1. **Introduction:**

Tickborne diseases (TBDs) are an ongoing public health concern in the United States (US), where the number of reported cases of TBDs per year doubled between 2004 and 2016, resulting in nearly half a million cases (Rosenberg et al., 2018). Lyme disease constituted over 400,000 of the reported TBD cases over the 13 year period, though the true number of cases is likely to be an undercount by an order of magnitude (Kugeler et al., 2021; Nelson et al., 2015; Schwartz et al., 2021). Over 90% of TBD cases reported between 2004 and 2016 are caused by pathogens spread by *Ixodes scapularis* (the blacklegged tick) (Burgdorfer et al., 1982; Chen et al., 1994; Dumler et al., 2001; Spielman et al., 1985; Telford et al., 1997). Not coincidentally, much of the scientific effort to characterize the changing risk of TBDs involves modelling the eco-epidemiological cycles of *Ixodes scapularis* and associated pathogens, particularly their sensitivities to exogenous stimuli (Gilbert, 2021; Sharma et al., 2024).

State variables within *I. scapularis* eco-epidemiological cycles, i.e., tick and host population densities and the prevalence of various pathogens, can be impacted by changes to environmental conditions like biodiversity, landscape composition, and potentially, climate change (Cunze et al., 2022; Keesing et al., 2006; McClure et al., 2016; Ogden et al., 2021; Ostfeld and Keesing, 2000a, 2000b; VanAcker et al., 2023, 2019). These factors likely influence the tickborne disease system simultaneously, and untangling their respective influences remains difficult. Relating biodiversity to TBD risk is particularly challenging as it is difficult to measure at spatial scales where biodiversity-specific phenomenon are relevant (Diuk-Wasser et al., 2021; O’Connor et al., 2024b). Many of the studies examining the impact of biodiversity on TBD risk assess so-called “dilution” and “amplification” effects (Diuk-Wasser et al., 2021; Ogden and Tsao, 2009). Briefly, the dilution effect is a mechanism in the *I. scapularis-*pathogen system where an increase in biodiversity would hypothetically increase the relative number of pathogen-incompetent hosts, ultimately reducing pathogen prevalence and risk for TBDs (Ostfeld and Keesing, 2000a). Conversely, the amplification effect suggests a directionally positive relationship between biodiversity and tick fecundity could increase pathogen transmission, particularly if pathogen transmission is primarily density-dependent (Ogden and Tsao, 2009). Evidence for both mechanisms exists, though it is likely both are occurring over different contexts and spatial scales (Diuk-Wasser et al., 2021; Keesing et al., 2006; Kilpatrick et al., 2017; LoGiudice et al., 2003; Ratti et al., 2021; VanAcker et al., 2019).

Efforts to better understand the dilution and amplification mechanisms involves categorizing individual hosts according to their dilution and amplification properties and relating these properties to landscape-level biodiversity (Diuk-Wasser et al., 2021). Two primary properties of concern are a host’s reservoir competency and role in the *I. scapularis* reproduction system (Faust et al., 2017; Kilpatrick et al., 2017; Ratti et al., 2021). For example, the white-footed mouse (*Peromyscus leucopus*), Eastern chipmunk (*Tamias striatus*) and short-tailed shrew (*Blarina brevicauda*) have been identified as important natural reservoirs for *I. scapularis*-borne pathogens (Keesing et al., 2012; Mather et al., 1989). Conversely, white-tailed deer (*Odocoileus virginianus*) increase the reproductive success of *I. scapularis,* yet do not act as reservoirs for many *I. scapularis*-borne pathogens, and in some cases, may be borreliacidal (Massung et al., 2005; Pearson et al., 2023; Telford et al., 1988). Superficially, presence of reservoir competent small-mammals and white-tailed deer should increase risk for TBDs, as risk is generally estimated as the joint distribution between pathogen prevalence and tick density (Mather et al., 1996). However, when considering the dual role of white-tailed deer as drivers of *I. scapularis* density and hosts that dilute the pool of pathogen-competent hosts, the exact relationship between white-tailed deer density and TBD risk becomes difficult to resolve (Diuk-Wasser et al., 2021; Ratti et al., 2021).

Describing the competing facets of the role of white-tailed deer as dilution or amplification hosts can be aided by considering various environmental and biological contexts. Relating biodiversity to TBD risk often relies on using forest connectivity as a proxy for biodiversity, whereby evidence for dilution and amplification effects rely on key assumptions about the mammalian host populations remaining in less connected landscapes (Diuk-Wasser et al., 2021; Nupp and Swihart, 2000, 1998, 1996; Rosenblatt et al., 1999). Specifically, the dilution effect is predicted to occur when species richness increases in more connected forests, while conversely, keystone species like white-tailed deer and white-footed mice remain in smaller forest fragments. The validity of white-tailed deer as dilutors in fragmented landscapes can be assessed by comparatively examining pathogens both capable and incapable of infecting white-tailed deer in fragmented and connected landscapes. A possible candidate for analysis is the bacteria *Anaplasma phagocytophilum,* which presents in nature as several genetic variants each exhibiting varying reservoir host competencies (Rikihisa, 2011). Human infection with the Ap-ha (“human-active”) variant of *A. phagocytophilum* results in the disease anaplasmosis, of which the majority of cases are found in the northeastern United States (Massung et al., 2002; Rosenberg et al., 2018). Like the ecological cycle of *B. burgdorferi*, Ap-ha *A. phagocytophilum* is maintained in nature via white-footed mice and other small mammals (Keesing et al., 2014). A second genetic variant of *A. phagocytophilum*, Ap-v1 (“variant-1”) does not cause disease in humans and is maintained in nature using white-tailed deer as a reservoir (Massung et al., 2005). Importantly, Ap-v1 *A. phagocytophilum* is unable to infect white-footed mice, thereby separating the ecological cycles of the two variants for use in analysis; the reproduction mechanism of *I. scapularis* is the same for both variants and the species of bacteria is the same. Previous analyses have indicated that infection of the reservoir hosts is mutually exclusive to each variant, though recent research has indicated there is a chance that white-footed mice can be infected with Ap-v1 and white-tailed deer can be infected with Ap-ha (Robert F. Massung et al., 2003; Robert F. Massung et al., 2003; Tufts et al., 2024).

Anaplasmosis is the second most frequently occurring TBD in New York State (NYS), a sub-national geographic area in the northeastern US. Within NYS, incidence of anaplasmosis has risen over the last 15 years in a distinct spatial cluster on the state’s eastern border (Russell et al., 2021). The emerging anaplasmosis cluster has been attributed to an increase in the AP-ha variant within *I. scapularis* ticks in the eastern portion of NYS, compared to a greater proportion of Ap-v1 infected *I. scapularis* in western NYS (Prusinski et al., 2023). The changes in the distribution of *A. phagocytophilum* genetic variants in *I. scapularis* populations over time can provide key insights into the relationship between tick-borne pathogens, mammalian hosts, landscape connectivity, and the dilution and amplification effect debate. Recent research used statistical analysis from field-collected *I. scapularis* ticks genotyped for *A. phagocytophilum* variants to examine the propagation of *I. scapularis* populations and Ap-ha and Ap-v1 prevalence compared to white-tailed deer connectivity in NYS (O’Connor *et al.* in review). Results indicate that white-tailed deer act as dilution hosts to the Ap-ha variant, such that increases white-tailed deer density (via functional connectivity as a proxy) do not increase risk for Ap-ha. Conversely, Ap-v1 was amplified by white-tailed deer density in the same manner. However, this analysis utilized statistical modeling techniques that are unable to fully control for effects from colliders and preceding causal variables.

To better define dilution and amplification mechanisms within the complex system of *A. phagocytophilum* genetic variants, biodiversity, and landscape structure, future analytical efforts may require concerted efforts to model the dynamics of this system, rather than its static, statistical relationships. Advances in computer processing capabilities have allowed researchers to develop simulation models designed to study dynamic systems from a “bottom-up” approach (Epstein and Axtell, 1996; Heath and Hill, 2010). Such simulations generally involve programming individual entities, or agents, that possess variability in their characteristics and behavior rules (Bonabeau, 2002). The resulting model system is observed for emergent behavior according how it responds to changes in parameterized agent behavior (Batty et al., 2003). Models developed with the aim of observing behavior from the bottom-up approach using discrete entities are often referred to as agent-based models (ABMs) or individual-based models in ecology (Grimm et al., 2006). For the remainder of this paper, we will refer to both as ABMs. Recently, ABMs have been implemented to study tick ecology and TBD epidemiology at varying spatial scales and using different tick and host species (Gaff and Nadolny, 2013; Gaff, 2011; Halsey and Miller, 2020, 2018; Healy et al., 2020; Li et al., 2016; Nadolny and Gaff, 2018; Tonelli and Dearborn, 2019; Wang et al., 2015, 2012). Typically, the spatial scale of an ABM relates to the purpose of the model. For example, Tonelli and Dearborn (2019) built an ABM with a spatial resolution of 1° latitude by 1° longitude grid cells to examine dispersal of *I. scapularis* by ovenbirds and wood thrushes over long distances (the east coast of the US). Li et al. (2016) built an ABM with 1km2 grid cells to examine the pathogen dispersal of *B. burgdorferi* throughout Scotland as *I. ricinus* responds to climate change. Conversely, Halsey and Miller (2018) built an ABM, the spatially explicit individual-based tick interaction model (SEIB-TIM), with an environment of 100x100 grid cells of 1m2 (10,000 m2 total)to assess the interaction between *I. scapularis* and its hosts *P. leucopus* and *O. virginianus*. Later, Halsey and Miller (2020) applied the same ABM to test dilution effect mechanisms by varying the species richness and abundance of various small mammal hosts with different reservoir competencies for *B. burgdorferi*. Notably, neither of the models described by Halsey and Miller (2018) or Halsey and Miller (2020) test dilution effect mechanisms as they pertain to forest connectivity using single pathogens or otherwise. Here, we describe a spatially explicit ABM, the Spatial Transfer of Ectoparasite Pathogens from Tick Interpatch Connectivity (STEPTIC) model, that utilizes a network modeling approach to incorporate the multiple spatial scales relevant to *I. scapularis* ecology in northeastern US forests. Specifically, STEPTIC uses between-patch forest connectivity to model white-tailed deer movement between relatively smaller-scale modeling environments containing small-mammal host communities (e.g., white-footed mice). We use STEPTIC to examine dilution and amplification mechanisms as they pertain to forest connectivity and the *A. phagocytophilum* genetic-variant landscape. The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006), as updated by Grimm et al., (2020).

1. **Model Description**
   1. *Purpose and Patterns*

The purpose of STEPTIC is two-fold: First, this model aims to build upon the SEIB-TIM described by Halsey and Miller (2018) by incorporating *I. scapularis* lifecycle dynamics at multiple spatial scales. Second, STEPTIC simulates the pathogen dissemination of the Ap-ha and Ap-v1 variants of *A. phagocytophilum* to better understand their gene flow with respect to landscape connectivity and the dilution and amplification effects. Model evaluation is performed by comparing the following three patterns to simulated results:

1. Spatiotemporal *I. scapularis* population expansion from patches with established populations to new patches occur faster and with greater intensity in patches with greater forest connectivity. The relationship between forest connectivity and *I. scapularis* density is modeled statistically in O’Connor et al. (in review) for both nymphal and adult *I. scapularis* and the simulated results here are expected show a similar relationship.
2. The relationship between forest connectivity and white-tailed deer density varies according to broader, landscape-level forest connectivity. Existing literature indicates that in certain environmental contexts, i.e., highly fragmented landscapes, the forest connectivity of individual patches may increase white-tailed deer density. In less urbanized ecosystems, the opposite is typically true, as depicted in (O’Connor et al., 2024a) using a geographically weighted regression model.
3. White-tailed deer should appear as dilution hosts and white-footed mice as amplification hosts. O’Connor et al. (in review) indicates white-tailed deer dilute the available pool of Ap-ha competent reservoir hosts to the point where deer density has no relation to TBD risk despite their increasing *I. scapularis* populations. This model should corroborate this finding.

*2.2 Entities, state variables and scales*

STEPTIC includes seven entities. Three entities are agents with specific behavioral rules: small-mammals (i.e., white-footed *mice*), white-tailed *deer*, and *ticks*. The remaining four entities include: the *environment*, *forest networks*, *forest patches* (individual units within the *forest network*), and *grid cells* (individual cells within the forest patches). *Forest networks* are shown in Figure 1.

Small-mammal agents (henceforth, *mice*) represent *P. leucopus* present in northeastern US forest patches. White-tailed *deer* agents represent *O. virginianus* with the capability to move through a *forest network*. *Tick* agents represent *I. scapularis* ticks that become established in *forest patches* where habitat is suitable. State variables for the *mice*, white-tailed deer, and *tick* agent entities are provided in Table 1. *Grid cells* represent specific geographic locations occupied by the agents. *Forest patches* consist of a collection of *grid cells* corresponding to the size of the *forest patch*. *Forest networks* represent a collection of forest patches navigable by white-tailed deer agents according to a calculated metric. The environment represents the total model environment incorporating the seasonality of the northeastern US. *Forest networks* were selected based landscape-level forest connectivity and the presence of *A. phagocytophilum* genetic variants from field collected *I. scapularis* specimens. Forest patches in the network are those within a theoretical white-tailed deer’s home range (1,675 meters) from the field-collection site. State variables for non-agent entities are presented in Table 2.

*2.3 Process overview and scheduling*

The process of STEPTIC includes the movement of the three agent types through their respective *forest network*. During this process, non-tick agents will move according to a *daylight* variable in the *environment* while *tick* agents will quest and attach to hosts at this time. Mouse agents will move within *forest patches* by traveling between *grid cells* via random walk. *Deer* agents will move within *forest patches* by traveling between *grid cells* of varying distances via random walk. If a *deer’s* random walk takes it outside of a forest patch, it will “jump” to a new forest patch according to a probability gathered from a matrix of between-patch forest connectivity gathered from a shortest, least-cost path algorithm. *Tick* agents will move with the hosts they are feeding on. Upon successful feeding, *tick* agents will go through their life cycle by molting at specified times according to the *season* state variable in the *environment* and have several opportunities to fail to move on to the next life stage via grooming, desiccation, failing to molt, etc. A tick completing its lifecycle will involve reproduction and the creation of new tick agents. Throughout this process, Ap-ha and Ap-v1 *A. phagocytophilum* bacteria will be transferred between tick agents and non-tick agents according to their reservoir competency.

The schedule of this model involves a series of 14 steps performed iteratively after the user sets the initial *environment* starting *year,* *day of* *year,* and *hour of the day*. The steps of the model schedule are listed below:

1. Update the *environment*: This step updates the entire model *environment* with each new timestep by adding one hour to the *hour of the day* variable, changing the *day* variable if the *hour of the day* equals 24, changing the *year* variable if the *day* variable reaches 365, changing the *daylight* variable according to a yearly sunlight calendar with hourly resolution, and changing the *season* variable if the *day* variable reaches a preset day. The *hours of the day* variable exists to control the *daylight*, which in turn controls *tick* questing and *deer* and *mice* agent movement.
2. Move *mice* agents: This step updates the location of the *mice* agents by performing a random walk one grid cell away using queen’s adjacency. Each adjacent cell has a 1 in 9 chance of being selected, and *mice* also have a 1 in 9 chance at remaining stationary. *Mice* movement only occurs if the *daylight* environmental variable is set to “day”. At this stage, *mice* are assigned a tiebreak probability if two mice should become co-located with the same *tick* agent.
3. Move *deer* agents: This step updates the location of the *deer* agents in one or two steps and only occurs when the *daylight* environmental variable is set to “day”. First, *deer* perform a random walk to a new *grid cell* within any combination of 100 *rows* up or down and 100 *columns* left or right. If *deer* “walk” to a *grid cell* outside of their current *forest patch*, they travel to a new *forest patch* using a lookup probability table of between-patch connectivity indicating which patch is the most likely a deer will travel to. At this stage, a Bresenhem’s line algorithm is used to highlight which *grid cells* were crossed by which *deer* to attach questing *tick* agents, and *deer* are assigned a tiebreak probability should two *deer* cross the same location of a *tick*-agent.
4. Attach *ticks*: Here, *tick* agents attach (“link”) to *mice* and *deer* agents based on their new *locations*. If non-egg *tick* agents are co-located with a *mice* agent or a *grid cell* a *deer* agent crossed, they potentially attach to their hosts according to a random draw of an attachment parameter. If more than one of the same types of non-*tick* agents, e.g., two or more *mice*, exist on the same grid cell as a non-egg *tick* agent, the tie is broken via the tiebreak probability variable described in schedule step 2 and 3. If more than one non-*tick* agents of different types exist or crossed the same *grid cell* as a non-egg *tick* agent, the tie is broken according to parameterized life stage specific host preference.
5. Transfer pathogens: Following *tick* attachment, Ap-ha and/or Ap-v1 pathogens can be transferred between *tick* agents and host agents (*mice* and *deer*). Here, if a *tick* has been attached to a host for greater than 24 hours and either the *tick* or the host has a non-negative state for their *infection status* variables, a random binomial draw occurs to determine if the pathogen will be transferred. The probability for this draw is parameterized. Note, only *mice* agents can become infected with Ap-ha, and only *deer* agents can become infected with Ap-v1, while *tick* agents can become infected with either.
6. Groom ticks: If *ticks* are attached, they can be groomed from their respective hosts. This process only occurs when the *daylight* environmental variable is set to “day”. *Mice* and *deer* each groom ticks at their own parameterized rate. Successful grooming is governed by a random binomial draw, where the probability parameter is equal to this rate. If the binomial draw returns a value of 1, one *tick* is randomly removed from the host and “killed” by removing it from the model *environment* and from the *tick links* state variable of their formerly linked host.
7. Mate ticks: If two adult *ticks* with “male” and “female” *sex* state variables are attached to a *deer* agent, they will undergo the mating process. When males mate, they die and are removed from the environment and from their respective *tick links* state variable of their formerly linked host. When females mate, their mated state variable changes to 1.
8. Tick timer: This step updates three state variables in the *tick* agents. The *age* of each non-egg *tick* is increased by 1. If a *tick* is attached, the *time on host* variable increases by one. If a *tick* is attached and is has been attached to its host for a parameterized amount of time, the state variable *fed* changes to 1.
9. Tick drop-off: This step occurs for non-egg *tick* agents where *fed* equals 1 and *dropped* equals 0. *Tick* agents that fulfill these criteria drop from their hosts, setting their *links* variable equal to 0, and changing their *forest patch* and *grid cell* state variables to match the *location* of the host agent. If a larvaltick matches the *fed* and *dropped* criteria, they will drop-off of their host randomly over a period of 12 days. Because all 1,000 larvae that hatch from eggs will exist on the same *grid cell*, this ensures that not all 1,000 larval ticks are dropped in the same grid cell and instead are dispersed throughout the network as their hosts move. This process is achieved by creatingnew larval tick agents with *number of ticks* set to 1 and subtracting the *number of ticks* value from the original agent by the number that drop off.
10. Lay eggs: This step occurs for adult ticks whose *sex* state variable is “female”, *fed* state variable is 1, *mated* state variable is 1, and *dropped* state variable is 0. This step only occurs during a specific *day of the year* in the environment (during the “spring” *season*). This step changes the tick agent’s *life stage* variable from “adult”to “eggs”, the *number of ticks* variable from 1 to 1,000, the *sex* variable from “female” to “none”, the *infection status* variable to “negative” (if not already), the *age* variable to 0, the *Agent ID* variable to a new unique number, and *dropped, fed,* and *mated* to 0.
11. Tick molting: At this step, *ticks* move on to the next stage of their lifecycle if specific criteria are achieved and if the *day of the year* *environmental* variable matches a parameterized value. The non-environmental criteria are if *fed* and *dropped* equal 1. If those criteria are achieved, ticks have an opportunity to molt but may also die according to a life stage-specific molt success probability. A successful molted tick will change *fed* and *dropped* to 0, eggs will become larvae, larvae will become nymphs, and nymphs will become adults. During the nymphal to adult molt, a random “male” or “female” *sex* state variable is assigned.
12. Tick death: At this step, *ticks* can randomly die according to replete and unreplete death probability parameters specific to the *tick* agent’s *age* state variable. If a *tick* dies based on this probability, it is removed from the model environment.
13. Host infection timer: This step uses two parameterized values for when an infected host’s immune system is expected to remove any Ap-ha or Ap-v1 *A. phagocytophilum* infection. At each time step, the *Ap-ha / Ap-v1 infection timer* state variable is updated by adding 1. If this value reaches the equivalent of 28 days for *deer* agents or 55 days for *mouse* agents, the *infection status* state variable returns to “negative”.
14. Compile results: This step exists outside of the *environment* and simply collects data at each timestep. Data collected are Ap-ha and Ap-v1 percentages for *deer*, *mice*, and *ticks* at each *forest patch*.

*2.4 Design concepts*

*2.4.1 Basic principles*

STEPTIC is built to expand upon previous ABMs of tick ecology by expanding its spatial scale to better approximate metapopulations of *I. scapularis* ticks and their movement between disjoint forest patches according to multi-scale host movement. Though previous models exist that operate over different scales and incorporate reproductive and reservoir hosts (Halsey and Miller, 2018; Li et al., 2016; Tonelli and Dearborn, 2019), STEPTIC is the first to incorporate multiple spatial scales through separate, hierarchical processes. Conceptually, STEPTIC acts like a hybrid-ABM with the purpose of bridging the gap between an hyper-realistic, computationally-intensive model and one that incorporates a systems focused ecological phenomenon at a higher spatial scale (O’Sullivan et al., 2016). STEPTIC achieves this by running two types of models at different spatial scales. The smallest scale, i.e., the scale an *I. scapularis* tick interacts with a small-mammal host is modeled in every forest patch within the forest network, separately. White-tailed deer, who are larger and travel further distances, also interact in these small-scale environments, but scale is adjusted here by effectively treating them as a vector (in a mathematical sense), rather than a scalar as white-footed mice are. The larger scale elements of the environment are modeled by a forest connectivity network defined by least-cost paths calculated from a raster built to model resistance to white-tailed deer. Thus, as deer move through the individually running ABMs, they can move between them according to an ecological theory operating at a coarser spatial scale. This concept combines elements from Crooks and Hailegiorgis (2014), Anderson and Dragićević, (2016), and Anderson and Dragićević, (2018), by using multiple, disjoint models connected by a larger network to facilitate agent and pathogen movement between the models, thus modeling dispersal distances of multiple scales.

*2.4.2 Emergence*

THIS WILL BE ADDED WITH RESULTS

*2.4.3 Adaptation*

Adaptation is represented in STEPTIC through two behaviors, tick attachment and deer movement, both of which can be characterized as direct objective seeking. Adaptive behavior occurs during tick attachment when tick agents select hosts to attach to (in the event of a tie) based on predetermined life stage-specific preferences. Adaptive behavior occurs during deer movement when deer agents leave forest patches and select new ones to travel to based on the path of least resistance.

*2.4.4 Objectives*

The objective gained from tick adaptability during questing pertains to the intended outcome for a tick based on their life stage*.* Adult ticks climb higher on vegetation to attach to potentially larger hosts, feasibly to increase mating success. Juvenile ticks quest at lower heights and are less preferential. In this way, ticks will “adapt” to different options available to them, albeit using a predetermined ruleset from probabilities calculated from field-collected data: larvae will attach to *mice* 77.76% of the time, nymphswill attach to *mice* 46.78% of the time, and adults will always attach to *deer*.

Although STEPTIC does not feature a resource consumption mechanic guiding *deer* movement, *deer* movement adaptability achieves the objective of traveling to a new *forest patch* using the least amount of energy possible based on a calculation of least-cost path inverse sinuosity in the *network*. Least-cost path inverse sinuosity and new *forest patch* probability calculation is described in section *2.5 Initialization*.

*2.4.5 Learning*

STEPTIC does not feature adaptive learning.

*2.4.6 Prediction*

STEPTIC does not use adaptive prediction.

*2.4.7 Sensing*

STEPTIC uses sensing for the adaptive behaviors described in section *2.4.3 Adaptation* and *2.4.4 Objectives*. Tick agents are assumed to be able to sense the type of host they share a *grid cell* with, consistent with *life stage* specific host preferences. Deer agents are assumed to be able to sense which *forest patch* they are in within the *forest network* and are further assumed to have some ability to estimate the path of least resistance between their *forest patch* and other *forest patches.*

*2.4.8 Interaction*

Interaction appears in STEPTIC in four ways, both of which occur during *tick* attachment. First, hostagents directly interact with *tick* agents by allowing *tick* agents to attach. Attachment is considered direct interaction because it results in the *tick* agent changing its location as the *host* agent moves throughout the *forest patch* or *forest network*. Second, *host* agents interact with *tick* agents after they have attached by subjecting them to the grooming process. Grooming can result in killing ticks and removing them from the *environment*. Third, *tick* agents interact with *mice* and *deer* agents by transferring pathogens, i.e., altering the *infection status* state variables. Lastly, mediated interaction appears in STEPTIC during attachment. Attachment is necessary for *tick* agents to complete various stages of their life cycle, specifically feeding and mating. In this way, *host* agents mediate the feeding and mating processes but are not directly affected themselves.

*2.4.9 Stochasticity*

Many processes in STEPTIC are stochastic, starting with agent creation during initialization. STEPTIC is initialized by introducing a random number of *mice* agents based on density measurements at the *forest patch* level. The number of *deer* agents are assigned deterministically according to an equation described in section *2.5 Initialization.* Agents are assigned a *grid cell* within a *forest patch* stochastically to start the model. STEPTIC also uses field data of Ap-ha and Ap-v1 *A. phagocytophilum* infection at the *forest patch* level to stochastically assign t*ick* agents an infection status. Stochasticity is used for initialization because agent location at 1m2 resolution is not available. *Deer* and *mouse* agents are assigned *age* state variables at random up to their maximum lifespans because deer and mice age distribution data is not available.

Model subroutines also feature stochasticity using pseudorandom number generation. *Mice* agent movement is stochastic via a queen’s adjacency random-walk, and *deer* movement is stochastic via a within-*forest patch* random walk and between-*forest patch* movement governed by the least-cost path inverse sinuosity. Near completely random movement is included to simplify the model computation while still allowing for the examination of *I. scapularis* and *A. phagocytophilum* dispersal through *forest networks* governed by connectivity. Stochasticity is also featured in the tick attachment process during tiebreak events and a parameterized probability of attachment. Stochasticity during probability of attachment is used to regulate the rate of successful questing. Ap-ha and Ap-v1 transfer occurs stochastically to best match with variability in reservoir competencies within species. *Tick* grooming occurs stochastically to regulate the rate of *tick* death while attached to hosts. Stochasticity is introduced during *tick* mating if there exists an unequal number of male and female *ticks* on a host. In this instance, some *ticks* will only have one matched *tick* of the opposite *sex* to mate with, leaving some *ticks* unable to find a mate. The model does not have or require the resolution to pair ticks together, so they are selected randomly. Larvaedrop from *deer* agents at random times after they are fed for the purpose of separating the collective and spreading *ticks* throughout the *forest network*. *Ticks* randomly undergo successful molting, replete and unreplete death in forest habitat to control regulate the rate of *tick* death while having already had chances to move throughout the *forest network* and spread pathogens. *Deer* and *mice* undergo random death up to their parameterized maximum lifespan to effectively mimic all-cause death processes in a forest environment for the purpose of clearing pathogens from the host reservoir pool.

*2.4.10 Collectives*

Collectives are represented in STEPTIC as eggagents and larvalagents prior to molting. The collectives exist for the purpose of increasing the computational efficiency of the model due to large numbers of eggand larvalagents. These agents remain as collectives when they exist on the same *grid cells* after the egg laying process and before larvalagents molt into nymphalagents. The collective attaches to hosts together and is represented by the *number of ticks* state variable. Eggagents collectively hatch with *number of ticks* set to 1,000, and hatched larval *ticks* may die according to stochastic rules, reducing the *number of ticks*. After *larval ticks* attach, feed, and drop off from a host, they are no longer a collective.

*2.4.11 Observation*

The model is observed via the data collection process indicated in step 14 of *section 2.3 Process overview and scheduling.* At each timestep, the total number of each type of agent in each *forest patch* are recorded. Additionally, the total number of Ap-ha infected *ticks* and *mice* and Ap-v1 infected *ticks* and *deer* are counted. State variables in the *environment* are also counted including *season, day of year* and *year*.

*2.5 Initialization*

This model is initialized using data collected from 8 real forest networks surrounding field sites examined by the New York State Department of Health Vector Ecology laboratory. Site selection from the larger database first involves calculating a patch-level connectivity metric, the SCR index, at each study site. Sites were then tested for increasing or decreasing relationships between counts of *A. phagocytophilum*-positive *I. scapularis* and year of collection. Using the calculated criteria, sites were selected for modeling according to several parameters: connectivity (high or low), relationship between Ap-ha counts and year of collection (positive or negative), relationship between Ap-v1 counts and year of collection (positive or negative), and frequency of site visits. The selected sites are shown in Table 3 and Figure 1.

Once sites are selected, a GIS layer of forest patches gathered from the National Land Cover Database is intersected with the coordinates of the study sites, and all forest patches within 1,675 meters (the parameterized white-tailed deer home range) of each site are selected as the *forest network* (Homer et al., 2020; Homer and Fry, 2012). Additionally, a GIS layer of wildlife management units (WMUs) containing counts of deer take in NYS is overlaid over the selected *forest patches* to be used for deer density estimation. The number of deer agents per *forest patch* is calculated in three steps: the mean total deer take per WMU in 2006, 2007 and 2008 multiplied by proportion of area of *forest patches* in the *forest network* compared to all patches in the WMU. The resulting number is then multiplied by the inverse of the SCR index. Here, the inverse is taken to match the relationship between forest connectivity and deer populations. Last, the resulting number is divided by the ratio of total deer killed in NYS to an estimate of 1 million deer statewide from the NYS Department of Environmental Conservation (<https://extapps.dec.ny.gov/docs/administration_pdf/deer2.pdf>). For *forest patches* less than 1 hectare, a truncated minimum of 2 deer is assigned to that patch. The formula for calculation of *deer* agents is used to provide a better estimate for deer density when using hunter-killed deer take data. Hunter-killed deer data is inherently biased to overestimate deer populations where hunting is legal and more popular among residents. For *mice* agents, a random truncated normal distribution of mice with a minimum of 1 agent per hectare, mean of 50 agents per hectare and a standard deviation of 5 agents. Both *deer* and *mice* agents are randomly assigned locations within their specific *forest patch* as described in section *2.4.9 Stochasticity*.

After the *deer* and *mice* agents are initialized, *tick* agents are assigned locations based on field-collected values for tick density. *Tick* agents are only selected to start in *forest patches* matched to field-collected data and are split between nymphaland adultticks. The number of *tick* agents is calculated as the field-collected tick density multiplied by the *forest patch* area. *Tick* agents are randomly assigned locations within their specific *forest patch* as described in section *2.4.9 Stochasticity*. Additionally, *tick* agents are randomly assigned an infection status according to the field-collected *A. phagocytophilum* prevalence data.

The between-patch deer movement probabilities are calculated next using least-cost path inverse sinuosity. First, least-cost paths are calculated using a resistance raster for white-tailed deer described in O’Connor et al., (2024a). This resistance raster includes GIS raster data for roadways, elevation, and land cover type. Least-cost paths between *forest patches* within each *forest network* are calculated using Dijkstra’s algorithm implemented by the ‘leastcostpath’ R package (Dijkstra, 1959; Lewis, 2023). The resulting least cost paths are used to calculate the *forest patches* crossed in a “shortest paths” network using the ‘igraph’ R package (Csárdi et al., 2023). Each *forest patch* is then matched to *forest patches* that are a first-order distance away. The least-cost path inverse sinuosity is then calculated for the pairs of *forest patches.* The least-cost path inverse sinuosity of each destination forest patch is then divided by the sum of all least-cost path inverse sinuosity values for its corresponding origin *forest patch* to achieve the between-patch *deer* movement probabilities.

The final steps for model initialization include setting the model timing and total timesteps. For the burn-in period, this model is set with the timing of the *environment* variable *year* equal to 0, *day* equal to 265 (the fall equinox), *season* equal to fall. The model always starts at midnight because the *environmental* variable *day hour* is calculated as the *timestep* modulo 24. The *day of year, year,* and *season* variables are selected to ensure that adultticks are given the full amount to complete their lifecycle, i.e., fall questing, over-wintering, and spring-questing. Nymphalticks emerge the following year using the initialized data.

*2.6 Input data*

STEPTIC uses two types of input data to mediate time-varying processes. The first is the sunlight calendar data described briefly in section *2.3 Process overview and scheduling.* The sunlight calendar is used to control the status of the *daylight* in the *environment.* *Deer* and *mice* agents go through movement procedures when *daylight* is equal to “day”, which can alter the spatial distribution of ticks as they drop from their hosts. The sunlight calendar is gathered from the R package, ‘suncalc’, and is rounded to hourly increments (Thieurmel and Elmarhraoui, 2017). The cleaned sunlight calendar data provides a sunrise and sunset hour for each day of the year.

The second input data is coded at various points throughout the model to control the timing of the tick life cycle. These data are represented with units of “day” and are programmed for changes to the *season* variable where spring, summer, fall and winter begin on days 79, 171, 265, and 355 respectively. Lifecycle specific timing include the day adult *ticks* lay eggs, eggshatch to larvae, larvaemolt to nymphsand nymphsmolt to adults*,* which are represented by day values of 111, 202, 111 and 258.

*2.7 Submodels*

*2.7.1 Mice movement*

*Mice* movement can best be described as a 1 cell, queen’s adjacency random walk with the added possibility of a *mice* agent remaining stationary. At each *timestep*, *mice* have a 1 in 9 probability of moving to the cell it was on at the previous *timestep* or any of the 8 cells adjacent to it. These probabilities are modeled by the current location of *mice* agents, such that a *mice* agent cannot leave its current *forest patch*. For example, if a *mice* agent is located at *grid cell* with *row* equal to 1 and *column* equal to 1, the agent can only stay in the same location or move either directly right, down, or diagonally down and to the right. When each *mice* agent moves, the *location* state variable is updated*.*

*2.7.2 Deer movement*

*2.7.2.1 Deer movement 100 grid cell random walk*

*Deer* movement is performed in a series of steps. First, a value of 100 *grid cells* is added and subtracted to the current *row* and *column* of the *grid cell* each *deer* agent is located as potential possible landing locations. These possibilities are then randomly sampled to generate a new *grid cell* location. When a new *grid cell* is selected, the *location* and *old location* state variables are updated. If any of the new *row* or *column* values are negative, the *deer* agent moves to the between-patch movement submodel (below).

*2.7.2.2 Between-patch movement*

*Deer* agents with negative new *grid cell rows* or *columns* calculate a new *forest patch* to travel to according to the between-patch probability network described in section *2.5 Initialization*. The probability network remains static throughout the model run and building this network was described in section *2.5*. The first step in this process is to select a new *forest patch* according to the probabilities described, at which point the minimum and maximum values for *grid cell rows* and *columns* in the new *forest patch* are listed. A new *grid cell* is then selected from these *rows* and *columns.* Last, the *deer* agent’s *location* and *old location* values are updated. When *deer* agents move between patches, their paths are recorded as described in section *2.7.2.3 Create deer paths* (below).

*2.7.2.3 Create deer paths*

“Deer paths” are essentially a list of *grid cells* a *deer* agent will have traveled through during section *2.7.2 deer movement.* Deer paths are created using a Bresenham line algorithm to compute all *grid cells* each deer traveled through by comparing *location* to *old location*. Once all *grid cells* traveled through by each deer are found, they are recorded in a table along with the *deer* agent’s *ID*. Each deer is assigned a random tiebreak probability for use in section *2.7.4 Attach ticks* (below).

*2.7.4 Attach ticks*

The tick attachment procedure works in four steps. First, *tick* agents are filtered to include only non-egg *tick* agents with *links* and *dropped* state variables of 0. These *tick* agents are matched with the *grid cell* list created during section *2.7.2.3 Create deer paths*. If a *tick* agent is matched to multiple *grid cells* for different *deer* agents, the *deer* agent with the highest tiebreak probability is selected. Second, this process is repeated using the current *location* of *mice* agents. Third, *tick* agents are checked for ties between *deer* agents and *mice* agents by selecting them according to the following logic: *adult tick* agents will always attach to *deer* agents and *nymphal* and *larval tick* agents will attach to *mice* and *deer* agents according to probabilities previously defined in section *2.4.4 Objectives*. To reiterate, larvae *tick* agents will attach to *mice* 77.76% of the time, nymphswill attach to *mice* 46.78%. The final step in the tick attachment procedure is to update the *linked ticks* state variables for *mice* and *deer* agents. This is completed by adding any newly attached *tick* agents to the *linked ticks* list column for *mice* and *deer* agents.

*2.7.5 Transfer pathogens*

Transferring pathogens between *tick* and host agents involves two steps. First, attached *tick* agents without a *sex* variable set to *male* are compared against their corresponding host agents for their current *infection status*. If a *tick* agent has an *infection status* state variable set to either *Ap-ha +* or *Ap-v1 +* while the corresponding host agent has an *infection status* state variable set to *negative*, the host agent will have their *Ap-ha infection status* state variable set to *positive* if they are a *mice* agent or their *Ap-v1 infection status* state variable set to “positive” if they are a *deer* agent.. If a *tick* agent has an *infection status* state variable set to *“*negative*”* and their corresponding host’s *infection status* state variable is set to “Ap-ha +”or “Ap-v1 +”, the *tick* agent’s *infection status* state variable changes to Ap-ha or Ap-v1 positive, depending on the host.

*2.7.6 Groom ticks*

*Ticks* are groomed from their hosts randomly at a parameterized rate of 0.00734 ticks per hour for *mice* agents and 0.00495 ticks per hour for *deer* agents. *Tick* agents have a 20% chance of surviving when selected to be groomed by their host. These procedures are performed using a random binomial draw according to those probabilities. If *tick* agents are successfully groomed by their host, they are filtered from the *environment,* and the *tick links* state variable for that host is updated by removing the *ID* of the *tick* agents from the list column.

*2.7.7 Mate ticks*

The “mate ticks” subroutine works in two steps. First, the *links* state variable of all *tick* agents where the *mated* state variable is set to 0 are compared to indicate if they are attached to the same *deer* agent host. *Tick* agents attached to the same *deer* agent are then counted by their *sex* state variable, to indicate how many male and female matching pairs there are. If there are an equal number of *tick* agents with “male” *sex* state variables to “female” *sex* state variables, all *tick* agents with *“female” sex* state variables set their *mated* state variable equal to 1. All *tick* agents with “male” *sex* state variables die, are filtered from the *environment* and are removed from their corresponding *deer* agent’s *tick links* state variable. If there are more *tick* agents with their *sex* state variable equal to “female” than those set to “male” in the matching pairs, all *tick* agents with their *sex* state variable set equal to “male” will die, are filtered from the *environment* and are removed from their corresponding *deer* agent’s *tick links* state variable. Then, the equivalent number of *tick* agents with their *sex* state variable set equal to “female” *w*ill change their *mated* state variable to equal 1. If there are more *tick* agents with their *sex* state variable equal to “male” than those set to “female” in the matching pairs, all *tick* agents with their *sex* state variable set equal to “female” *w*ill change their *mated* state variable to equal 1. Then, the equivalent number of *tick* agents with their *sex* state variable set equal to “*male*” *w*ill die, are filtered from the *environment* and are removed from their corresponding *deer* agent’s *tick links* state variable.

*2.7.8 Update tick timer*

The tick timer subroutine works by simply adding (1/168) to the *age (weeks)* state variable for *tick* agents, changing the *fed* state variable equal to 1 if the *time on host* state variable is equal to 3, 5, or 10 days for larvae, nymphs, and adults,respectively, and conditionally adding 1 to the *time since fed* state variable if the *fed* state variable is equal to 1.

*2.7.9 Tick drop off*

The tick drop off subroutine works differently for adultand nymphalticks compared to larvalticks, because this subroutine works to separate larvalticks from their collective during the drop off period. First, larvae *collectives* with the *fed* state variable equal to 1 and *dropped* state variable equal to 0 are identified, and a random number of the larvaeare selected to drop from their host. The maximum number of larvaethat can drop is equal to the *number of ticks* state variable and the probability of any larvaedropping off is 1 / (12 – *time since fed*). This number is assigned to the *dropped* state variable and then subtracted from the *number of ticks* state variable. The process is repeated iteratively, such that each new timestep changes the probability so when *time since fed* equals 12, the remainder of the larvaewill drop from their host. At every timestep, larvae *tick* agents are created according to the *number of ticks* state variable dropped from a host. When new larvaetick agents are created, they are assigned new *ID*s and their *number of ticks* and *dropped* state variables are set to equal “1”.

Once the new larvaeare created, all *tick* agents with *dropped* state variables set to “1” have their *location* state variable changed to reflect the *location* state variable of their linked host and have their *links* state variable changed to 0. These *tick* agents are then filtered from the *tick links* variable of the *deer* agents they were linked to.

*2.7.10 Lay eggs*

The egg laying subroutine occurs when the *day of the year environmental* variable reaches 111. At this point, *tick* agents with *sex* state variables equal to *“female”,* *mated* state variables equal to 1 and *dropped* state variables equal to 1, change their state variables in the following way: *Infection status* is set equal to “None”, *number of ticks* is set equal to 1,000, *time since fed* is set equal to 0, *dropped* is set equal to 0, *sex* is set to “None”, *mated* is set to 0, a new *ID* is assigned, and *life stage* is changed to “Eggs”.

*2.7.11 Tick molting*

*Larval and nymphal tick* agents undergo molting when their *dropped* state variables are equal to 1 and the *day of the year environment* variables have reached a certain point (111 for larvae and 258 for nymphs). Eggagents “molt”, i.e., hatch, when *day of the year* equals “202”. Both larval and nymphal tickagents have a “molt success probability” parameter that is implemented here through a binomial trial. Larvae and nymphs have a 41.5% and 27.6% chance of molting successfully, respectively. If larvae or nymphsdo not successfully molt, they are filtered from the *environment.* At this point, state variables change like so: *fed, time since fed, dropped, mated,* and *links* allequal 0. Eggs, larvae, and nymphschange their *life stage* state variable to “larvae”, “nymphs”, and “adults”*,* respectively, and nymphs are assigned a random *sex* state variable equaling either “male” or “female”.

*2.7.12 Tick death*

The tick death subroutine is essentially a series of conditional binomial trials potentially resulting in removal from the *environment* if the trial returns a 1. There are three types of “death” in this subroutine. The first is “replete death”, which occurs for non-egg *tick* agents with *fed* and *dropped* state variables that equal 1. For each *tick* agent fulfilling these criteria, they undergo a binomial trial with the following probabilities: 1.31E-4 for larvae, 9.59E-5 for nymphs, and 9.12E-5 for adults. The second is “non-replete death”, which occurs for nymphal and adult tick agents in two ways, if *day of the year environmental* variable is less than 40 and if it is greater than or equal to “40”. Non-replete death probabilities when the *day of the year environmental* variable is less than 40 are 3.12E-6, and 1.83E-7 fornymphaland adultticks, respectively. Non-replete death probabilities when the *day of the year environmental* variable is greater than or equal to “40” are 3.64E-4, and 3.61E-4 fornymphaland adultticks, respectively. The third type of “death” is for *collective* agents, i.e., egg *tick* agents and non-replete larvalagents. This death occurs using a binomial trial probability of 3.02E-5 for eggagents, 2.13E-4 for larvaewhen the *day of the year environmental* variable is less than 40 and 5.17E-4 when the *day of the year environmental* variable is greater than or equal to 40. In this scenario, the maximum number of *tick* agents dying in each *collective* is equal to the *number of ticks* state variable. Any ticks that die during the *collective* process are tracked by subtracting the result of the binomial trial from the *number of ticks* state variable.

*2.7.13 Host infection timer*

The host infection timer subroutine tracks the length of time that a host has been infected with either Ap-ha or Ap-v1 *A. phagocytophilum*. If a *deer* agent’s *infection timer* state variable reaches 672 (28 days 24 hours), that agent’s *Ap-v1 infection status* state variable gets set to “negative”. If a *mice* agent’s *infection timer* state variable reaches 1,320 (55 days 24 hours), that agent’s *Ap-ha infection status* state variable gets set to “negative”.

**3. Results**

**4. Discussion**

**5. Tables and Figures**

  
Table 1: Agent entities (*tick, mice, and deer* agents) and their corresponding state variables.



Table 2: Non-agent entities (*Environment, networks, forest patches* and *grid cells*) and their corresponding state variables.



Table 3: Eight field sites with historical data for *I. scapularis* collection and *A. phagocytophilum* pathogen testing. Each site includes their corresponding sinuous connection reduction index connectivity, changes in Ap-ha and Ap-v1 over time, number of adjacent field site patches and frequency of site visits.

Table 4: THIS WILL BE THE PARAMETER TABLE WITH CITATIONS.

Table 5: THIS WILL BE A STATISTICAL RESULTS TABLE  
A screenshot of a computer screen

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Figure 1: Maps of eight field sites with historical data on *I. scapularis* collection and *A. phagocytophilum* pathogen testing. Patches are colored according to whether they include field data. Least-cost path networks used to generate between-patch movement probability table are shown as dark lines between forest patches.

ADDITIONAL FIGURES WILL INCLUDE:

MODEL SCHEDULING LOGIC DIAGRAM

DIAGRAM OF HOST MOVEMENT IN MODEL

1 OR 2 STATISTICAL RESULT PLOTS

**6. References**

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