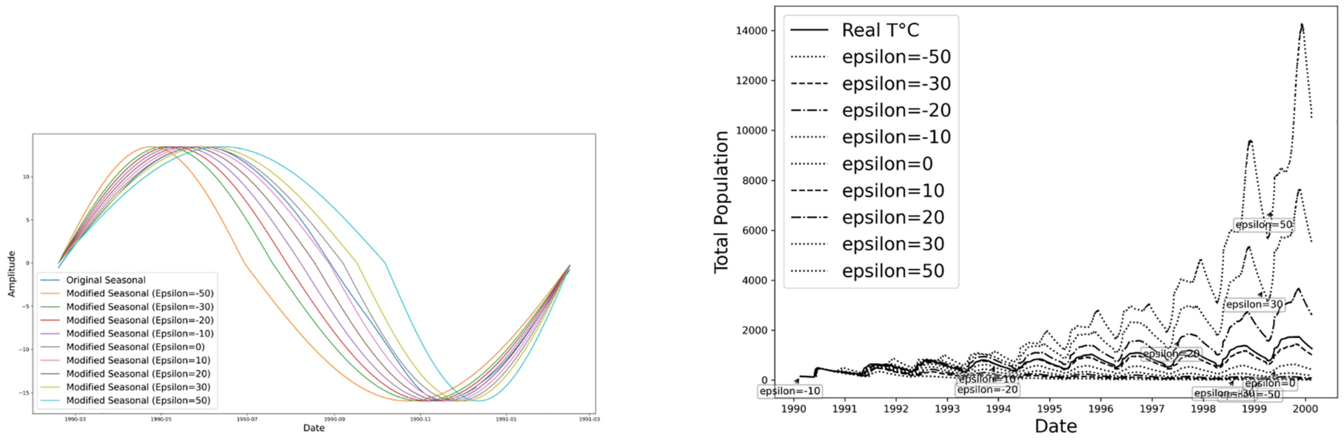
This approach assumes that the transition rate between compartments is constant, implying that the time distribution until an event occurs (*e.g.* The waiting time distribution WTD) for an event at a constant per-capita rate follows an exponential distribution. In this scenario,



a: The T_{S5} signal for all values of ε over one year. b: Total population abundance for the scenario S5.

Fig 10. The reconstructed temperature signal T_{S5}, depicted for various values of ε, is a valuable tool for assessing the effect of positive and negative temperatures throughout the annual cycle on the tick population. By observing how T_{S5} fluctuates with different ε values, we can indirectly evaluate the impact of altering the length of optimal temperature intervals. It captures the temperature variations over one year, considering different values of ε, influencing the duration of the warm and cold seasons. As ε varies, indicating shifts in the relative duration of these seasons, the resulting T_{S5} signal exhibits the corresponding changes in its temperature profile. It also depicts how warm and cold season length alterations affect the overall temperature pattern over ten years.

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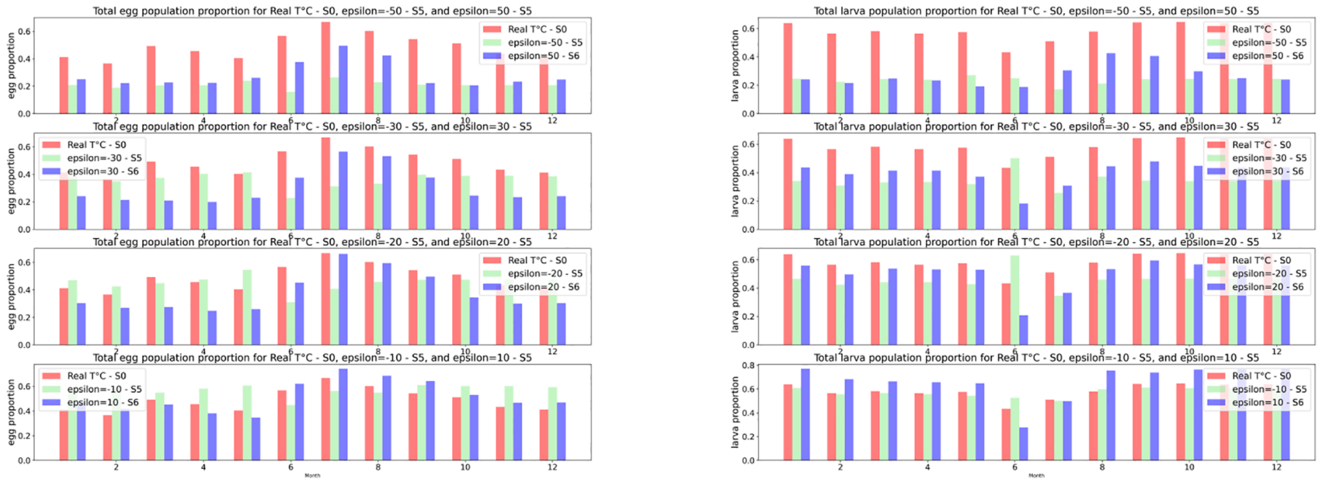
most individuals leave the compartment quickly, while a small proportion remains for a long time. However, a cohort's time in a stage strongly depends on temperature fluctuations [51].

Later, this approach was modified to account for temperature-dependent transition rates. Although this modification improves the model's fit to the data, it does not accurately represent climate-dependent mechanisms. By construction, the transition rates are calculated from population densities and are not directly related to temperature [52].

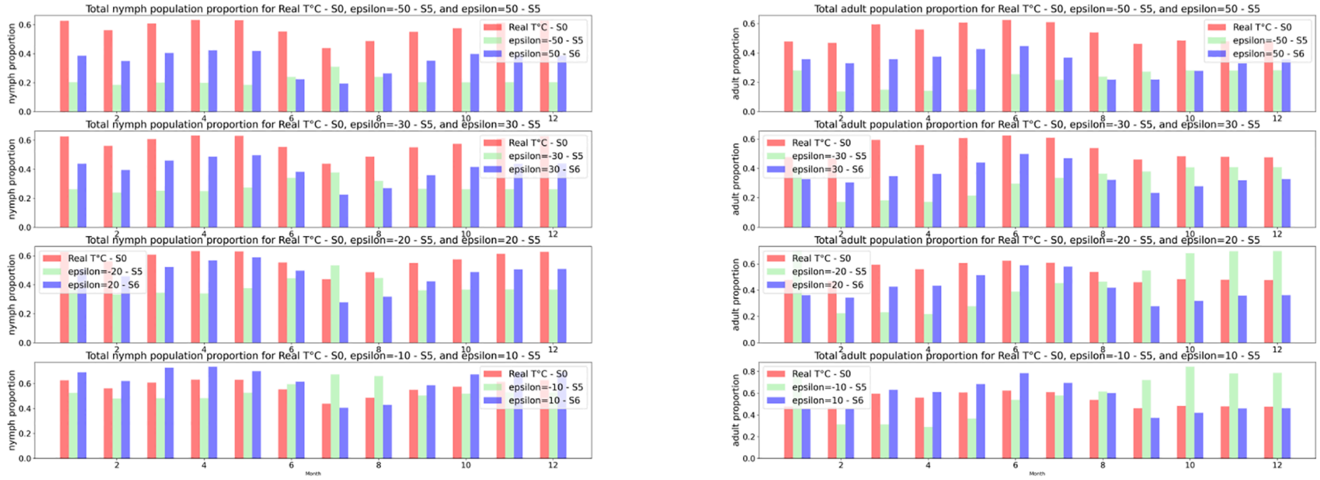
Climatic parameters affect metabolic speed and, consequently, the growth rate within physiological stages (*e.g.* eggs, larvae, nymphs, or adults) [53]. Growth involves the creation and modification of certain organs or functions, requiring energy to create structures (*e.g.* organs) and information (i.e. entropy growth) to enable the functioning of these organs [54]. Therefore, the transition between stages results from this growth process. On the other hand, tick survival is governed primarily by fat reserves from their blood meal [55]. A tick that has not yet fed in a particular stage relies on reserves from the previous stage. The consumption of these reserves begins as soon as the tick starts to molt right after its blood meal. The tick dies once it has depleted its reserves. Energy consumption is minimal during diapause, but reserve consumption increases rapidly once the diapause ends. Therefore, a tick's physiological age, corresponding to its time at the same stage, can be defined by its maturity level, which depends on metabolism speed influenced by temperature and the degree of depletion of the reserve [54].

Our model explicitly represents the different life stages of ticks, incorporating climatic parameters—especially temperature. Specifically, we considered two critical aspects: the consideration of molting (i.e. transition between stages) and the speed of transition within a life cycle. This approach was initially developed by [56,57], who used biological development rates to predict the phases of parasitic development depending on temperature. This requires evaluating a weighted development fraction for each day of development that accounts



a: Total egg population per month for scenarios S5 for all ε values

b: Total larva population per month for scenarios S5 for all ε values



c: Total nymph population per month for scenarios S5 for all ε values

d: Total adult population per month for scenarios S5 all ε values

Fig 11. The per-stage monthly total population for scenario S5 and different ε values.

https://doi.org/10.1371/journal.pcsy.0000065.g011

for daily temperature changes and a threshold temperature necessary for development to proceed.

More recently, the consideration of the life cycle and moulting has been studied by [49], where the tick life cycle was structured into four stages, assuming each stage is subdivided into an infinite number of discrete stages approximating a continuous life cycle framework

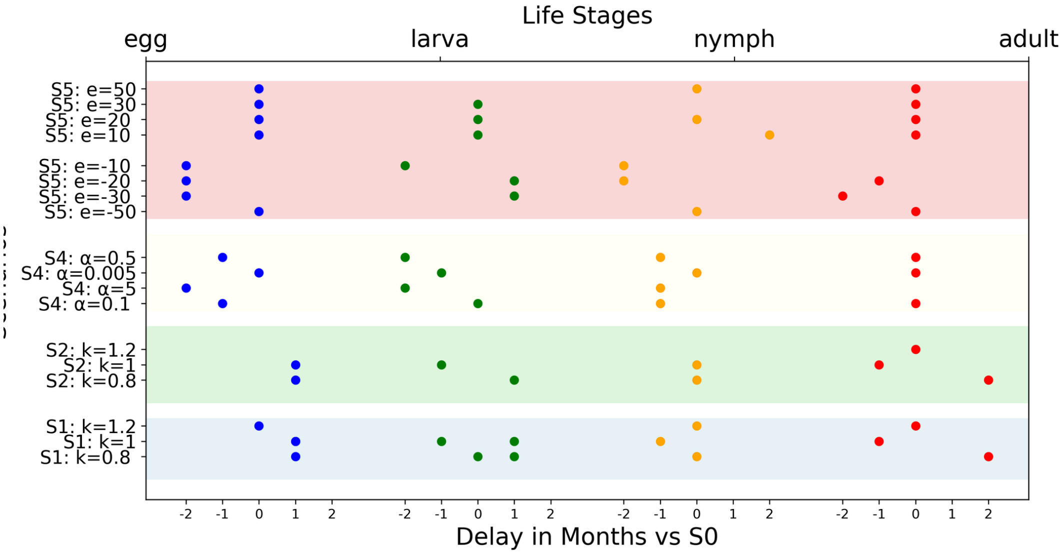


Fig 12. Comparison of delay of per-stage pics between scenarios. The cases where there was a total phase shift between peaks are not included in this graph.

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[58,59]. This approach has a generic form that explicitly models the life cycle of ticks, laying the foundation for modeling the life cycles of macroparasites in general.

The importance of a bottom-up and multi-agent approach

A distinctive feature of our model is its use of different time steps for processes underlying the interactions between and within agents. The bottom-up approach allows us to account for the inter-individual variability of ticks and, more importantly, the variability of their hosts, especially rodent hosts that move randomly. This method enables us to replicate closely the observed behavior of the system (ticks and hosts) and represent its operational mode as a network of interacting elements [60].

Our model also navigates intrinsic scales, covering various temporal dimensions. These multiple scales are critical to represent the dynamics of the system accurately. Firstly, the model differentiates between two primary time scales: one for ecological processes, such as host mobility, and another for physiological processes, including daily life cycle activities. For example, behavioral stages like feeding and oviposition are updated daily, as physiological processes—particularly development—are continuous phenomena. The molting process, which typically lasts between twenty days and a month to a month and a half [61], is discretized into time steps of 1/15 or 1/30 units, while ecological processes, which occur on a shorter time scale, use hourly time steps.

Choosing the same time step for both processes would complicate the model by introducing unnecessary complexity, mainly when correlating specific features of growth and host encounters. Therefore, our approach helps maintain the model's clarity and focus on the essential interactions.

The third time scale emerges from the model parameterization and directly relates to the tick life cycle's semelparous and periodic nature. Since each cycle repeats annually due to the periodicity of temperature, the model incorporates an annual demographic time scale, where the tick seasonal cycle is completed once a year. This scale is inherently connected to the physiological processes through the development speed within each life stage, which is temperature-dependent. This interconnection between physiological and demographic scales influences the unfolding of the life cycle and the general demography of the population.

Effects of noise suppression and seasonality on tick population

We employed reconstructed temperature signals to identify the specific features most significantly impacting our model's short-term outputs. Our objective was to examine how various components of a temperature signal influence tick population phenology, both in the short term by eliminating temperature fluctuations and in the long term by evaluating trend effects. This comprehensive approach improves our understanding of population dynamics and their potential shifts in response to climate variations.

Our key findings confirm that temperature significantly affects population abundance: Higher amplitudes promote growth, while lower amplitudes cause declines, regardless of trend variations. Suppressing temperature noise while maintaining the trend (Scenario S1) generally reduces the population abundance compared to the original scenario (S0). However, removing the temperature trend (Scenario S2) allows for higher population levels. The results vary significantly with different scaling factor values, indicating that slight temperature fluctuations, akin to short-term intra-annual variations, are crucial in determining population dynamics.

This phenomenon has been observed in the field by several studies. For instance, [62] confirmed that warmer climatic regions, seasons, and years contribute to increased winter tick (*Dermacentor albipictus*) infestations. Additionally, higher summer temperatures are associated with more significant tick infestations in moose, with increased density also leading to higher tick activity [63]. Interestingly, we found that extreme temperatures positively affect the tick population density, while daily temperature noise has a negative effect. This distinction underscores the need to separate these factors when analyzing climate impacts.

In Scenario S5, when hot and cold seasons were equal ($\varepsilon = 0$), we observed a stable population with a rising trend. Extending the warm season ($\varepsilon = 20, 30, 50$) led to a population explosion, while increasing the cold season resulted in low population abundance and declining trends. [64] observed a similar trend using projected data from the RCP 8.5 scenario to simulate the density and activity patterns of *Ixodes ricinus* ticks, finding that increasing temperatures before summer shifts the peak of questing nymphs to earlier in the year. An increase in inter-season periods is associated with more winter and spring days supporting tick activity. These shifts, often resulting from milder winters or prolonged summers, shift peak activity to earlier in the year [6,65,66]. Similarly, [2] demonstrated that warmer years from May to August were associated with a nearly three-week advance in the seasonality of nymph and larva stages compared to colder years. However, the rapid transition from a cold winter to a hot summer can accelerate tick population growth.

It is noteworthy that climate warming alters the questing behavior of ticks from cooler climates, prompting them to initiate questing at lower temperatures than those from warmer climates (*e.g.* European tick *I. ricinus*). This adaptability suggests that *I. ricinus* could advance their activity season by a month under climate change, potentially increasing the risk of tick-borne diseases and altering their epidemiological patterns [67].

Climate change also affects vegetation density, influencing the distribution and availability of hosts [68]. Determining whether tick distribution and abundance changes are primarily due to temperature variations or other factors remains challenging. Field data establishing a correlation between climate change and tick population or disease incidence changes do not necessarily prove causation. Therefore, models of tick populations under climate change are crucial for inferring potential drivers of these changes [10].

Limitations and possible extensions

Humidity, including relative humidity, vapor pressure, precipitation, and snow cover for northern species [69,70], strongly influences tick populations and their questing behavior [11,71,72]. We acknowledge that humidity plays a crucial role in the survival of ticks in general, and *Ixodes scapularis* in particular. Many studies have emphasized the significant impact of humidity on the development of various tick species (*e.g.* [73–75]). Although, humidity is not explicitly considered a limiting factor in our model, it remains a critical ecological variable that shapes tick population dynamics by influencing survival, behavior, and reproduction. Ticks rely on moisture to maintain water balance; high humidity prolongs their activity and increases the likelihood of finding a host, while low humidity causes desiccation, reducing survival rates and questing behavior. Tick survival, particularly for hard tick species like *Ixodes scapularis* and also *Ixodes ricinus*, depends on maintaining hydration under desiccating conditions, requiring a relative humidity of at least 80% [28]. Both temperature and relative humidity affect their survival, with the saturation deficit temperature and humidity combined significantly impacting ticks at up to 30-35 °C. As temperatures rise, the saturation deficit increases, drying out ticks and reducing their survival [28,76]. High temperatures, especially in dry conditions, can significantly reduce tick questing activity [26]. Climate change exacerbates these effects by altering tick biology and behavior, potentially impacting their abundance and distribution. As temperatures rise and weather patterns shift, ticks may change their habitats and activity patterns, potentially altering tick populations in various regions [77]. The relationship between blacklegged tick activity, specifically, and hard ticks in general, and their physical and biological environment is complex, shaped by interactions among multiple factors [73]. The most notable limitation of our model is its restriction to temperature as the only climate variable influencing tick development, thereby excluding other potentially significant factors as humidity. However, the main objective of our study was to isolate and examine the effect of temperature variability and its signal components on tick population dynamics, assuming constant and non-limiting humidity. This approach enabled us to specifically assess the role of temperature in shaping blacklegged tick dynamics. In addition to humidity and temperature effects, diapause plays a crucial role in tick population dynamics. Diapause is an essential mechanism for surviving unfavorable environmental conditions, occurring in two forms: developmental diapause (a temperature-independent process) and behavioral diapause (a temperature-dependent process). In this study, we only considered temperature-dependent behavioral diapause, which influences questing activity and seasonal dynamics. However, developmental diapause, which halts development irrespective of temperature, is equally important and should be incorporated into future models to better capture the full complexity of tick life cycles and their interactions with the environment. Ticks play a critical role as vectors of numerous diseases, including Lyme disease, babesiosis, and tick-borne encephalitis, contributing to the epidemiological burden of tick-borne diseases worldwide. Their ability to act as disease vectors is amplified by their adaptability to environmental changes and their reliance on humidity and temperature for survival. Future epidemiological studies need to incorporate broader environmental factors, such as precipitation patterns, snow cover, and vapor pressure, to provide a more comprehensive understanding of tick ecology and vector potential. More epidemiological context is needed to highlight the role of ticks in driving disease dynamics, particularly in the context of climate-driven shifts in their distribution and abundance. Expanding future research to account for the effects of humidity and other environmental variables, such as microclimatic conditions, will be crucial for a more comprehensive understanding of tick ecology. This includes assessing how variations in humidity affect questing behavior, host-seeking activity, and vector competence. Recognizing the significance of humidity, we intend to develop a future optimized new version of the model that integrates both temperature and humidity as key limiting factors, enabling a more accurate representation of their combined impact on tick dynamics. Additionally, understanding how these interactions influence disease transmission will provide critical insights into managing tick-borne diseases in a changing climate.

Conclusions

We used an agent-based model to simulate natural tick-host systems, focusing on temperature-dependent processes and population dynamics over a decade. Using reconstruction signal techniques with temperature data from 1990-2000, we assessed the impacts of extreme fluctuations, trends, and seasonality on tick abundance. Our findings confirm that temperature significantly influences the dynamics of the tick population, with higher amplitudes promoting growth and lower amplitudes causing declines. Additionally, we distinguished between the effects of extreme temperatures and daily fluctuations, noting that the former positively affects tick population density, while the latter has a negative impact. Our model highlights the importance of considering intra- and inter-annual temperature variations when analyzing tick phenology. These insights contribute to a broader understanding of tick population responses to climate variations, underscoring the need for further research incorporating other climatic factors, such as humidity, to improve predictive accuracy.

Supporting information

S1 Appendix. Please refer to the appendix file.
(PDF)

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Software: Cyrine Chenaoui, Ahmed Louhichi, Nicolas Marilleau, Slimane Ben Miled.

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Visualization: Cyrine Chenaoui.

Writing – original draft: Cyrine Chenaoui.

Writing – review & editing: Cyrine Chenaoui, Mohamed Aziz Darghouth, Nicolas Marilleau, Slimane Ben Miled, Ahmed Louhichi.

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