

**AN EVALUATION OF EMERGENT AND ESTABLISHED TICK SPECIES AT
MULTIPLE GEOGRAPHIC SCALES:
COMMUNITY IMPACTS AND ECOLOGICAL PREDICTORS**

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ABSTRACT

Tick species and their associated pathogens are rapidly expanding their geographic range due to climate change, accidental introductions, and globalization. In the United States (US), exotic and invasive species such as *Haemaphysalis longicornis* interact with established tick species in the environment and on animal hosts. In addition, tickborne pathogens (TBP), novel and domestic, are continuing to expand geographically. Therefore, four research studies were dedicated to understanding ecological interactions of native and exotic tick species and their associated pathogens on human, companion, livestock, and wildlife hosts at varying geographic scales. First, forestry-related environmental variables were analyzed for their association on the abundance of ticks on human hosts in the southeastern US. Here we learned that each tick species, *Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis*, responds differently to biotic and abiotic variables which could be potentially mediated by their abundance. Next, we created environmental niche models (ENM) using GPS data from foresters encountering the tick species, *A. americanum*, *D. variabilis*, and *I. scapularis*. These maps are an important tool for implementing management strategies to control each tick species and can be used to reduce encounters with hosts. Next, ticks were collected through a Tennessee-statewide surveillance study from livestock and companion animal hosts and screened for *Ehrlichia*, *Anaplasma*, and *Theileria* pathogens to understand their current prevalence. Here we detected the occurrence of the devastating novel pathogen *T. orientalis* Ikeda in eastern Tennessee and an expanded geographic range of *Ehrlichia* and *Anaplasma* in the state. Finally, wildlife was sampled on farms in three eastern Tennessee counties infested with *H. longicornis* to understand ecological interactions between *H. longicornis*, on hosts, and established tick species. We demonstrated that the presence of *H. longicornis* can be predicted by host and established tick

species life history characteristics. Through these research projects we identified host, tick, and environmental variables that are specific to established and an exotic tick species which can be targeted for tick control. We recommend that future studies further investigate how these variables affect tick presence on hosts and in the environment.

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**CHAPTER I. FOREST-ASSOCIATED HABITAT VARIABLES INFLUENCE HUMAN-
TICK ENCOUNTERS IN THE SOUTHEASTERN UNITED STATES**

Abstract

Due to the increased frequency of human-tick encounters and expanding ranges of ticks in the United States there is a critical need to identify environmental conditions associated with tick populations and their likelihood to contact human hosts. In a passive tick surveillance partnership with United States Department of Agriculture Forest Inventory and Analysis (FIA) program we identified environmental variables associated with tick encounters by forestry personnel. Ticks were identified to species and life stage and site-specific variables were associated with each tick using FIA forest inventory datasets and generalized linear and zero-inflated models. Of the 55 FIA variables available, we identified biotic and abiotic environmental variables associated with *Amblyomma americanum* (carbon in litter material and standing dead tree aboveground dry biomass), *Dermacentor variabilis* (seedling species unevenness and elevation), and *Ixodes scapularis* (carbon in dead woody material and seedling species unevenness). We propose conducting future controlled studies using these forestry-related environmental variables to test their ability to alter tick abundance on plots. Land management decisions not only affect common flora and fauna, but changes to these habitats can also influence the way ticks parasitize hosts and use vegetation to find those hosts. These results can be used with land management decisions to prevent future human-tick encounters and highlight risk areas.

Introduction

The geographic ranges of many tick species are expanding (Alkishe et al. 2021, Eisen and Paddock 2021; Rochlin et al. 2022) and this is likely associated with the continued increase in human tick encounters in the United States (U.S.). In the southeastern U.S., lone star tick (*Amblyomma americanum* L.), American dog tick (*Dermacentor variabilis* Say), and blacklegged tick (*Ixodes scapularis* L.) are three commonly encountered tick species (Nieto et al. 2018, Trout Fryxell and Vogt 2019, Gallagher et al. 2022). Combined, these three ticks cause the majority of vector-borne diseases in the U.S. (Beard et al. 2021, Eisen and Paddock 2021). Specifically, these three species are responsible for tick-associated illnesses caused by bacteria (e.g., *Anaplasma*, *Borrelia*, *Ehrlichia*, *Francisella*, and *Rickettsia*), viruses (e.g., Heartland, Bourbon, Powassan), protozoans (e.g., *Babesia*), and food allergies (alpha-gal syndrome) (Dyer et al. 1931, Green 1931, Bell 1945, Spielman 1976, Burgdorfer et al. 1982, Grayson 1996, Ewing et al. 1997, Levin and Ross 2004, Steinke et al. 2015, Godsey et al. 2016, 2021). Southeastern states have previously reported an average annual rate of Lyme disease (0.0-10.8) per 100,000 persons from 2008-2015, Rocky Mountain spotted fever incidence >30 from 2000-2007, and an incidence rate (1-75) per million persons per year for human granulocytic anaplasmosis from 2008-2012 (Openshaw et al. 2010; Dahlgren et al. 2015; Schwartz et al. 2017).

The U.S. Centers for Disease Control and Prevention (CDC) now report expanding ranges of these important species. Expanded distributions and increased abundances of *A. americanum* into northern states are driven by biological (e.g., deer) and geographic variables (e.g., elevation or temperature) (Springer et al. 2015, Linske et al. 2020, Rochlin et al. 2022). Although the population west of the Rocky Mountains is now *Dermacentor similis* n. Lado et al. (2021), *D. variabilis* is historically common in the central U.S.. Recent studies documented this

tick encompassing a more expansive home range than previously thought with potential for populations expanding westward and northward (Boorgula et al. 2020). It is possible that tick-host use of dogs, raccoons, and other medium-sized mammals and climatic variables are responsible for this shift (e.g., Costero and Grayson 1996; Ewing et al. 1997). Concurrently, *I. scapularis* populations are slowly spreading from their historical northeastern habitats via bird migration and deer expansion (Eisen et al. 2016, Hickling et al. 2018). Because the ranges for these ticks are changing, the human-reported diseases associated with these ticks are becoming more prevalent in those regions (e.g., (Madhav et al. 2004, Eisen and Eisen 2018, Xu et al. 2020).

Ticks are dependent on their hosts for movement and nutrition, so it is likely that these range expansions also align with changes in host populations as they respond to climate, human land use, and land management practices (Gubler et al. 2001, Mills et al. 2010). Environmental variables influence tick distributions and pathogen transmission cycles by altering host, tick, and pathogen dynamics (Estrada-Peña et al. 2012, Robinson et al. 2015). For risk assessment and tick management, it is important to identify habitats associated with high tick abundance. Although tick ecology and human encounters have been well recorded in the Northeast and Midwest (Esteve-Gassent et al. 2016), tick ecology is less well understood in the Southeast because of the historical focus on Lyme disease in the northeast (Ginsberg et al. 2021, Hamilton et al. 2022). Previously, Trout Fryxell et al. (2015) investigated environmental variables associated with tick abundance of common southeastern tick species at a site with habitats common throughout the southeastern U.S., but few variables were identified as explaining tick distribution. The authors noted that investigated variables did not include those associated with host use and proposed that

variables associated with host habitats may be more important indicators (Trout Fryxell et al. 2015).

Here, we partnered with the Forest Inventory and Analysis (FIA) Program of the Forest Service, U.S. Department of Agriculture (USDA), knowing the program inventories sites throughout the southeastern U.S., to describe and identify environments where foresters are likely to encounter common human-biting ticks. Foresters that inventory sites encounter ticks, which we can then use to better understand the environmental conditions conducive to increased tick abundance or habitat suitability. Our goal was to estimate habitat suitability and risk of tick encounters with environmental variables. Specifically, we used tick encounter data to analyze associations between tick abundance and environmental variables assessed during encounters.

Materials and methods

Tick collection

Data for this study were obtained through a partnership with the USDA-FIA. Ticks were collected voluntarily according to methods outlined in Trout Fryxell and Vogt (2019) by FIA foresters conducting standard inventory operations over a period of five years (2017-2021) in the southeastern U.S.. Ultimately, ticks were submitted from crews in Kentucky, Tennessee, Florida, Alabama, Arkansas, Georgia, South Carolina, and Louisiana (**Table 1.1**). We requested crews to check themselves before, during, and after visiting each site. Forestry crews were given a field safety talk, and tick collection kits, which had instructions for removing ticks, forceps, and 80% ethanol filled vials. Each crew placed all collected ticks into a single vial labeled with the date, crew id, and GPS. We include information only if a crew submitted a tick to our program; we did not receive information on sites without ticks or sites where crews did not submit ticks (e.g., ticks were killed or returned to the wild). If a particular tick species was not collected at a site, it

was recorded as a zero since other ticks were encountered and collected at that site. Collections in 2020 and 2021 were limited due to Covid-19 pandemic.

While on or traveling to/from FIA plots, crews encountered ticks and placed those ticks into provided vials containing 80% ethanol. Crews labeled those vials with the date, a plot identifier, number of foresters present the day of collection, and GPS coordinates of plots. Submitted ticks were then identified to species and life stage using taxonomic keys (Yunker et al. 1986, Durden 1996, Keirans and Durden 1998).

Environmental variable collection

Vegetation data were collected by USDA-FIA crews on permanent ground sampling plots located across the study area at a sampling intensity of 1 plot per 2,428 ha (Reams et al. 2005). Depending on the state, each forest plot is assigned to 1 of 5, 7, or 10 spatially balanced panels and 1 panel of plots is measured every year so that each state is completely inventoried once every 5-10 years on an ongoing basis. Inventory data for this study were collected on a five-year cycle for most states, except for Alabama and Louisiana, which are on a seven-year cycle. Each forest inventory plot is a cluster of four points (subplots) arranged where one point is central and the other three lie 36.5 m from it at azimuths of 0, 120, and 240 degrees. Each point is the center of a circular subplot with a fixed 7.32 m radius. Plots that are partially forested or that straddle heterogeneous forest conditions are subdivided by a procedure known as condition mapping (Bechtold and Scott 2005). Conditions are distinguished based on land use, forest type, stand size, ownership, stand density, regeneration status, and reserved status (**Table 1.2**). A new condition is defined and mapped each time one of these variables changes during plot measurement. Trees greater than or equal to 12.7 cm diameter are measured in the subplots. Each subplot in turn contains a circular microplot with a fixed 2.07 m radius. Trees 2.5 cm to 12.7 cm

diameter and seedlings less than 2.5 cm diameter are measured in the microplots. Forest metrics collected at the plot, condition, or subplot level and included in this study were elevation, distance to improved road, forest type, slope, stand age, stand size, and water presence (**Table 1.2**). Additional forest characteristics (e.g., live tree density) were derived from the tree-level metrics and summarized for each plot condition to a per 0.40 ha (1-acre) basis (**Table 1.2**). In total, 54 environmental variables describing physical geography and forest stand structure were selected as possible predictors of tick abundance due to their ability to affect tick and tick-host survivability (**Table 1.2**). Details about the specific metrics collected at each plot location, as well as metrics derived from the field-collected variables, were previously described (United States Forest Service 2016; Burrill et al. 2021).

Environmental modeling of tick abundance with FIA data

We conducted independent two-tailed analyses ($\alpha = 0.05$) in Statistical Analysis Software (SAS Institute, Cary, NC, ver. 9.4) to test the effect of environmental variables collected by foresters on the abundance of *A. americanum*, *D. variabilis*, and *I. scapularis* separately. Given the large number of environmental variables available, a correlation analysis was performed prior to modeling to minimize potential multicollinearity. Less biologically meaningful or less statistically significant correlated (PROC CORR) (> 70%) environmental variables were removed from further consideration (**Table 1.2**). In addition, Moran's I (PROC VARIOGRAM) (> 70%) was used to measure autocorrelation among geographic areas and environmental variables; however, there was no multicollinearity observed between variables and sites for each species. We used a generalized linear model (PROC GLIMMIX) with a negative binomial distribution to analyze the relationship between number of *A. americanum* ticks encountered at each plot and environmental variables. Whereas zero-inflated models with a negative binomial

distribution were used to analyze the relationship between *D. variabilis* and a Poisson distribution for *I. scapularis* abundance and environmental variables and two-way interactions were observed. A stepwise regression was used for iterative removal of nonsignificant terms was conducted to find the most parsimonious model. For plots with multiple condition classes (approximately 30 instances), environmental variables were taken from the first forest condition encountered on the plot. This was done to account for categorical variables collected on plots instead of averaging condition classes together. Finally, because there were differences in the number of foresters in each crew size and the amount of time was not recorded that foresters spent at each plot, we cannot account for any effects of temporal exposure length on the abundance of ticks per plot. To account for unequal crew sizes in data collection the crew size was used as an offset in each individual model.

Results

A total of 1,221 ticks were collected during the study period from 198 sites: 1,094 (89.60%) *A. americanum* from 151 sites, 88 (7.21%) *D. variabilis* from 52 sites, and 39 (3.19%) *I. scapularis* from 30 sites. Of the *A. americanum* records, 286 (23.42%) were adult females, 220 (18.01%) were adult males, 578 (47.33%) were nymphs, and 10 (0.82%) were larvae. The remaining ticks were 51 (4.18%) *D. variabilis* females, 36 (2.95%) *D. variabilis* males, 1 (0.08%) *D. variabilis* nymph, 14 (1.15%) *I. scapularis* males, and 25 (2.05%) *I. scapularis* females (**Table 1.1; Figure 1.1**).

Each tick species responds differently to environmental variables

Fifty-four environmental variables were included as potential predictors of tick abundance for all three tick species (**Table 1.2**). Carbon in litter material ($P = 0.0498$) and standing dead tree aboveground dry biomass ($P = 0.0031$) had a significant effect on *A.*

americanum, in which increases in each variable resulted in a decrease in tick abundance (**Table 1.3** and **Figure 1.2 a** and **b**). A one unit increase in carbon in litter material resulted in a 1.84 increase in *A. americanum* abundance and a one unit increase in standing dead tree aboveground dry biomass resulted in a 1.31 increase in *A. americanum* abundance. Seedling species unevenness ($P = 0.0216$) significantly impacted the number of *D. variabilis* ticks collected on human hosts, in which tick abundance decreased as the variable increased (**Table 1.3** and **Figure 1.2 c**). Elevation ($P = 0.038$) was significantly associated with *D. variabilis* abundance, in which tick numbers increased as the variables increased (**Table 1.3** and **Figure 1.2 d**). A one unit increase in seedling species unevenness resulted in a 1 tick increase and a 1 unit increase in elevation resulted in a 1 tick increase for *D. variabilis* abundance. Carbon in dead woody material (carbon in down dead) ($P < 0.0001$) and seedling species unevenness ($P = 0.0307$) significantly affected *I. scapularis* on human hosts, in which increases in each variable resulted in an increase in tick abundance (**Table 1.3** and **Figure 1.2 e** and **f**). A one unit increase in seedling species unevenness resulted in a 3-tick increase and a one unit increase in carbon in dead woody material resulted in 13 tick increase for *I. scapularis*.

Discussion

The chances of a tick surviving to find its next host depends on the environment where it either molts to the next life stage or hatches from an egg and then finds its next host. Here, we identified environmental conditions that indicate an increased chance of encountering a common tick species and where those encounters are more likely to occur in the southeastern U.S. Our study not only identified where ticks are encountered, but also provides information for possible tick management (e.g., landscape change) or avoidance (e.g., increased use of personal protection in areas suitable for ticks).

In our study, the most encountered tick throughout the region was *A. americanum*. Forestry crews were less likely to encounter *A. americanum* at sites when carbon in litter material was higher. Thus, foresters were less likely to encounter this tick species whenever organic material on the forest floor, in the form of humus, woody debris, or roots, increased. Gilliam et al. (2018) found a similar result in which increasing leaf litter cover decreased adult *A. americanum* numbers, but not for larvae or nymphs. Additionally, Schulze and Jordan (2005) found reduced litter resulted in increased *A. americanum* encounters, which could be the result of this tick's higher resistance to desiccation and ability to occupy microhabitats. Immature and adult *A. americanum* are known to quest on vegetation above the leaf litter (Schulze et al. 1997) and increases in litter could inhibit their ability to climb flora and find hosts. Snags are known to support a variety of animal species and decreases in human tick encounters as snags increased could be due to more available hosts obtaining ticks in these habitats and ultimately reducing encounters (Pugliese and Rosà 2008). Decreased encounters could also be the result of wildlife, which harbor *A. americanum*, using vertical space in standing dead tree matter, contrary to encountering ticks questing on vegetation (Stokland 2001). Reducing tick-host contact could deny ticks from obtaining a blood meal and molting into the next life stage (Wilson et al. 1988).

There was a decrease in *D. variabilis* abundance as seedling species unevenness increased; in other words, tick abundance increased as the proportion of seedling density increased for the most predominant species. Habitats with ample seedling unevenness present could include areas such as timber plantations, which are numerous in the southeastern U.S. (Miller et al. 2003; Miller et al. 2009). Plantation forestry operations are also known to have fewer wildlife species (Stephens and Wagner 2007) which could cause a decrease in *D. variabilis* populations. Previously, Trout Fryxell et al. (2015) found no relationship between *D.*

variabilis and habitat type diversity in the Southeast. Because *Dermacentor variabilis* is known to parasitize a variety of host types (small, medium, and large mammals) throughout different life stages (Butler et al. 2020; Kollars and Kengluocha 2001; Foster et al. 2003) and homogenous forests typically have lower mammal diversity (Stephens and Wagner 2007) our result could be due to decreased host availability on these plots. Increases in elevation resulted in an increase in human-*D. variabilis* encounters, but there were no ticks collected above 600 meters mean sea level. Butler et al. (submitted) found *D. variabilis* to be absent from areas with low elevation such as the Mississippi Alluvial Plain region and high elevations such as the Appalachian Mountains. Many of these low elevation sites are characterized as swampland habitats (Faulkner et al. 2011) and although *D. variabilis* has been reported to survive submerged underwater for a period of time (Fielden et al. 2011) these habitats may not be conducive to their hosts (Kollars et al. 2000, Schwartz and Schwartz 2016).

Ixodes scapularis were more often associated with sites with increased carbon in down dead woody material; in other words, tick abundance increased as stumps and their associated root system and woody material on the forest floor increased. This variable aligns with larval and nymph stages of *I. scapularis* found on small mammals and those mammals often use coarse woody debris and habitats for refuge (Piesman and Spielman 1979, Wolff and Hurlbutt 1982, Pearce and Venier 2005). Increases in dead tree biomass and carbon could support a larger population of rodents, which are also primary hosts for immature *I. scapularis* (Hurlbutt 1982, Buskirk and Ostfeld 1995). Rodents, which serve as hosts for immature *I. scapularis* ticks, are known to feed on invertebrates (Hamilton 1941) and coarse woody debris is associated with increased vertebrate diversity. Additionally, down-woody material supports carbon in down dead and therefore our results indicate areas with these characteristics likely serve as a refuge for tick-

infested hosts (Riffell et al. 2011). Mammal activity patterns at the forest stand level have the ability to impact *I. scapularis* tick populations (Coyle et al. 2013). *Ixodes scapularis* abundance increased with an increase in seedling species unevenness. Unevenness in plant communities often results from dominance of certain species rather than heterogeneity (Strong 2002). Although the reason for the significance of seedling density unevenness is unclear, seedling species such as Tulip poplar (*Liriodendron tulipifera* Dippel) (Jenkins and Parker 1998) can dominate canopy openings after disturbance which often increases edge effects (Dupuch and Fortin 2013). White-tailed deer (*Odocoileus virginianus* Zimmerman), a species that thrives in edge habitats (Rohm et al. 2007) and known to commonly browse seedlings (Runkle 1981), have been reported to prefer consuming tulip poplar seedlings compared to beech or pine species (Seagle and Liang 2001). Additionally, white-tailed deer browsing can reduce understory species richness (Horsley et al. 2003) and seedling abundance is known to decrease as deer abundance increases (Leland Russell et al. 2001). Elevated tick encounters on plots with increased seedling density unevenness could be due to increase white-tailed deer movement. Increases in tick numbers in these areas could be due to dominance of species preferred by deer whose presence facilitates adult tick dispersal (Varela-Stokes 2007, Bradshaw and Waller 2016).

Land management can alter tick populations by making areas more or less attractive to wildlife (Medlock et al. 2013, Gallagher et al. 2022). Oftentimes human-modified habitats result in environments which support tick populations by promoting increased host use. For example, prescribed burning may remove tick and mammal habitats that promote the abundance of tick populations (Pascoe et al. 2020). Our research found *I. scapularis* positively associated with carbon in down dead and leads to more questions about burning to reduce tick and mammal habitats to subsequently lower blacklegged tick abundance. Although prescribed fire is often

achieved to increase mammal habitats frequent burning may decrease rodent populations, which support *I. scapularis* abundance, by reducing woody debris and shrubs (Converse et al. 2006; Morris et al. 2011). Some studies found controlled burns can reduce the abundance of ticks and the prevalence of tickborne pathogens in an area (Stafford et al. 1998, Gleim et al. 2019). Because *I. scapularis* populations were associated with carbon in dead woody material, future studies should investigate the role of controlled burns at reducing carbon in dead woody material to reduce tick population in areas with high Lyme disease incidence. However, other studies indicated tick populations surge after prescribed fires, which could be due to reduced litter material or increased host use in burned areas (Allan 2009). Because *I. scapularis* prefers a higher relative humidity for survivability, burn treatments could be important for reducing this ticks abundance by altering forest microclimate (Bertrand and Wilson 1996; Refsland and Fraterrigo 2018). Increased carbon in litter material was associated with a decrease in *A. americanum* abundance. Immature and adult ticks often search for hosts higher up on litter or vegetation (Huang et al. 2021; Mangan et al. 2022); therefore, increased litter material could make questing for this species more difficult. Litter material remains an important aspect of forest ecology regulating moisture and energy content between the soil and above air (Ogée and Brunet 2002). Litter thickness is associated with soil moisture promoting a buffer to reduce soil exposure from environmental conditions (Cawson et al. 2020) reducing soil evaporation (Ogée et al. 2001). In addition, moist soils are associated with more diverse and abundant array of microbial biomass (Baldrian et al. 2010), whereas dry soils are associated with a decrease in mass (Sardans and Peñuelas 2005). Previous studies documented microbes commonly found in soil can cause tick mortality (Gomathinayagam et al. 2002, Sun et al. 2011, Samish et al. 2014). Results from this study could be due to decreased tick survivorship from increased microbial

communities and moisture within leaf litter and soil. Because decreasing litter material with prescribed burns would likely cause a rise in human-tick encounters for *A. americanum*, management strategies targeting tick hosts would likely be more productive.

As with most ecological studies, limitations for this research included unequal tick collections acquired by individual forestry crews. Although most crews participated in tick collection some crews were not avid collectors, resulting in unequal tick collections acquired by individual forestry crews but this was corrected for by using an offset in each model. Differences in participation could be due to a variety of reasons including, but not limited to, demographics, education, risk-tolerance, previous experience with a tickborne disease, or limited time to perform tick checks. Unbalanced tick collections also affected data collection geographically in which most collections were located in Kentucky, but there were limited collections in other states. Although geographical differences in tick collections could alter our results by not considering environmental conditions occurring with tick abundance in other states, our Moran I-values indicated there were no correlations ($> 70\%$) among location for each tick species.

In conclusion, carbon in litter material and standing dead tree aboveground dry biomass were associated with *A. americanum*; elevation and seedling species unevenness were associated with *D. variabilis*; and carbon in dead woody material and seedling species unevenness were associated with *I. scapularis* encounters. Future studies which include forest management strategies to test the effects of manipulating these variables to control tick populations are needed. Management could include prescribed burning to eliminate variables associated with tick species (e.g., carbon in dead coarse woody material). Educational materials could be targeted to those who use the land (e.g., foresters, recreational users, hunters) as they engage in outdoor activities in habitats that support tick populations. Forest management strategies such as thinning

and tree-species selection could help control tick populations by forming more warm and dry microclimates (Brennan et al. 2023). Additionally, our results supported that different tick species could respond negatively or positively to certain management regimes based on environmental variables associated with increased abundance. Therefore, it is important to test different control strategies which would best manage a selected tick species. Because the forest variables in our study are associated with wildlife habitat and food sources, management strategies (in urban and rural areas) are vital for controlling tick populations. In the future, we will aim to integrate tick encounter data and site variables at different scales (the site and area around the site) to focus on management of forestry-related environmental variables and their effects on tick populations.

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Appendix

Table 1.1. Total number of ticks encountered by forest inventory crews (total number of tick encounter sites) in the southeastern United States for the years 2017-2021, by state.

State	<i>Amblyomma americanum</i>	<i>Dermacentor variabilis</i>	<i>Ixodes scapularis</i>
Alabama	35 (1 site)	17 (1 site)	1 (1 site)
Arkansas	4 (4 sites)	0 (0 sites)	2 (1 site)
Florida	107 (19 sites)	2 (2 sites)	9 (7 sites)
Georgia	1 (1 site)	0 (0 sites)	1 (1 site)
Kentucky	648 (74 sites)	41 (25 sites)	12 (7 sites)
Louisiana	3 (3 sites)	2 (2 sites)	3 (3 sites)
South Carolina	33 (24 sites)	11 (10 sites)	8 (7 sites)
Tennessee	263 (25 sites)	15 (12 sites)	3 (3 sites)
Total	1094 (151 sites)	88 (52 sites)	39 (30 sites)

Table 1.2. Definitions for environmental variables used to test associations with *Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis* separately (198 plots total).

Variable	Definition ^a	Potential predictors of tick abundance
Stand age	Average total age, to the nearest year, of trees in the stand-size class of the condition.	<i>D. variabilis</i> and <i>I. scapularis</i>
Carbon in down dead	Carbon, in tons per acre, of woody material >3 inches in diameter on the ground, and stumps and their roots >3 inches in diameter. Estimated from models based on geographic area, forest type, and live tree carbon density (Smith and Heath 2008).	<i>I. scapularis</i>
Carbon in litter	Carbon, in tons per acre, of organic material on the floor of the forest, including fine woody debris, humus, and fine roots in the organic forest floor layer above mineral soil. Estimated from models based on geographic area, forest type, and (except for nonstocked and pinyon-juniper stands) stand age (Smith and Heath 2002).	<i>A. americanum</i>
Carbon in soil organic material	Carbon, in tons per acre, in fine organic material below the soil surface to a depth of 1 meter. Does not include roots. Estimated from models based on geographic area and forest type (Smith and Heath 2008).	<i>A. americanum</i> and <i>D. variabilis</i>
Carbon in standing dead trees^b	Carbon, in tons per acre, in standing dead trees ≥1.0-inch diameter, including coarse roots, is estimated from models based on geographic area, forest type, and (except for nonstocked stands) growing-stock volume (Smith and Heath 2008).	<i>D. variabilis</i>
Ecological subsection code	Code identifying an area of similar surficial geology, lithology, geomorphic process, soil groups, subregional climate, and potential natural communities.	None
Carbon in understory above ground	Carbon, in tons per acre, in the aboveground portions of seedlings and woody shrubs. Estimated from models based on geographic area, forest type, and (except for nonstocked and pinyon-juniper stands) live tree carbon density (Smith and Heath 2008).	None

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Live tree basal area per acre (square feet)	Cross-sectional area, including bark, at the point of diameter measurement ^c of all live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	<i>I. scapularis</i>
Live tree density	Number of all live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis.	<i>A. americanum</i>
Live tree belowground carbon (pounds) per acre	Carbon, in pounds, of coarse roots >0.1 inch in root diameter for live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis	<i>I. scapularis</i>
Live sapling density	Number of all live trees >1.0 inch d.b.h./d.r.c. and <5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis.	<i>D. variabilis</i> and <i>I. scapularis</i>
Live sapling aboveground dry biomass (pounds) per acre	Oven-dry biomass in the aboveground portion, excluding foliage, of all live trees ≥ 1.0 inch d.b.h./d.r.c. and <5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>D. variabilis</i>
Seedling species unevenness (1)	Proportion of total seedling density for the most dominant species in the condition class, i.e., the species with the greatest proportion of seedling density. Note: as a formula this is $\max(\text{seedling density for species } i \text{ on plot } j / \text{total seedling density on plot } j)$.	<i>I. scapularis</i>
Seedling species unevenness (2)	Proportion of total seedling density for the second most dominant tree species in the condition class, i.e., the species with the second greatest proportion of seedling density.	None
Live tree above ground dry biomass	Oven-dry biomass in the aboveground portion, excluding foliage, of all live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>I. scapularis</i>
Live tree above ground carbon	Carbon in the aboveground portion, excluding foliage, of all live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>I. scapularis</i>

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Standing dead tree basal area	Cross-sectional area, including bark, at breast height (4.5 ft above the ground) of all standing dead trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	<i>A. americanum</i>
Standing dead tree density	Number of all standing dead trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis.	<i>A. americanum</i>
Standing dead tree aboveground dry biomass (pounds) per acre	Oven-dry biomass in the aboveground portion, excluding foliage, of all standing dead trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>A. americanum</i>
Standing dead tree belowground dry biomass	Oven-dry biomass of the belowground portion, including coarse roots with a root diameter ≥ 0.1 inch, of all standing dead trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>A. americanum</i>
Standing dead tree aboveground carbon (pounds) per acre	Carbon in the aboveground portion of all standing dead trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>A. americanum</i>
Standing dead tree belowground carbon (pounds) per acre	Carbon of coarse roots > 0.1 inch in root diameter of all standing dead trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>A. americanum</i>
Live tree quadratic mean diameter	Diameter, in inches, corresponding to the mean basal area of all live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class.	<i>I. scapularis</i>
Live sapling basal area	Cross-sectional area, including bark, at breast height (4.5 ft above the ground) of all live trees ≥ 1.0 inches to < 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	<i>D. variabilis</i>

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Live sapling below ground dry biomass	Oven-dry biomass of the belowground portion, including coarse roots with a root diameter ≥ 0.1 inch, of all live trees ≥ 1.0 inches to < 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>D. variabilis</i>
Live sapling above ground carbon	Carbon in the aboveground portion, excluding foliage, of all live trees ≥ 1.0 inches to < 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>D. variabilis</i>
Live sapling belowground carbon	Carbon of coarse roots > 0.1 inch in root diameter of all live trees ≥ 1.0 inches to < 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in pounds per acre.	<i>D. variabilis</i> and <i>I. scapularis</i>
Hardwood live tree basal area	Cross-sectional area, including bark, at the point of diameter measurement of all live Angiospermae trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	<i>I. scapularis</i>
Live hardwood tree density	Number of all live Angiospermae trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis.	<i>D. variabilis</i>
Softwood live tree basal area	Cross-sectional area, including bark, at the point of diameter measurement of all live Gymnospermae trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	<i>D. variabilis</i> and <i>I. scapularis</i>
Live softwood tree density	Number of all live Gymnospermae trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis.	<i>I. scapularis</i>
Hardwood live sapling basal area	Cross-sectional area, including bark, at breast height (4.5 ft above the ground) of all live Angiospermae trees ≥ 1.0 inches to < 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	None
Live hardwood sapling density	Number of all live Angiospermae trees ≥ 1.0 inches to < 5.0 inches d.b.h./d.r.c. in the condition class, on a per acre basis.	<i>I. scapularis</i>

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Tree species unevenness (basal area; primary)	Proportion of total live tree basal area for the most dominant tree species in the condition class, i.e., the species with the greatest proportion of live tree basal area.	<i>D. variabilis</i>
Tree species unevenness (basal area; primary)	Proportion of total live tree basal area for the most dominant tree species in the condition class, i.e., the species with the greatest proportion of live tree basal area.	<i>D. variabilis</i>
Tree species unevenness (basal area; secondary)	Proportion of total live tree basal area for the second most dominant tree species in the condition class, i.e., the species with the second greatest proportion of live tree basal area.	<i>D. variabilis</i>
Live seedling density	Number of all live trees <1.0 inch diameter and ≥ 6 inches tall (softwoods) or ≥ 12 inches tall (hardwoods) in the condition class, on a per acre basis.	<i>A. americanum</i>
Live hardwood seedling density	Number of all live Angiospermae trees <1.0 inch diameter and ≥ 12 inches tall in the condition class, on a per acre basis.	<i>A. americanum</i>
Tree species unevenness (density; primary)	Proportion of total live tree density for the most dominant tree species in the condition class, i.e., the species with the greatest proportion of live tree density.	<i>D. variabilis</i> and <i>I. scapularis</i>
Tree species unevenness (density; secondary)	Proportion of total live tree density for the second most dominant tree species in the condition class, i.e., the species with the second greatest proportion of live tree density.	None
Elevation	Distance the plot is located above (or below, if negative) sea level. Rounded to the nearest foot.	<i>D. variabilis</i>

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Proportion of the total live tree basal area	This variable comes from a tree species summary. Substituting $prop_baf_i = \left(\frac{ba_{ij}}{\sum_{i=1}^n ba_{ij}} \right)$ for x, this was where ba_{ij} is the total live tree basal area per acre of species i on plot j and n is the total number of species observed on plot j.	<i>D. variabilis</i>
Proportion of the total number of live trees per acre		<i>D. variabilis</i>
Live tree average actual height	Average length (height) in feet of all live trees ≥ 5.0 inches d.b.h./d.r.c., as measured from ground level to the highest remaining portion of the tree still present and attached to the bole, in the condition class	<i>A. americanum</i>
Species code	FIA tree species code	None
Physiographic class code	The general effect of landform, topographical position, and soil on moisture available to trees.	None
Site productivity class code	Code indicating the classification of forest land in terms of inherent capacity to grow crops of industrial wood based on the culmination of mean annual increment of fully stocked natural stands. Code 1: 225+ cubic feet/acre/year Code 2: 165-224 cubic feet/acre/year Code 3: 120-164 cubic feet/acre/year Code 4: 85-119 cubic feet/acre/year Code 5: 50-84 cubic feet/acre/year Code 6: 20-49 cubic feet/acre/yea. Code 7: 0-19 cubic feet/acre/year	None

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Total live tree basal area (square feet) per acre	Cross-sectional area, including bark, at the point of diameter measurement of all live trees ≥ 5.0 inches d.b.h./d.r.c. in the condition class. Expressed in square feet per acre.	<i>D. variabilis</i> and <i>I. scapularis</i>
Subplot percent slope	The predominant or average angle of the slope across the subplot, to the nearest 1 percent. Valid values are 0 through 155.	<i>I. scapularis</i>
Basal area per acre of live trees	Basal area in square feet per acre of all live trees ≥ 1.0 inch d.b.h./d.r.c. in the condition class.	<i>I. scapularis</i>
Forest type	A descriptor of the species with the plurality of stocking for all live trees in the condition class that are not overtopped. Primarily derived using a computer algorithm (Arner et al. 2003).	None
Horizontal distance to improved road	The straight-line distance from plot center to the nearest improved road, which is a road of any width that is maintained as evidenced by pavement, gravel, grading, ditching, and/or other improvements. Code 1: ≤ 100 ft Code 2: 101 ft to 300 ft Code 3: 301 ft to 500 ft Code 4: 501 ft to 1000 ft Code 5: 1001 ft to 0.5 mile Code 6: 0.5 mile to 1.0 mile Code 7: 1 mile to 3 miles Code 8: 3 miles to 5 miles Code 9: > 5 miles	None

Table 1.2 continued

Variable	Definition ^{aa}	Predictor
Water type on plot	Water body <1 acre in size or a stream <30 feet wide that has the greatest impact on the area within the sampled portions of any of the four subplots. Code 0: None – no water sources within the sampled condition class(es) Code 1: Permanent streams or ponds too small to qualify as noncensus water^d Code 2: Permanent water in the form of deep swamps, bogs, marshes without standing trees present and less than 1.0 acre in size, or with standing trees Code 3: Ditch/canal – human-made channels used as a means of moving water, e.g., for irrigation or drainage, which are too small to qualify as noncensus water Code 4: Temporary streams Code 5: Flood zones – evidence of flooding when bodies of water exceed their natural banks	None
Stand size	A classification of the predominant (based on stocking) diameter class of live trees^e within the condition. Assigned using an algorithm (Arner et al. 2003). Code 1 (large diameter): Stands with an all-live stocking value of at least 10 (base 100); with more than 50 percent of the stocking in medium and large diameter trees; and with the stocking of large diameter trees equal to or greater than the stocking of medium diameter trees. Code 2 (medium diameter): Stands with an all-live stocking value of at least 10 (base 100); with more than 50 percent of the stocking in medium and large diameter trees; and with the stocking of large diameter trees less than the stocking of medium diameter trees. Code 3 (small diameter): Stands with an all-live stocking value of at least 10 (base 100) on which at least 50 percent of the stocking is in small diameter trees.	None

^a Definitions are presented in the U.S. Customary units used by the Forest Inventory and Analysis Program. 1 inch = 2.54 cm. 1 foot = 0.3048 m. 1 mile = 1.609 km. 1 acre = 0.40 ha. 1 pound = 0.453 kg.

^b To qualify as a standing dead tree, the dead tree must be ≥ 1.0 inch diameter, have a bole that has an unbroken actual length ≥ 4.5 feet, and lean < 45 degrees from vertical as measured from the base of the tree to 4.5 feet.

^c For timber species, diameter is measured at breast height (d.b.h.), which is usually 4.5 feet above the ground line on the uphill side of the tree. For woodland species, which are often multi-stemmed, diameter is measured at the ground line or at the stem root collar (d.r.c.), whichever is higher.

^d Noncensus water is defined as lakes, reservoirs, ponds, and similar bodies of water 1.0 acre to 4.5 acres in size, and rivers, streams, canals, etc., 30.0 feet to 200 feet wide. Census water is defined as lakes, reservoirs, ponds, and similar bodies of water 4.5 acres in size and larger, and rivers, streams, canals, etc., more than 200 feet wide.

^e Large diameter trees are ≥ 11.0 inches diameter for hardwoods and ≥ 9.0 inches diameter for softwoods. Medium diameter trees are ≥ 5.0 inches diameter and smaller than large diameter trees. Small diameter trees are < 5.0 inches diameter.

Table 1.3. Model results for *Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis* separately collected on forest inventory crews in the southeastern United States for the years 2017-2021.

Model	Variable	Estimate	Standard error	Degrees of freedom	T value	F value	P value
<i>Amblyomma americanum</i>	Standing dead tree aboveground dry biomass	-1.3565	0.4531	1, 183	-2.99	8.96	0.0031
	Carbon in litter material	-1.1479	0.5812	1, 183	-1.98	3.90	0.0498
Model	Variable	Estimate	Standard error	Degrees of freedom	Wald Chi-square		P value
<i>Dermacentor variabilis</i>	Elevation	0.0034	0.0016	1	4.3		0.038
	Seedling species unevenness	-2.2719	0.9891	1	5.28		0.0216
<i>Ixodes scapularis</i>	Seedling species unevenness	1.7515	0.8105	1	4.67		0.0307
	Carbon in down dead woody material	3.6489	0.6774	1	29.02		< 0.0001

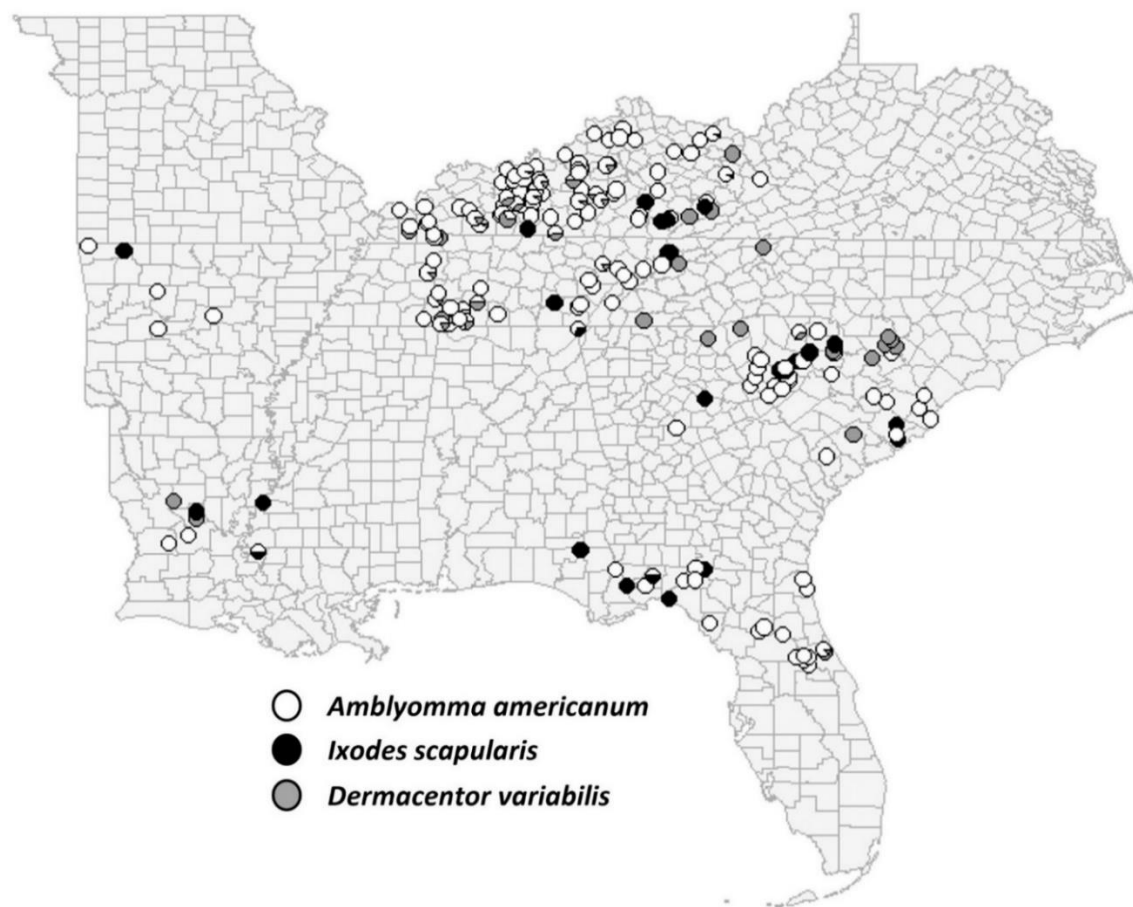


Figure 1.1. Approximate location of sites where *Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis* were collected by FIA (Forestry Inventory and Analysis) foresters in the southeastern United States 2017-2021.

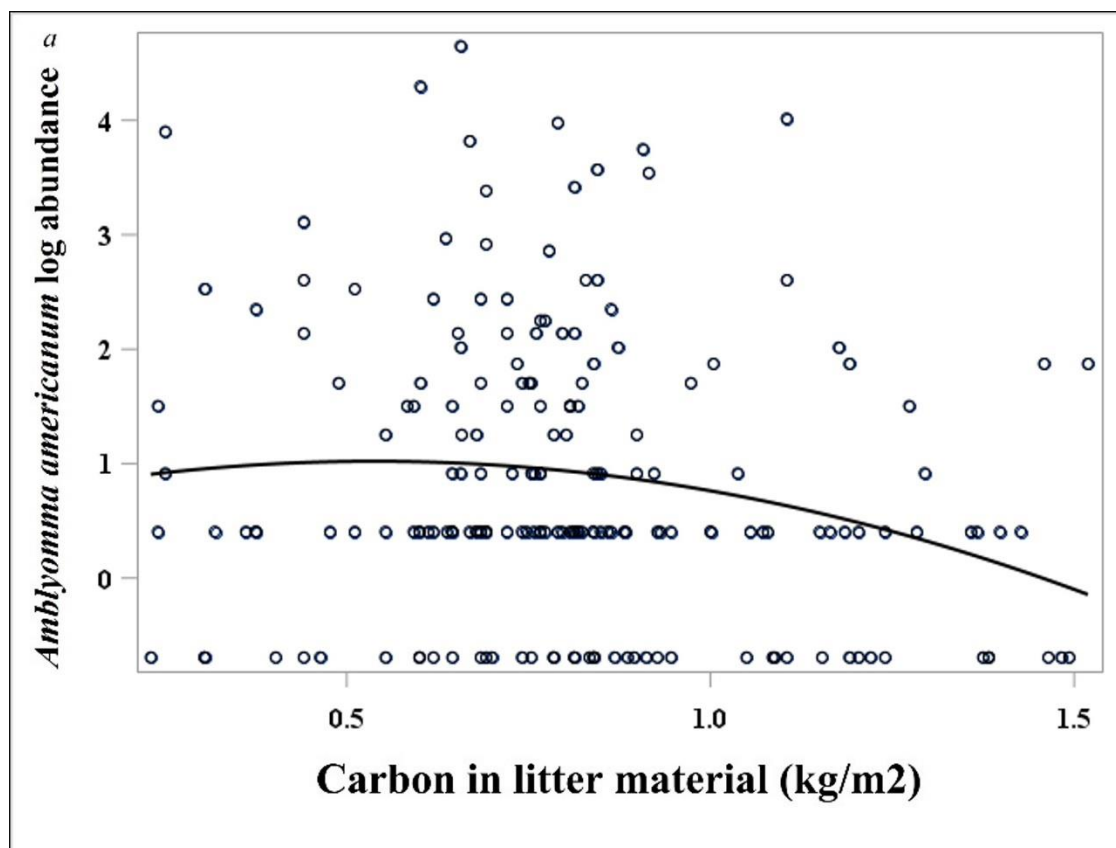


Figure 1.2. Relationship between carbon in litter material (kg/m²) associated with the abundance of *Amblyomma americanum* on FIA (Forest Inventory and Analysis) foresters in the southeastern United States (US) (2017-2021).

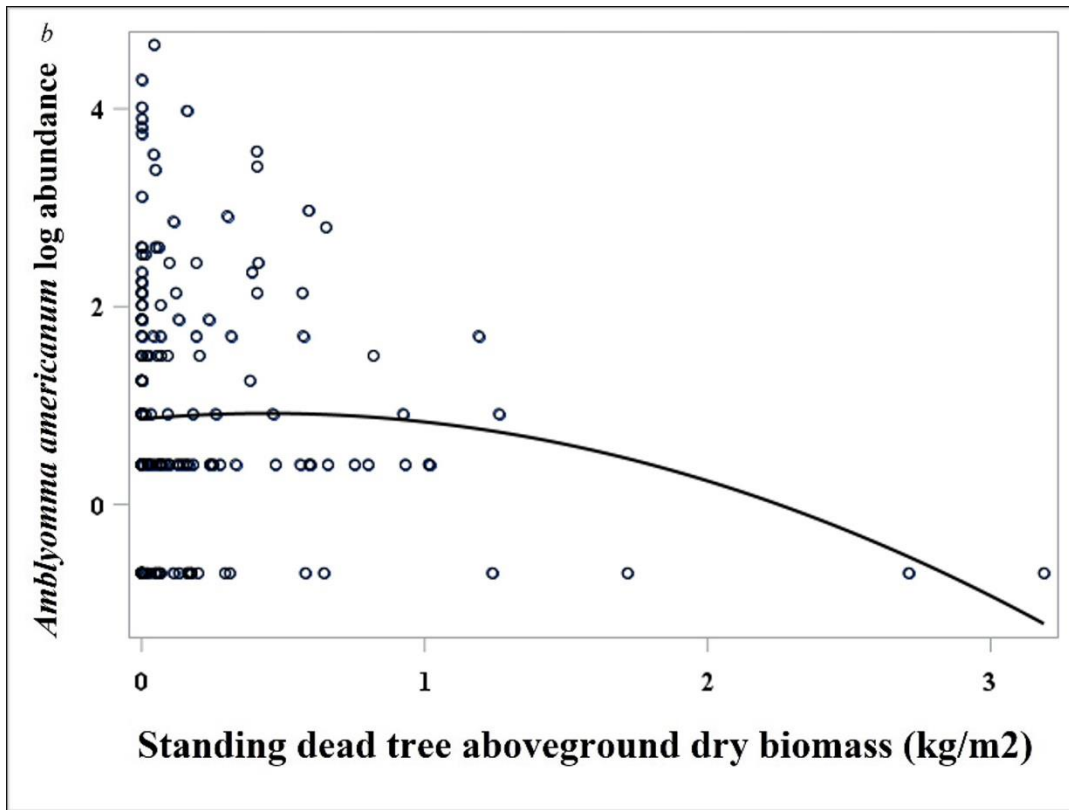


Figure 1.3. Relationship between standing dead tree aboveground dry biomass (kg/m2) associated with the abundance of *Amblyomma americanum* on FIA (Forest Inventory and Analysis) foresters in the southeastern United States (US) (2017-2021).

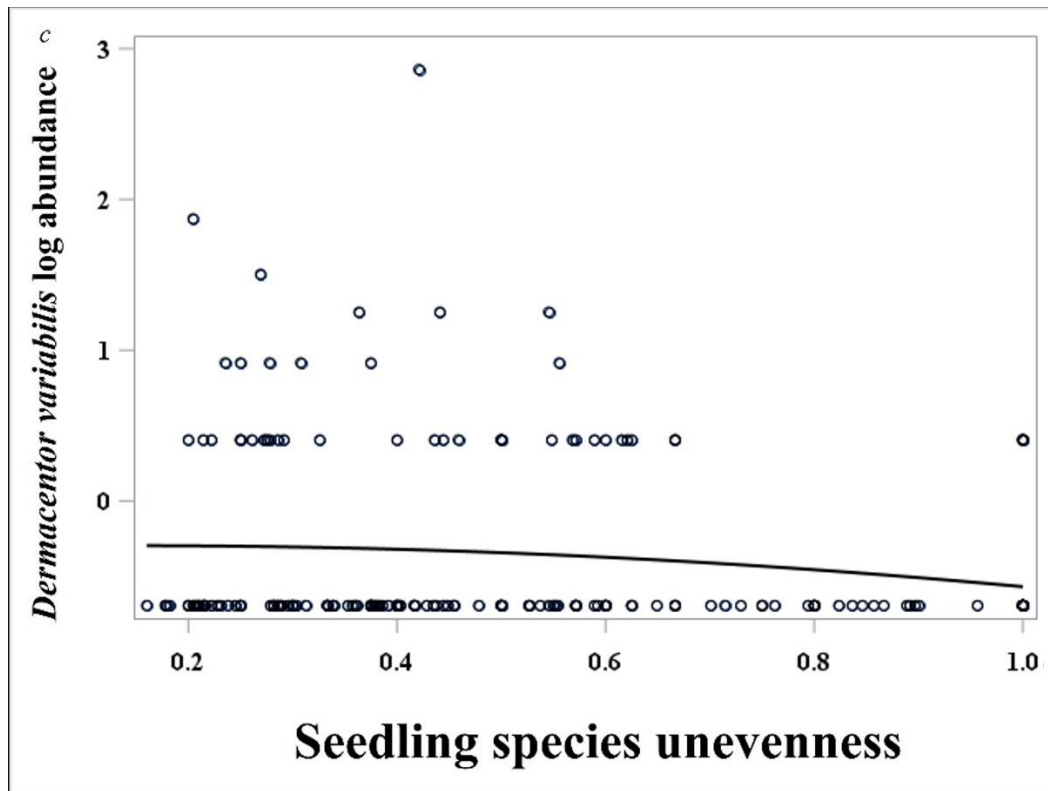


Figure 1.4. Relationship between seedling species unevenness associated with the abundance of *Dermacentor variabilis* on FIA (Forest Inventory and Analysis) foresters in the southeastern United States (US) (2017-2021).

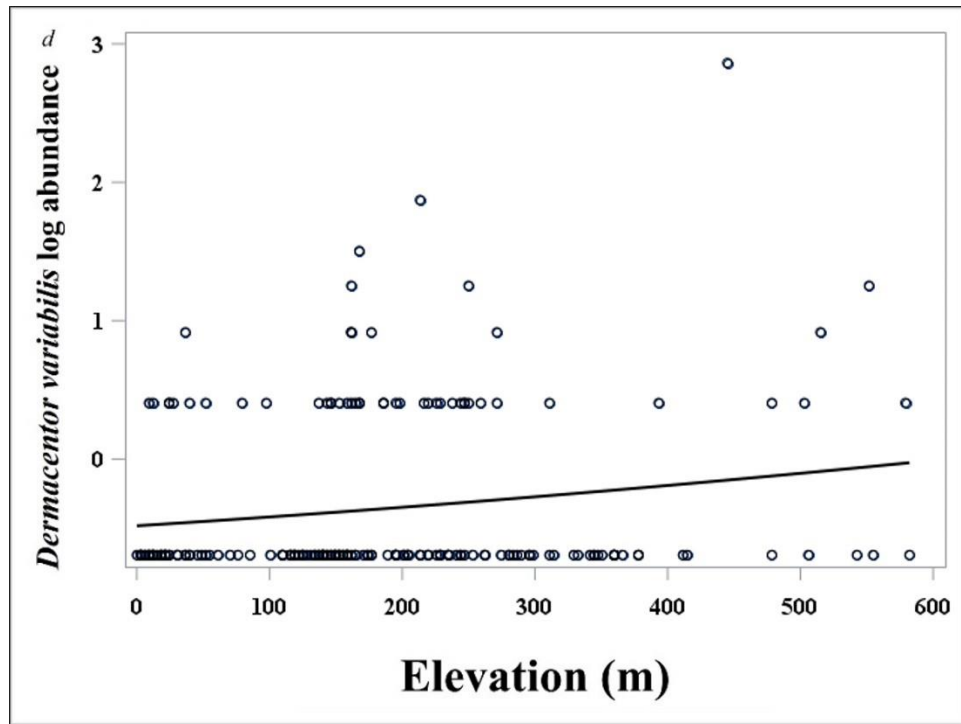


Figure 1.5. Relationship between elevation (m) associated with the abundance of *Dermacentor variabilis* on FIA (Forest Inventory and Analysis) foresters in the southeastern United States (US) (2017-2021).

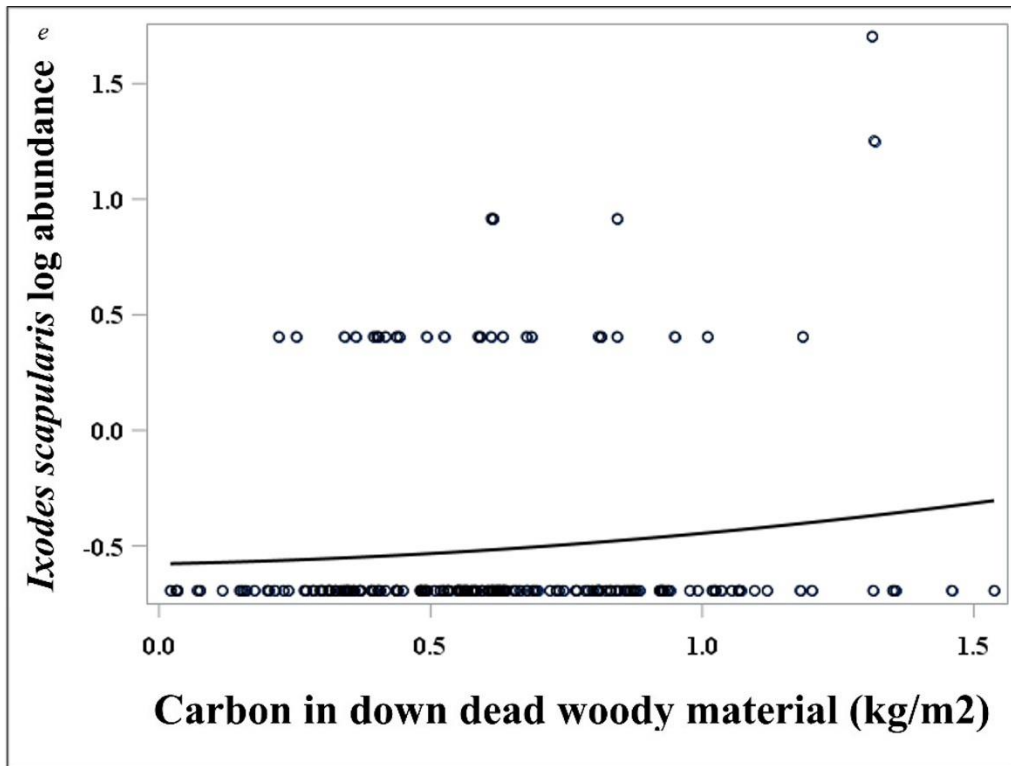


Figure 1.6. Relationship between carbon in down dead woody material (kg/m²) associated with the abundance of *Ixodes scapularis* on FIA (Forest Inventory and Analysis) foresters in the southeastern United States (US) (2017-2021).

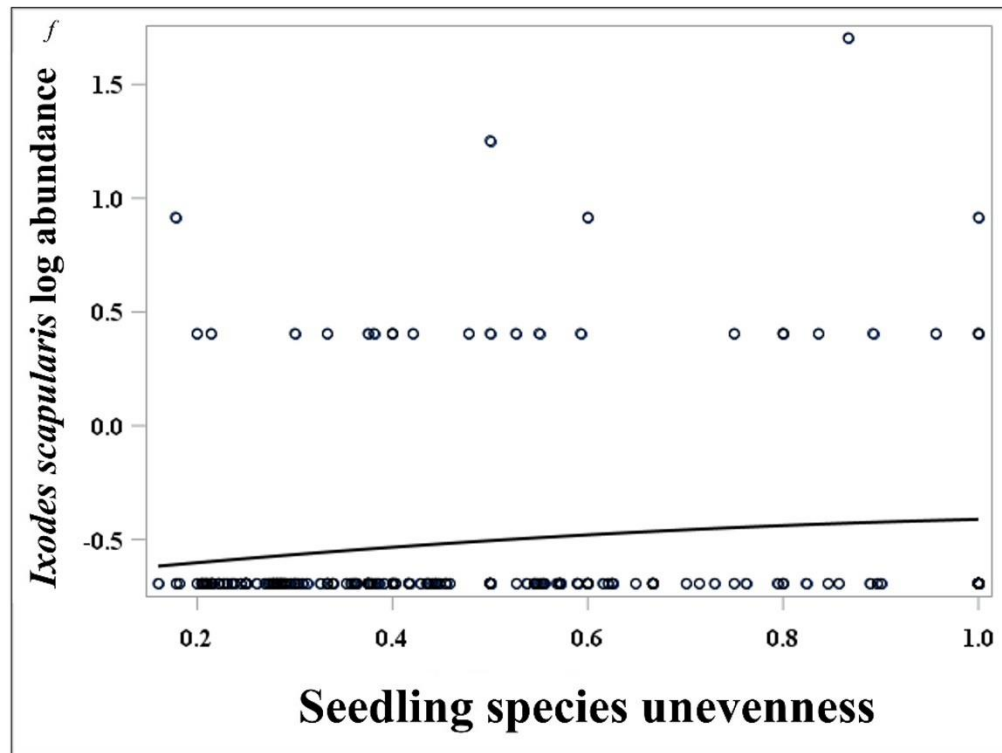


Figure 1.7. Relationship between seedling species unevenness associated with the abundance of *Ixodes scapularis* on FIA (Forest Inventory and Analysis) foresters in the southeastern United States (US) (2017-2021).

**CHAPTER II. HUMAN RISK TO ENCOUNTER TICK SPECIES IN THE
SOUTHEASTERN UNITED STATES ESTIMATED WITH SPATIAL DISTRIBUTION
MODELING**

Abstract

The expanding geographic distribution and increased populations of ticks has resulted in an upsurge of human-tick encounters in the United States (US), leading to an increase in tickborne disease reporting. Limited knowledge of the broadscale spatial range of tick species is heightened by a rapidly changing environment. Therefore, we partnered with the Forest Inventory and Analysis (FIA) program of the Forest Service, U.S. Department of Agriculture and used passive tick surveillance to better understand spatiotemporal variables associated with foresters encountering three tick species (*Amblyomma americanum* L., *Dermacentor variabilis* Say, and *Ixodes scapularis* L.) in the southeastern US. Eight years (2014-2021) of tick encounter data were used to fit environmental niche and generalized linear models to predict where and when ticks are likely to be encountered. Our results indicate temporal and environmental partitioning of the three species in the southeastern US. *Ixodes scapularis* were more likely to be encountered in the autumn and winter seasons and associated at sites with soil organic matter, vegetation indices, evapotranspiration, temperature, and gross primary productivity. By contrast, *A. americanum* and *D. variabilis* were more likely to be encountered in spring and summer seasons at sites with elevation, landcover, temperature, dead belowground biomass, vapor pressure, and precipitation. Regions in the southeast least suitable for encountering ticks included the Blue Ridge, Mississippi Alluvial Plain, and the Southern Florida Coastal Plain, whereas suitable regions included the Interior Plateau, Central Appalachians, Ozark Highlands, Boston Mountains, and the Ouachita Mountains. Resulting predictive models were supported with field work at predicted low-risk sites and by comparing them to known county-level databases. Spatial and temporal patterns of different tick species can inform foresters and outdoorsmen on tick

avoidance measures, reduce tick populations by managing suitable tick habitats, and monitoring areas with unsuitable tick habitat for potential missed encounters.

Introduction

The geographic distribution of human-tick encounters for medically important tick species is rapidly increasing in the United States (US) (Jordan and Egizi 2019; Molaei et al., 2022). Range expansion for commonly encountered tick species (*Amblyomma americanum* L., *Dermacentor variabilis* Say, and *Ixodes scapularis* L.) has resulted in an upsurge of tick-borne disease cases in the last two decades including Spotted Fever Group Rickettsiosis, Anaplasmosis, Ehrlichiosis, Alpha-gal syndrome, Powassan virus, and Lyme disease (Hamer et al. 2010; Dahlgren et al. 2011; Scott Dahlgren et al. 2016; Mitchell et al. 2020; Álvarez-López et al. 2021).

Current distribution range maps for these tick species are commonly based on known occurrences at the continental or county level which is important for surveillance and management of ticks for regional and county health departments (Springer et al. 2014; Lehane et al. 2020). These range maps or distribution maps are often based on administrative landmarks (county boundaries) rather than tick and host biological patterns because these maps encompass large spatial areas with imprecise environmental factors for the species distribution (Collins et al. 2017). Environmental niche models (ENM) estimate distribution maps based on interactions of the species with climatic and environmental variables in time and space (Peterson 2006). Recent ENMs for *A. americanum* predicted this species to inhabit regions in the northern, southeastern, and western regions of the US and Mexico, as well as in the Midwest from eastern Texas to Kansas, Oklahoma, and Missouri (Raghavan et al. 2019; Ma et al. 2021; Rochlin et al. 2023). Similarly, the potential distribution for *D. variabilis* was predicted to occur in parts of Canada and Mexico, as well as northern, southern, and midwestern regions of the US, including parts of California (Minigan et al. 2018). Predictions for *I. scapularis* were distributed throughout

regions in the eastern and midwestern US (Peterson and Raghavan 2017). Understanding the effects that environmental variables have on each tick species' distribution is vital because of the recent and predicted impacts of climate and land-use change on their population dynamics (Sagurova et al. 2019; Boorgula et al. 2020; Ginsberg et al. 2020; Tran et al. 2021).

Ixodid ticks spend the majority of their lives in the environment relative to time spent on hosts, thus it is also important to understand how soil properties affect tick populations (Estrada-Peña 2008). For example, soil properties such as percent litter coverage and soil moisture are associated with *A. americanum* abundance (Semtner et al. 1971 and Raghavan et al. 2016). Additionally, land management decisions (e.g., burning) were associated with decreased immature *I. scapularis* (Mather et al. 1993) and *A. americanum* populations (Gleim et al. 2014; Gallagher et al. 2021). Specifically, Gallagher et al. (2021) reported that prescribed burns reduce tick abundance by heat exposure or decreasing soil moisture. Climatic variables (e.g., temperature, vapor pressure, and precipitation) have been associated with *A. americanum*, *D. variabilis*, and *I. scapularis* (e.g., Diuk-Wasser et al. 2012, Bacon et al. 2022). Landscape variables associated with forests (e.g., land cover, primary productivity) are important for host populations and likely regulate infesting tick populations (e.g., Ferrell and Brinkerhoff 2018, Titcomb et al. 2017). For example, the normalized difference vegetation index (NDVI), a measure of greenness, has been associated with the abundance of *A. americanum* (Spare et al. 2021). Knowing whether an environmental variable is associated with tick presence can be an important surveillance tool for monitoring and a potential management tool for controlling the species off its host.

As tick populations are expanding in a rapidly changing environment, we collaborated with the Southern Research Station's Forest Inventory and Analysis (FIA) Program of the Forest

Service, U.S. Department of Agriculture (USDA) to evaluate the environmental conditions that could increase likelihood of encountering ticks. We chose to work with FIA because foresters are known to collect data at a variety of sites with varying environmental conditions and their forest crews are consistently exposed to ticks in the environment. In other words, crews were at a variety of sites collecting environmental data and encountering ticks. Specifically, foresters collected encountered ticks while working on sites around the southeastern US. We used eight years (2014-2021) of tick encounter data to create environmental niche and generalized linear models to understand where and when ticks are likely to be encountered. Here we test the hypothesis that temporal, climatic, physiographic, and soil variables are important predictors of the presence of *A. americanum*, *D. variabilis*, and *I. scapularis* in the southeastern U.S.

Materials and methods

Tick encounter data

Ticks were collected from forest crews employed by FIA. Passive tick collections were opportunistic and occurred when crews worked at plots in the southeastern U.S. between 2014 and 2021. Crew members placed encountered ticks into a single vial containing 80% ethanol and labeled it with the date, forestry crew identification number, and GPS coordinates where the crew was working (Trout Fryxell and Vogt 2019). Encountered ticks were sent to the University of Tennessee, Knoxville Medical and Veterinary Entomology laboratory where they were identified to species and life stage using taxonomic keys (Yunker, et al., 1986; Durden, 1996; Keirans and Durden 1998; Egizi et al. 2019).

Statistical analysis

Generalized linear models were created from (PROC GLIMMIX) in Statistical Analysis Software (SAS, ver. 9.4, Cary, North Carolina) with two-tailed hypotheses ($\alpha = 0.05$) to analyze

how season affects the presence of each tick species. The date of tick collection was transformed into categorical variables (winter, spring, summer, and autumn) based on solstice or equinox. Season was used to determine the probability of detecting tick presence for each species separately in the binary logit models. Odds ratios and their 95% confidence intervals were calculated for independent variables that were successful at predicting the presence of each tick species. Relative tick encounters, similar to seasonality, were graphed by summing tick abundance for each month per years collected and transformed as a percentage. **(Figure 2.1).**

Environmental niche modeling of potential suitability for ticks

FIA crews used hand-held GPS receivers to record the latitude and longitude of each FIA plot. The coordinates used for niche modeling are within 1.6 km (1 mile) of the actual encounter sites because (1) many of the plots are located on private lands and these exact locations are kept confidential (<https://www.fia.fs.usda.gov/tools-data/spatial/Policy/default.asp>) and (2) ticks may have been encountered traveling to or from plots or while working at the plot. We coarsened the spatial resolution of the model to account for differences between plots and pseudopigraphic locations. We used these approximate locations (maximum uncertainty of 1.6 km) as tick presence data to train environmental niche models from 258 sites where *A. americanum* were encountered, 90 sites where *D. variabilis* were encountered, and 36 sites where *I. scapularis* were encountered. We evaluated 20 environmental rasters (gridded data) as predictor variables in niche models acquired from EarthData (<https://earthdata.nasa.gov/>) or EarthExplorer (<http://earthexplorer.usgs.gov>) (**Table 2.1**). Each encounter was matched temporally to rasters with the same or nearest date available. We averaged rasters from every date each tick was collected from human hosts to encompass all environmental conditions when tick species were active on human hosts (FIA crews). To compensate for potential spatial sampling errors of ticks

we aggregated (coarsened) the original spatial resolution of rasters from 500 meters to 4.8 km. All raster processing steps were completed in ESRI ArcMap 10.7. ENMs were fitted using presence data and environmental variables in the maximum entropy algorithm Maxent (Version 3.4.0) that estimates species' potential geographic distributions (Phillips et al. 2006). We removed duplicate presence records and ran independent models for each tick species with cross-validation and five replicates, each based on a maximum 5000 iterations. A 10% training presence threshold (allowing 10% of training presence data to be predicted absent) was applied to convert the model outputs of continuous probability of suitability to binary maps of suitable-unsuitable values. Because Maxent is a stable machine-learning platform for controlling correlated variables, environmental raster images were not assessed for autocorrelation beforehand but left to the algorithm to discern (Elith et al. 2011). Due to lower sample size for *I. scapularis* only the linear, quadratic, and product features were used in Maxent. Additionally, categorical variables (land cover) were removed from the environmental niche model for *I. scapularis* because the variable contribution was not balanced. For *A. americanum* and *D. variabilis*, an addition of the hinge feature was used to build a piecewise linear exponent because there were more encounters available for model training (Phillips and Dudík 2008).

To quantify model performance, we used area under the curve (AUC) of the receiver operating characteristics; $AUC \geq 0.9$ indicate excellent models, 0.8-0.9 good, 0.7-0.8 fair, 0.6-0.7 poor, and < 0.6 failed models (Safari et al. 2016). We observed the omission error for each model at a 10% training threshold. In addition, we overlaid U.S. ecoregions boundaries shapefile to evaluate risk based on regional similarities or differences (e.g., geology, soils, climate, vegetation) of distinct geographic areas (Omernik 1987; Omernik 1995; CEC 1997; McMahon et al. 2001; Omernik 2004; Omernik and Griffith 2014).

Independent model testing

To test each species ENM in addition to the internal cross-validation of Maxent algorithm, we used targeted field work and an independent dataset of previously reported tick records for each tick species by county.

We selected three USDA Southern Research Station Experimental Research Forests near the University of Tennessee, Knoxville to confirm the presence or absence of ticks in this area in 2021. The three experimental forests included Coweeta, Blue Valley, and Bent Creek in western North Carolina and northern Georgia in southern Appalachian Mountains. Each collection site in western North Carolina is representative of forests previously disturbed by logging and mining (McNab 1990; Adams et al., 2004; Swank and Crossley 2012). The Coweeta Hydrologic Laboratory has an area of 1600 ha and is dominated by mixed-oak forests with understories of noncontinuous mountain laurel and rhododendron (Clinton 2003). Soils in this region are comprised of Inceptosols and Ultisols (Adams et al., 2004). The Blue Valley experimental forest has an area of 526 ha dominated by eastern white pine and stand of oak-hickory in the Blue Ridge Mountains (Adams et al., 2004). This area contains acidic, infertile, well drained soils with vegetation primarily consisting of buckberry shrubs (Adams et al., 2004). Bent Creek experimental station is comprised of 2,550-ha of upland hardwood forests primarily dominated by oak-hickory stands and understory vegetation of rhododendron (Adams et al., 2004). The Asheville Basin region contains soils with low organic matter contents, clay layers, and reduced fertility whereas the Mountain Highland are Inceptisols and acidic (Adams et al., 2004). We provided vials to crews to collect encountered ticks, but we also conducted active surveillance in these forests. We set dry ice traps for overnight monthly trapping (March-June 2021) at five

different sites within each forest (Mays et al. 2015). Collected ticks were stored in ethanol filled vials, then identified to species and sex as described above.

Additionally, we compared county level records with our predicted distributions. County level records for *I. scapularis*, *A. americanum*, and *D. variabilis* were downloaded on May 14, 2022, from the Centers for Disease Control (<https://www.cdc.gov/ticks/surveillance/TickSurveillanceData.html>). True positives, used to calculate sensitivity, were identified as counties with available tick records and predicted suitable by the niche models. Here, we considered the CDC datasets to be the standard, so false positive counties were those predicted suitable but lacking tick presences, indicating model commission error, and false negative counties were those with known tick presences but predicted unsuitable by the niche models, representing omission error. Sensitivity tests were calculated in SAS using PROC FREQ. County-level validation of models calibrated with environmental variables with 4.8 km resolution and GPS records of ticks represents a compromise between the need to validate the models and the lack of higher resolution presence data readily available for each species.

Results

A total of 1,901 ticks were submitted during the study period from 384 sites: 1720 (90.5%) *A. americanum* from 258 sites, 136 (7.2%) *D. variabilis* from 90 sites, and 45 (2.3%) *I. scapularis* from 36 sites. Of the *A. americanum* records, 669 were adults, 851 were nymphs, and 200 were larvae. There were 135 *D. variabilis* adults, and one *D. variabilis* nymph. Finally, there were 45 *I. scapularis* adults. Ticks were primarily collected and submitted by crews in Kentucky, South Carolina, and Tennessee (**Table 2.2**).

Statistical analysis

Season was significantly associated with presence for all three species; *A. americanum* ($F_{3, 349} = 13.69$; $P < 0.0001$), *D. variabilis* ($F_{3, 349} = 6.07$; $P = 0.0005$), and *I. scapularis* ($F_{3, 349} = 22.14$; $P < 0.0001$). The likelihood of *A. americanum* being present was highest in spring compared to any other season, and higher in summer compared to autumn and winter.

Dermacentor variabilis encounters were greater in summer months compared to spring and winter months. Finally, encounters of adult *I. scapularis* were more likely to occur in autumn and winter months compared to spring and summer months. A detailed breakdown of each species monthly percent encounter throughout the eight-year study period is shown in (**Figure 2.1**).

Environmental niche modeling of potential suitability for ticks

Three of the five replicate niche models for *A. americanum* had AUC values greater than 0.8 (**Table 2.3**). We averaged the raster outputs (probability of suitability) of the three Maxent models to create a single map of potential suitability for *A. americanum* (**Figure 2.2**). Model 2 had the highest AUC and results indicated that elevation, landcover, minimum temperature, and vapor pressure were best at predicting habitat suitability (**Table 2.3**). In models one and three, the same three contributing variables predicted environmental suitability except maximum temperature had a higher contribution than minimum temperature in these two models. Resulting models indicated potential suitable environments where *A. americanum* are likely to be encountered; thus, crews working in forests throughout Tennessee, Kentucky, Northern Florida, Arkansas, North Carolina, and eastern Virginia have an increased likelihood of encountering *A. americanum* (**Figure 2.2**).

Similar to *A. americanum*, three *D. variabilis* models had AUC values greater than 0.8 (Table 2.2) so we averaged the outputs of the three models to generate the predicted suitability

map for *D. variabilis* (**Figure 2.3**). High contribution variables to all three models included elevation, landcover, and maximum temperature. Differences between models were represented by precipitation and vapor pressure in the first model, vapor pressure in the second model, and dead belowground biomass and precipitation in the third model (**Table 2.2**). Areas of potential suitability and thus concern for crews encountering *D. variabilis* included regions throughout Tennessee and Kentucky, northern North Carolina, Alabama, Arkansas, and eastern Virginia (**Figure 2.3**).

Only one model for *I. scapularis* had an AUC value greater than 0.8 (**Table 2.2**). The high contribution environmental variables were evapotranspiration, gross primary productivity, maximum temperature, vegetation indices, and soil organic matter (**Table 2.3**). The area of potential suitability for *I. scapularis* included all ecoregions in the southeastern US; however, there was a reduced risk to encounter *I. scapularis* ticks in southern Florida, eastern Tennessee and Mississippi, and western Arkansas (**Figure 2.4**).

Independent model testing

We tested each resulting niche model with data from passive and active surveillance at three experimental research forests and by comparing predicted suitability maps with published or available county-level tick records. Passive and active tick collections at these targeted forests resulted in a total of five *D. variabilis* provided by an individual camping in the area, but an exact location of encounter was not recorded. There were no ticks collected in any of the 15 traps placed in the three experimental research forests. The CDC tick surveillance datasets indicated *D. variabilis* was reported (less than five recovered in the county and only one life stage), but there were no county records for *A. americanum* and *I. scapularis* in Macon County, North Carolina where The Coweeta and Blue Valley Experimental Forests are located. It was also

documented that *D. variabilis* was established (more than five found in the county or more than one life stage), but there were no county records for *A. americanum* and *I. scapularis* in Buncombe County, North Carolina where The Bent Creek Experimental Forest is located. Our map models, for all three tick species, suggested suitable habitats were present in regions scattered throughout Macon County; however, suitable habitats were found scattered throughout Buncombe County for *D. variabilis* and *I. scapularis*, but not for *A. americanum*. Our models correctly predicted sites where dry ice traps were located to be environmentally unsuitable for all three tick species.

Overall, the CDC database identified 390 *I. scapularis*-positive counties and 674 no county records, 718 *D. variabilis*-positive counties and 346 no county records, and 561 *A. americanum*-positive counties and 503 no county records. When we compared our resulting predictive maps at the county level to previously recorded data, sensitivity values and associated confidence intervals for *A. americanum* were 0.9465 (0.9279-0.9651), for *D. variabilis* were 0.8175 (0.7893-0.8458), and for *I. scapularis* were 0.9956 (0.9905-1.00). This indicates that the models predicted suitable habitats (~encounter areas) similar to those reported by others. There was no observed difference between county status (established, reported, or new county record) and the number of *A. americanum* or *D. variabilis* submitted from foresters. Counties noted as established in the CDC database for *I. scapularis* were found to have multiple ticks collected compared to reported or new county records.

Discussion

Three-host ticks reside in the environment for the majority of their two- to three- year life cycle, leaving them susceptible to abiotic and biotic factors (Sonenshine and Roe 1993). Consequently, ecological niches often differ in suitability for each species to exist spatially and

temporally in a rapidly changing environment (Cuervo et al. 2021). In this study, we used ecological niche and generalized linear models to describe geographic regions (where) and temporal periods (when) humans are at risk for tick encounters in the southeastern US. We identified environmental variables associated with the presence of three common human-biting tick species, which are important indicators for tick encounters and could be targeted for management. The only common environmental variable significantly contributing to the presence of all three species was maximum temperature, which supports the expectation that where a tick occurs will change in warming climates (Ogden et al. 2004, 2005, Estrada-Peña et al. 2012). Additionally, long-term passive surveillance is an important tool for obtaining widespread occurrence records which can be used to monitor tick species geographic distribution shifts and public health risk (Schillberg et al. 2018, Kopsco et al. 2020). This dataset highlights the potential power of passive tick surveillance using trained scientists from federal agencies that generate accurate distributional information.

Amblyomma americanum

According to many published papers and citizen/community scientist reports, the most abundant and encountered tick in the southeastern US is *A. americanum* and the species is most likely to be encountered in the spring (Merten 2000; Petry et al. 2010). The likelihood of encountering *A. americanum* at a site was determined by four environmental variables (elevation, landcover, maximum temperature or minimum temperature, and vapor pressure). Previously, others reported variables such as precipitation, vapor pressure, diurnal range, and temperature as important contributors to predicting *A. americanum* suitability and potential range (Sagurova et al. 2019; Raghavan et al. 2019; Rochlin et al. 2022). Our environmental niche model highlighted regions at higher risk of encountering *A. americanum* that align with the Interior Plateau, Interior

River Valleys and Hills, Ozark Highlands, Boston Mountains, Arkansas Valley, Ouachita Mountains, northern region of the Southeastern Plains, northeastern Piedmont, Northern Southern Coastal Plain, Southwestern Appalachians, and western regions of the Central Appalachian ecoregions. These ecoregions suitable for *A. americanum* contain upland hardwood forests, grassy plateaus, and neutral elevations in between the Appalachian Mountains and regions in the Southern Plains (Sayler et al. 2016). A similar pattern to our results was observed based on ticks collected from wildlife hosts in Florida where *A. americanum* was more likely to be present in the northern region of the Southern Coastal Plain (Hertz et al. 2017).

Importantly, our results also predicted when and where *A. americanum* may not be encountered: fall and winter months and locations typically thought to have standing water. Less suitable areas comprised of wetlands and bottomland hardwoods (e.g., Mississippi Alluvial plain, Southern Florida Coastal Plain), in agreement with previous reports (Faulkner et al. 2011) (Rochlin et al. 2022). These areas have flat plains with wet soils, marshlands, and swampy land cover (Kambly and Moreland, 2009). Ticks were less likely to be found in the Southeastern Plains, a region that has historically gone through various land use changes such as plantation forestry and agriculture; these land management decisions could have impacts on tick abundance (Napton et al. 2010; Kerr et al. 2022). The Southeastern Plains in Tennessee are known to be occupied by *A. americanum* and their associated tickborne diseases such as human ehrlichiosis and spotted fever group Rickettsioses (Cohen et al. 2010, Moncayo et al. 2010). Similar to our ENM, *A. americanum* populations are less likely to occur in regions with high elevations such as in the Smoky Mountains (Sagurova et al. 2019). Importantly, because *A. americanum* was associated with both elevation and temperature variables, it is possible to investigate these relationships in more detail as higher elevations begin to warm. Future models could predict and

explain that, as areas warm, more tick encounters will occur at higher elevations where this species was previously absent (Sagurova et al. 2019).

Dermacentor variabilis

Foresters were frequently encountering *D. variabilis* adults in summer months, as previously reported (Burg 2001). Six environmental variables contributed to the environmental niche models and consistent variables included elevation and landcover; the contribution of the remaining four variables (maximum temperature, precipitation, vapor pressure, and dead belowground biomass) varied in each model. Similarly, previous research indicated precipitation, temperature, and meters above sea level associated with *D. variabilis* (Minigan et al. 2018). Ticks were most likely to be present throughout Kentucky and Tennessee, but the predicted suitability was fragmented in northern Arkansas, North Carolina, and Virginia. Like our *A. americanum* model, *D. variabilis* suitable areas included ecoregions with upland hardwood forests and fewer extreme elevation changes (e.g., Ozark Highlands, Boston Mountains, Arkansas Valley, Interior Plateau, Interior River Valleys and Hills, Southwestern Appalachians, Piedmont, Mississippi Valley Loess Plain, Ridge and Valley, and the Central Appalachians) (Sayler et al. 2016).

Prior to the range expansion of *A. americanum*, *D. variabilis* was the most commonly encountered tick (Lingren et al., 2005; De Jesus et al. 2019; Rochlin et al. 2022; Thompson et al. 2022). Areas where *D. variabilis* were least likely to be encountered included more southern areas of the study region such as the Southern Coastal Plain and Southeastern Plains, typically characterized as subtropical, low-elevation, sandy, and areas with marshlands in Florida (Sayler et al. 2016). Historically *D. variabilis* were reported throughout the Midwest and Southeast but not regions in the upper Northeast and Southwest (Bishopp and Trembley 1945). Recently, *D.*

variabilis encounters were predicted by warm temperatures and low precipitation, thus climate change could improve environmental conditions for this species, increasing their range into the upper Northeast US (Minigan et al. 2018).

The Southeastern Plains region is characterized by drought-prone and nutrient-poor soils, with most land use practices reverting to industrial forests, resulting in extreme clear cutting (Brown et al. 2005). These conditions could lead to unsuitable environmental conditions for this tick species due to its association with precipitation, landcover, and vapor pressure. Of interest is the potential role that dead belowground biomass has on *D. variabilis* because this variable can be manipulated with land and forest management decisions. Intense forest harvesting methods could increase dead belowground biomass due to remaining root structures underground (Butnor et al. 2001). Immature *D. variabilis* often quest below leaf litter (Conlon and Rockett 1982) making them difficult to collect with active surveillance and easier to collect with passive surveillance, from small sized hosts (Burg 2001; Petry et al. 2010; Butler et al. 2020b).

Ixodes scapularis

Historical encounters of *I. scapularis* in the Southeast are receiving more attention as recent reports are confirming more *I. scapularis* in the region (Arsnoe et al. 2019). This study confirms these more recent publications, with adult *I. scapularis* being encountered in the fall and winter and nearly the entire region environmentally suitable (Peterson and Raghavan 2017; Eisen and Eisen 2018; Lockwood et al. 2018). Although adult *I. scapularis* were encountered less frequently than *D. variabilis* and *A. americanum*, their predicted geographic range was larger. Specifically, *I. scapularis* was predicted to be present in all southeastern states and all ecoregions except the floodplains around the Mississippi River (Mississippi Alluvial Plains and Mississippi Valley Loess Plains). Environmental variables that contributed to this ENM included

evapotranspiration, gross primary productivity, maximum temperature, vegetation indices, and soil organic matter. Interestingly, the antagonistic effects of transpiration and relative humidity indicate that *I. scapularis* could withstand questing when evapotranspiration is high because it is buffered by drastic changes in relative humidity in forests (Cascone et al. 2019). Vegetation indices contributing to adult *I. scapularis* populations when they quest in colder months is likely associated with plant dormancy traits (Sundstrom et al. 2021). Previous research found the variables vapor pressure, elevation, forest cover, isothermality, and temperature associated with their models (Hahn et al. 2016, Peterson and Raghavan 2017). Similar to our *I. scapularis* model, ticks were less likely to be found at high elevations in the Appalachian Mountains or the Blue Ridge, or southern Florida or the Southern Florida Coastal Plain, and the Louisiana Coast or the Mississippi Alluvial Plain ecoregions (Sayler et al. 2016; Peterson and Raghavan 2017). In these ecoregions it could be difficult for *I. scapularis* to survive off host because they are dominated by wetland habitats (Sayler et al. 2016).

Studies of immature *I. scapularis* reported southern populations questing in leaf litter while genetically distinct northern populations questing higher on the vegetation, out of leaf litter (Arsnoe et al. 2015; Arsnoe et al. 2019). These behavioral and genetic differences might also be reflected in our ecological niches because variables associated with questing and surviving in an environment contributed to model calibration. Importantly, the *I. scapularis* submitted by foresters in this study were adults and were not genotyped. Follow up studies should compare the ecological niches of these genetically and behaviorally distinct populations.

Model testing

Our models could predict the presence of each tick species, but had difficulty predicting the absence of each tick species. This was confirmed with sensitivity testing as well as conducting targeted surveillance in predicted low-risk areas. These results were to be expected because the Maxent algorithm was only trained with presence records that had latitude and longitude coordinates (GPS records). Presence records were more readily available for this study because some crews were more vigilant tick collectors and absences could be due to lack of reporting and/or submitting. Nevertheless, our models were able to sufficiently predict tick absence when compared to current literature and active surveillance. Here, few encounters occurred in areas near the foothills of the Appalachian Mountains and our active surveillance supported that as well. Campers in the Bent Creek area helped us confirm the presence of *D. variabilis*, indicating they may be present in the region, but the likelihood of encounters at these sites is rare compared to other locations, a finding that is similar to other studies in the area (Seagle et al. 2021). These data support the overall findings that higher elevation areas are often unsuitable tick habitat, which could explain the decreased number of human-tick encounters in high elevation areas like Appalachia (Bunnell et al. 2003; Ford et al. 2015; Springer et al. 2015). Previous research documented that air temperature and density decrease as elevation increases (Zalakeviciute et al. 2018). A possible future research direction could be to monitor these sites as temperature and precipitation change in response to climate change (Portmann et al. 2009), because all three tick species in this study were associated with temperature and none were solely dependent on elevation. Using community science and passive surveillance data generated from this research could be an important tool for raising awareness of increased tick species distributions and used for tick avoidance and management regimes.

Potential for sampling bias

All three species were absent on human hosts in areas bordering the Mississippi river, coastlines around Louisiana, and southern Florida. This resulted in us reporting that ticks were absent (or low-risk of encounter sites) from areas comprising wetlands, analogous to previous studies (Bunnell et al. 2003; Stein et al. 2008). The absence of ticks on human hosts in these areas could also indicate sampling bias because fewer records were submitted by forest crews working in these areas. This is a known sampling limitation of this study: all data presented here are dependent on forestry crews submitting ticks. Future research should focus on confirming these findings by monitoring ticks in wetland habitats of these regions. Sensitivity and specificity tests indicated our niche models were efficient in their ability to detect known presences of all three species but had poor abilities in detecting a tick absence. Regardless, our relative activity and niche models can be used as a first approximation of risk for encountering ticks and their pathogens, as well as helping with tick management by forestry personnel.

Land management

Our results indicated that the burned area variable was not a good predictor of tick presence and therefore potentially not a suitable habitat. Prescribed burning may remove tick and mammal habitats that promote the abundance of tick populations (Pascoe et al. 2020), but several studies in the southeast have provided conflicting results that either support or refute the suggestion that prescribed burning may be used in tick management. Previously, prescribed burns reduced the abundance of ticks and the prevalence of tickborne pathogens in an area (Stafford et al. 1998; Gleim et al. 2019) which may be due to increased soil temperatures, decreased soil moisture, or destruction of tick habitats (Iverson and Hutchinson 2002; Gilliam et al. 2018). Conversely, a weak negative association between prescribed burns and the number of

ticks in an area could be due to increased host use of burned areas (Allan 2009) or little impact on tick species that quest and dwell within the soil (Padgett et al. 2009). Others propose that the methods for controlled burns, such as season, burning intensity, and frequency could be important factors for managing ticks in prescribed burns (Scifres et al. 1988). Future research to address the potential of controlled burns in large land management areas to reduce recreational and work-related tick encounters is warranted.

Conclusions

Passive tick surveillance data provided by FIA crews were valuable in delivering descriptions for when and where ticks were likely to be encountered and contributed to supporting our hypothesis. Data confirmed that ticks were active year-round in the southern US and habitats suitable for encounters can be explained by climatic and topographical features. Regions in the southeast that were least suitable for all three tick species included the Blue Ridge, Mississippi Alluvial Plain, and the Southern Florida Coastal Plain, whereas suitable regions for all tick species included the Interior Plateau, Central Appalachians, Ozark Highlands, Boston Mountains, and the Ouachita Mountains. Temporal periods associated with encountering each tick species in the southeastern US varied; *I. scapularis* was associated with cold seasons (autumn and winter) whereas *D. variabilis* and *A. americanum* were associated with warm seasons (spring and summer). This research provides important information for isolating regions for management of ticks when they are more seasonally active. This study also helps forestry managers alert field crews about tick activity and new county records of tick species. Additionally, this study provides crews with the opportunity to test management decisions against tick encounters. Future studies will aim to combine forest management strategies at high-risk geographic regions to understand associations on human-tick encounters.

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Appendix

Table 2.1. Spatial variables used in environmental niche modeling for common ticks in the southeastern US.

Environmental Variable	Definition	Reference
Elevation ^a	Height above sea level	Jenson and Domingue (1988)
Gross primary productivity ^b	Total amount of carbon produced by plants during photosynthesis	Running and Zhao (2015)
Net primary productivity ^b	The difference between carbon dioxide vegetation intakes during photosynthesis and the amount released during respiration	
Leaf area index ^b	Quantification of total canopy greenness	Myneni and Knyazikhin (2018)
Land cover ^b	Surface contents of within the visible landscape	Friedl and Sulla-Menashe (2019)
Land surface temperature ^b	Earth surface temperature at a particular location	Wan et al. (2015)
Evapotranspiration ^b	All forms of evaporation and transpiration	Running et al. (2017)
Vegetation indices ^b	A measure of greenness	Myneni and Knyazikhin (2018)
Precipitation ^b	Condensation of atmospheric water vapor affected by gravitational pull	Thornton et al. (2020)
Vapor pressure ^b	Point at which equilibrium pressure is acquired in a closed container	
Minimum temperature ^b	Lowest temperature recorded over a given amount of time	
Maximum temperature ^b	Highest temperature recorded over a given amount of time	

Table 2.1 continued

Burned area ^b	Surfaces which have been affected by burn scar from fire	Giglio et al. (2015)
Living aboveground biomass ^b	Living vegetation above the soil	Yu et al. (2021)
Living belowground biomass ^b	Living vegetation above below the soil	
Leaf Litter ^b	Decomposing plant material on the forest floor surface	
Soil organic matter ^b	Portion of the soil consisting of decomposing plant or animal tissue	
Dead aboveground biomass ^b	Dead vegetation above the soil	
Dead belowground biomass ^b	Dead vegetation below the soil	
Hydrologic soil group _b	Index of the rate that water infiltrates a soil	Ross et al. (2018)

^a Data were collected from <http://earthexplorer.usgs.gov>;

^b Data were collected from <http://earthdata.nasa.gov/>

Table 2.2. Total number of ticks encountered and submitted by Forest Inventory and Analysis Program crews of the Forest Service, US Department of Agriculture. Total number of tick-encounter sites is separated by state in the southeastern United States (2014-2021). In total there were 1720 *Amblyomma americanum* (200 larvae, 851 nymph, 310 males, and 359 females), 136 *Dermacentor variabilis* (1 nymph, 73 females, and 62 males) and 45 *Ixodes scapularis* (27 females and 18 males).

State	<i>Amblyomma americanum</i>	<i>Dermacentor variabilis</i>	<i>Ixodes scapularis</i>
Alabama	35 (1 site)	17 (1 site)	1 (1 site)
Arkansas	15 (13 sites)	5 (5 sites)	2 (1 site)
Florida	160 (31 sites)	3 (3 sites)	15 (13 sites)
Georgia	4 (3 sites)	0 (0 sites)	1 (1 site)
Kentucky	1030 (121 sites)	61 (40 sites)	12 (7 sites)
Louisiana	3 (3 sites)	3 (3 sites)	3 (3 sites)
Virginia	7 (4 sites)	0 (0 sites)	0 (0 sites)
Mississippi	1 (1 site)	0 (0 sites)	0 (0 sites)
North Carolina	9 (3 sites)	0 (0 sites)	0 (0 sites)
South Carolina	35 (26 sites)	13 (11 sites)	8 (7 sites)
Tennessee	421 (52 sites)	34 (27 sites)	3 (3 sites)
Total	1720 (258 sites)	136 (90 sites)	45 (36 sites)

Table 2.3. Model evaluation and variable contribution to environmental niche models generated with Maxent maximum entropy algorithm for ticks encountered by Forestry Inventory and Analysis (FIA) foresters from 2014-2021. Values for each variable represent that variables percent contribution to each model, bolded values were those identified as significant contributing variables to the model (greater than 0.1 or 10%).

Variable	<i>Amblyomma americanum</i>			<i>Dermacentor variabilis</i>			<i>Ixodes scapularis</i>
	model	model	model	model	model	model	model
	1	2	3	1	2	3	1
AUC values	0.83	0.85	0.80	0.87	0.85	0.86	0.82
<u>Variables Contributing to One or More Model</u>							
Elevation	16.7	20.2	15.3	24.9	21	16	7.7
Landcover	19.6	16.4	16.7	21	19.2	28.8	-
Vapor pressure	15.4	15.4	13	10.2	11.6	9	0
Precipitation	6.7	5.7	6.2	11.4	9.7	10.5	0
Maximum temperature	14.5	7	14.7	16.2	17.8	10.5	11.1
Minimum temperature	4.5	11.2	6.9	1.3	1	1.5	9.3
Dead belowground biomass	1.8	0.4	0.4	3.5	7.2	11.7	2.4
Evapotranspiration	0.9	2.4	1	3.3	1.8	3.2	11.9
Gross primary productivity	1.2	0.1	0.4	1.5	1.7	1.9	11.9
Soil organic matter	3.1	2.5	4.4	0.3	0	0.2	24.2
Vegetation indices	0	0	0	0.8	0.5	0.1	11.6
<u>Variables Assessed, but Not Contributing to a Model</u>							
Net primary productivity	5.1	2.6	6.4	2.4	1.6	1.4	2

Table 2.3 continued

Variable	<i>Amblyomma americanum</i>			<i>Dermacentor variabilis</i>			<i>Ixodes scapularis</i>
	model 1	model 2	model 3	model 1	model 2	model 3	model 1
<u>Variables Assessed, but Not Contributing to a Model</u>							
Hydrologic soil group	5.8	7.4	8.5	2.6	5	4.1	-
Land surface temperature	4.1	7.4	5.5	0	0.5	0.1	2
Litter	0.2	0.6	0.2	0.2	0.3	0.1	3
Living belowground biomass	0.1	0.6	0.4	0.4	1	0.9	0
Living aboveground biomass	0.1	0	0	0	0	0	0.1
Leaf area index	0	0	0.1	0	0	0	2.8
Burned area	0	0	0	0	0	0	0
Dead aboveground biomass	0	0	0	0	0	0	0

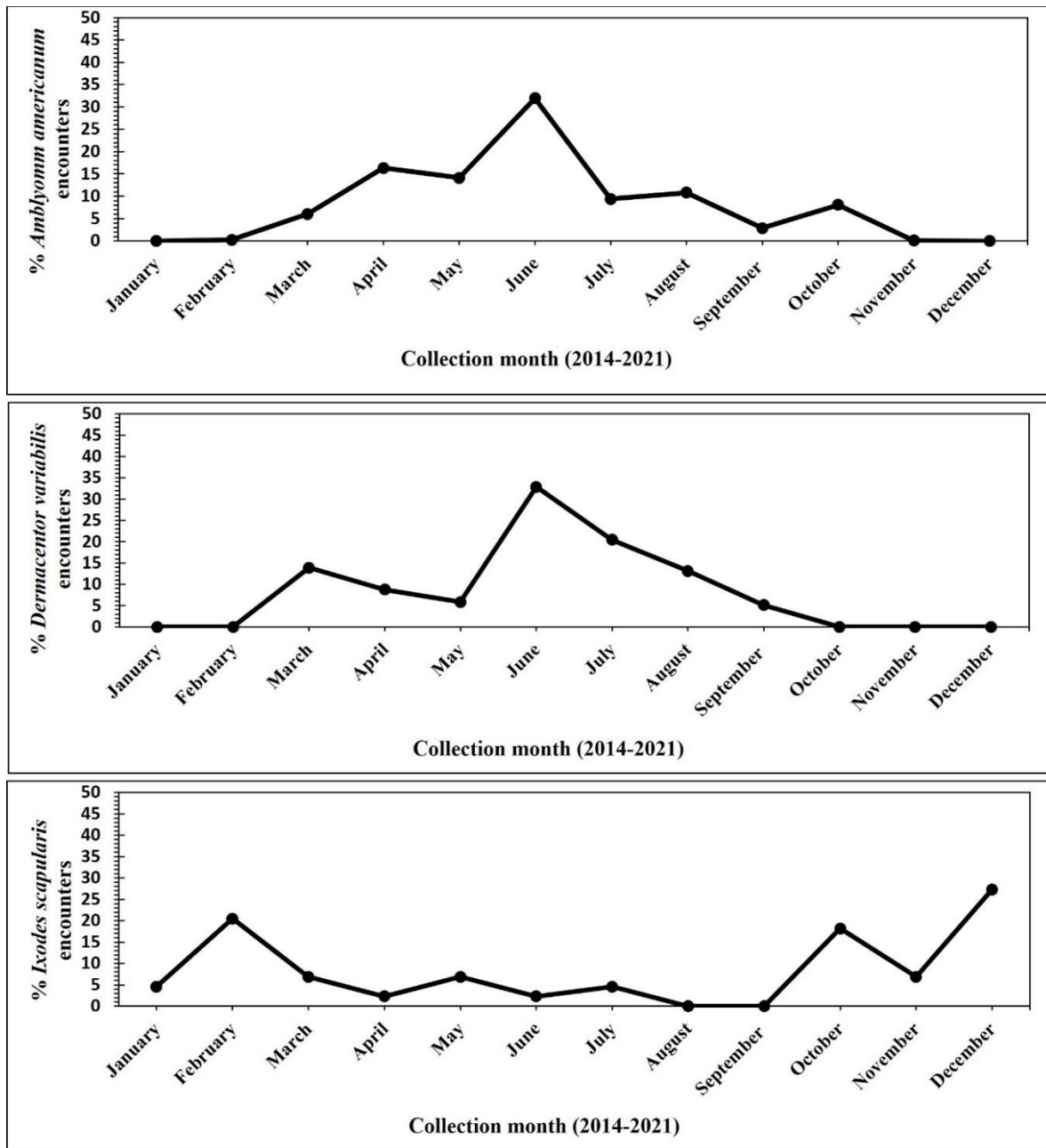


Figure 2.1. Relative activity of three species of ticks in southeastern United States. Percent monthly encounter for *Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis* encountered by Forestry Inventory and Analysis crews in the southeastern United States between 2014 and 2021.

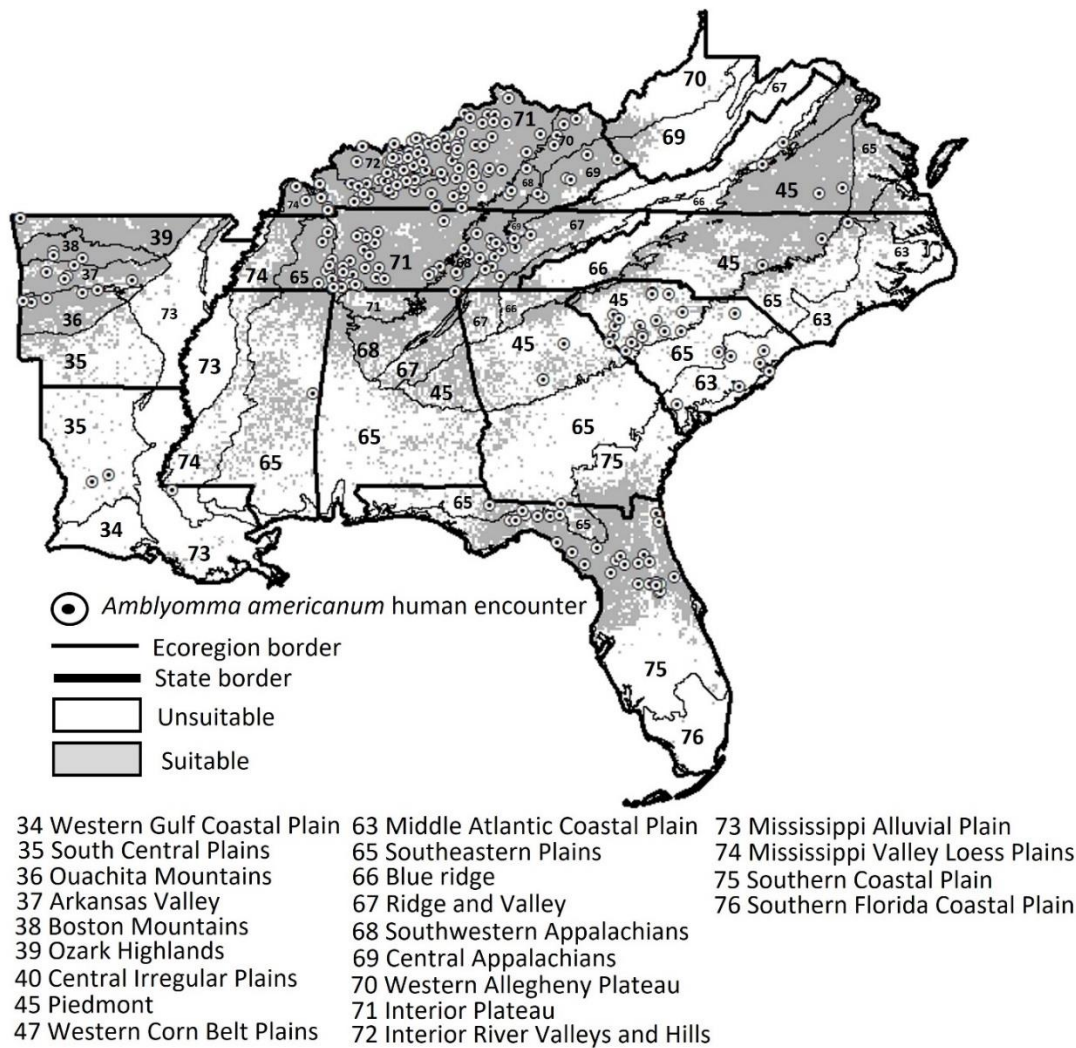


Figure 2.2. Potential distribution estimated with an environmental niche model for *Amblyomma americanum*. The model was based on tick encounters collected by Forest Inventory and Analysis Program of the Forest Service, US Department of Agriculture foresters in the southeastern United States (2014-2021). Landcover, elevation, maximum temperature, minimum temperature, and vapor pressure contributed the most to predicting this tick's geographic suitability.

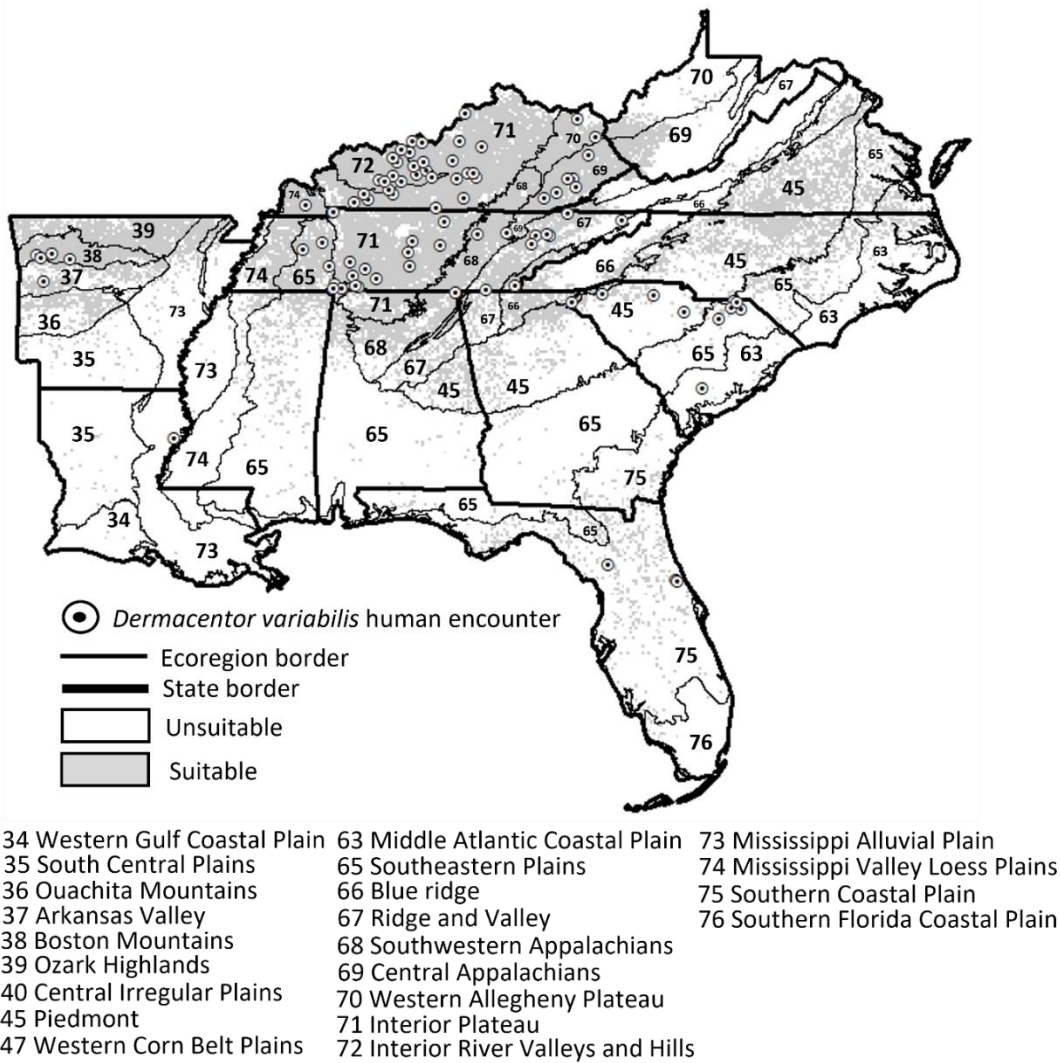


Figure 2.3. Potential distribution estimated with an environmental niche model for *Dermacentor variabilis*. The model was based on tick encounters collected by Forest Inventory and Analysis Program of the Forest Service, US Department of Agriculture foresters in the southeastern United States (2014-2021). Variables landcover, elevation, precipitation, vapor pressure, and dead belowground biomass contributed the most to predicting this tick's geographic suitability.

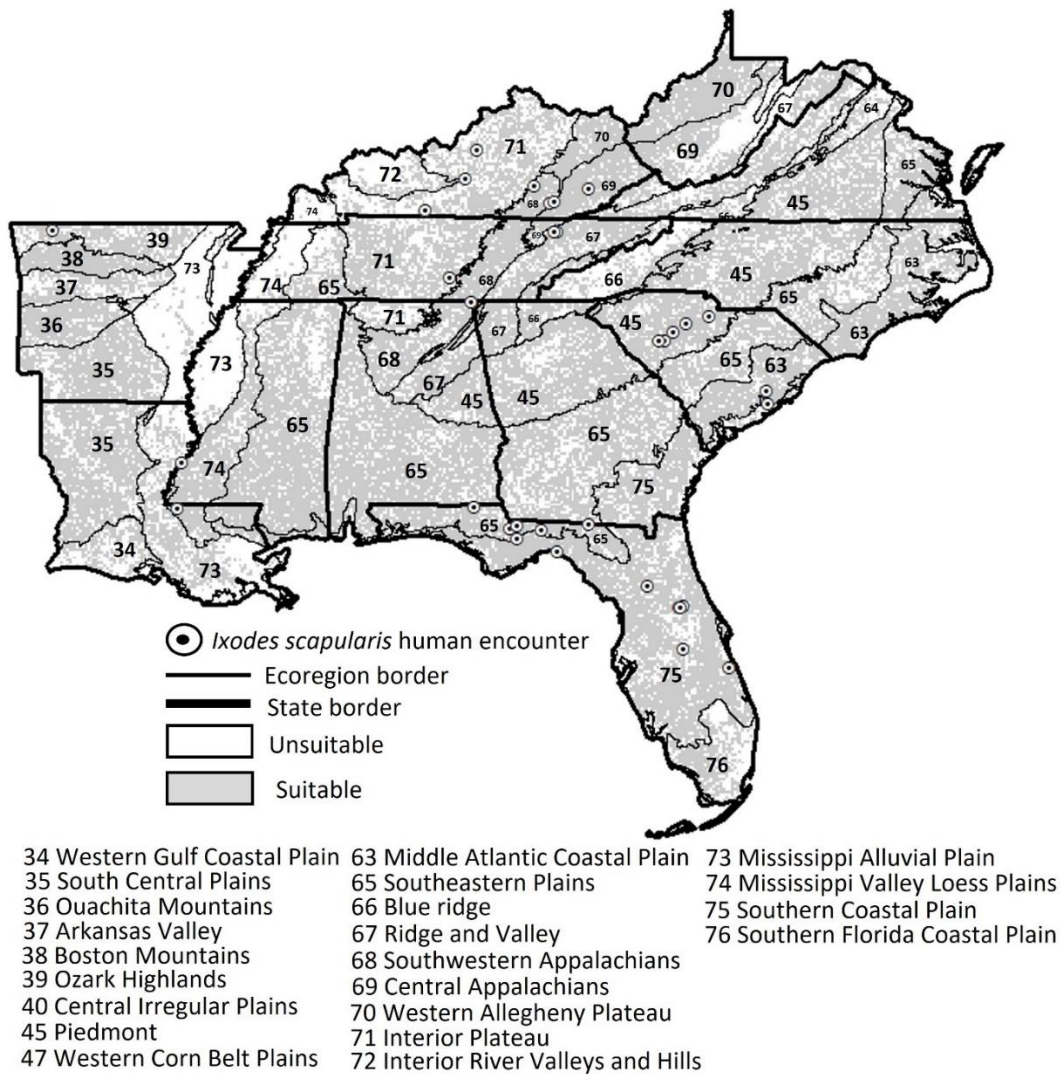


Figure 2.4. Potential distribution estimated with an environmental niche model for *Ixodes scapularis*. The model was based on tick encounters collected by Forest Inventory and Analysis Program of the Forest Service, US Department of Agriculture foresters in the southeastern United States (2014-2021). Variables soil organic matter, vegetation indices, maximum temperature, gross primary productivity, and evapotranspiration contributed the most to predicting this tick's geographic suitability.

**CHAPTER III. STATEWIDE PASSIVE SURVEILLANCE IDENTIFIES NOVEL
THEILERIA ORIENTALIS IKEDA AND AN INCREASE IN ANAPLASMA AND
EHRlichia PATHOGENS IN TENNESSEE COLLECTED TICKS**

Abstract

Animal diseases associated with ticks and their pathogens cause extensive economic loss and harm to livestock and companion animals. In the United States, this problem is exacerbated by the establishment of an exotic and invasive tick species, *Haemaphysalis longicornis* infected with a deadly protozoan (*Theileria orientalis* Ikeda genotype), representing a new and emerging vector and disease threat to the beef and dairy cattle industries. Knowing ticks and tick-borne pathogens rely on livestock and companion animals for dispersal and that they are widely understudied we aimed to understand the true prevalence of *Anaplasma*, *Ehrlichia*, and *Theileria* throughout Tennessee. We collected ticks from animals presented at animal shelters and livestock markets from 2019-2022. Ticks were identified to species and life stage and then a subset of those collections were screened for pathogens by amplifying *groEL* for *Anaplasma* and *Ehrlichia* and *MPSP* for *Theileria*. Results indicated that (8.20%) *groEL* (*Anaplasma* and *Ehrlichia*) was most prevalent in ticks feeding on canines and comprised of *E. ewingii*, *E. muris*, Panola Mountain *Ehrlichia*, *Ehrlichia chaffeensis*, and *A. phagocytophilum*. On the other hand (0.58%) *MPSP* (*T. orientalis* Ikeda) was amplified only from *H. longicornis* feeding on cattle. This study confirmed an increase in prevalence and geographic distribution of *groEL* associated pathogens and *T. orientalis* in the state of TN. In conclusion, a surveillance network using animal hosts to screen ticks for pathogens is important for tracking tick and tick-borne pathogen prevalence in understudied areas.

Introduction

The geographic ranges of tick species are reported to be increasing throughout the United States (US) resulting in an increase in reports of diseases transmitted by ticks (Hamer et al. 2010; Dahlgren et al. 2011; Scott Dahlgren et al. 2016; Mitchell et al. 2020; Álvarez-López et al. 2021). In addition to range expansion of established tick species, there has been an increase in the number of invasive tick species and their associated pathogens entering the US (Lohmeyer et al. 2011, Tufts and Diuk-Wasser 2021, Oakes et al. 2022). Tick-borne diseases (TBD) in companion animals and livestock often go underreported (Kocan et al. 2003; Modarelli et al. 2019) or misdiagnosed (Bowman et al. 2009; Schoeman 2009) which can lead to human exposure due to close relationships with these animals (Mahachi et al. 2020). Misconceptions are often due to a lack of knowledge regarding ticks and TBDs from veterinarians and doctors in their area of practice or the inability to screen patients due to lack of funds (Crist et al. 2022). Correctly reporting the prevalence of different TBDs in animal hosts is important because they can be also used as indicators for the risk of disease in human populations (Mahachi et al. 2020). Although serological testing is not always feasible because blood samples are unavailable, screening ticks for associated pathogens can be one mechanism to predict host risk for TBDs (Johnson et al. 2004). Studies that use ticks collected from the environment and on animal hosts can indicate the prevalence of TBD in human and non-human animal populations.

Several tick species are now common throughout Tennessee (Trout Fryxell et al. 2021) creating an urgent need to better understand the prevalence of their associated pathogens in the state. One of the first *Ehrlichia*-pathogen studies in the eastern region reported *E. canis* from canine blood samples (Seaman et al. 2004). This finding led to other studies documenting *E. canis* and *E. ewingii* prevalence in canine blood samples in TN (Beall et al. 2012) and

confirming that *Ehrlichia* was widespread throughout the state (Cohen et al. 2010). These results were also concerning due to the close associations between humans and canines and their ability to harbor human ehrlichiosis (Mahachi et al. 2020). In the central and eastern region of the state *Ehrlichia*-positive *A. americanum* collected from the environment were positive with *E. chaffeensis*, *E. ewingii*, and Panola Mountain *Ehrlichia*, but collections from companion animals were negative (Harmon et al. 2015). Human and bovine ehrlichiosis were both found in these field-collected ticks, which raised concern due to the infection risk for multiple host species. National canine data submitted by Idexx and Antech diagnostics reports Tennessee at a consistent high risk for ehrlichiosis in canines, in which 1 in 15 tested animals (6.35%) were found to be infected (CAPC 2023). Interestingly, tick and cattle associated studies found a low prevalence of *Ehrlichia*, which was found only in *A. americanum* ticks (Pompo et al. 2016); however, the status of the disease from this report is at least 10 years old and most of the state lacks a current risk assessment.

Anaplasma represents another common tick-borne pathogen known to infect cattle, canines, and humans (Ismail et al. 2010; Ganguly et al. 2018; Dewage et al. 2019). The prevalence of canine anaplasmosis from 2019-2022 in Tennessee indicated a medium-high risk with 1 in 20 screened dogs infected (5.23%) (CAPC 2023). Bovine anaplasmosis (BA) remains an understudied disease and is not frequently reported in the US, making it difficult to understand the true prevalence of the disease (Okafor et al. 2019a). Previously, Tennessee cattle-collected ticks were screened for *Anaplasma* bacteria, but none of the ticks were positive even though at the time of the study BA rates were nearly 11% (Pompo et al. 2016). Bovine anaplasma prevalence in Tennessee-adjacent states was 4.44% in Georgia (Okafor et al. 2019a), 28.99% in Mississippi (Okafor et al. 2019b), and 9.44% in Kentucky (Okafor et al. 2018). In

Tennessee there is a lack of published research on BA and therefore a need for statewide surveillance of the disease.

Recently, the exotic and invasive tick *Haemaphysalis longicornis* Neumann, which feeds on a variety of host species, was discovered throughout the eastern region of the US (Beard, Occi, Bonilla, Egizi, Fonseca, Mertins, and Bryon 2018, Rainey et al. 2018). The introduction of this tick soon brought the devastating bovine pathogen *Theileria orientalis* Ikeda genotype which is associated with bovine death in Virginia (Oakes, 2019). The rapid spread of the vector and the confirmation of *T. orientalis* Ikeda causing bovine theileriosis in the US is an agricultural food and health biosecurity threat and represents an exotic and emerging pest and disease (Watts et al. 2016, Oakes et al. 2019). Although other species of *Theileria* are known in the US such as *T. equi* in horses (Ueti et al. 2012), *T. buffeli* in cattle (Stockham et al. 2000), or *T. cervi* in white-tailed deer (Yabsley et al. 2005), the *T. orientalis* Ikeda genotype is globally known to cause destruction to cattle industries (Ota et al. 2009; Vink et al. 2016; Forshaw et al. 2020). In Tennessee, the cattle industry generates the most revenue compared to any other farm asset (USDA, 2019); therefore, introduction of *T. orientalis* could result in serious economic losses. Consequently, understanding the status of this pathogen through statewide surveillance is vital for reducing economic loss.

Our passive collections also indicated that *H. longicornis* co-feeds with common native ticks that are vectors of cattle and dog pathogens (Trout Fryxell et al. 2021). Specifically, it was found co-feeding with *Dermacentor variabilis* which transmit *Anaplasma marginale* causing BA in cattle and *Amblyomma americanum*, which transmit *Ehrlichia ewingii* causing canine ehrlichiosis in dogs. Our previous work in Tennessee confirmed *A. americanum*, *A. maculatum*, and *D. variabilis* collected from bovine across the state were only present on hosts in West and

Middle Tennessee (Pompo et al. 2016); however, just a few years later these species were discovered throughout the state including eastern Tennessee (Trout Fryxell et al. 2021). In depth surveillance of common ticks and their associated pathogens throughout the state is warranted to fully understand the expansion of ticks and associated pathogens.

Knowing these three tick species are common in Tennessee, found together feeding on hosts, and that *H. longicornis* can transmit all three pathogens, our goal is to obtain baseline pathogen occurrence data for these three host-tick-pathogen complexes. The purpose of this study is to determine the baseline prevalence and host characteristics associated with pathogen-positive ticks which can be used in future studies to develop and test strategies for tick-pathogen detection at livestock markets and animal shelters. We tested the hypothesis that ticks collected from cattle and dogs were infected with multiple tick-borne pathogens and that it was possible to quantify epidemiological predictors associated with those pathogen-positive ticks. Specifically, our objectives were to identify and confirm *Anaplasma*, *Ehrlichia*, and *Theileria* pathogens in *A. americanum*, *A. maculatum*, *D. variabilis*, and *H. longicornis* ticks, determine the prevalence of these pathogens in the different tick species; and identify characteristics of tick-infested hosts and pathogen-positive ticks.

Methods

Tick collection

Ticks were collected through a statewide surveillance network which included collaborating with a variety of animal shelters, veterinary clinics, livestock markets, and Extension agents. Details on the efforts were presented in Trout Fryxell et al. (2021). Ticks were stored in 80% ethanol and sent to the Medical and Veterinary Entomology laboratory at the University of Tennessee, Knoxville for identification to species and life stage using taxonomic

keys (Yunker, et al., 1986; Durden, 1996; Keirans and Durden 1998; Egizi et al. 2019). We randomly chose up to seven ticks for each species from each host animal for pathogen screening because tick numbers from submissions ranged from 1 - 795 per host (5.24 ± 20.857) and it was not possible to screen every individual tick due to resources. The number of hosts with zero ticks was not recorded by volunteers and it is not known how many ticks were missed by technicians.

Baseline pathogen presence in ticks

DNA extraction.

Ticks were individually screened for the presence of the *groEL* gene found in *Anaplasma* and *Ehrlichia* bacteria and *MPSP* protein found in *Theileria* bacteria. Each nymphal and adult tick was bisected with a disposable blade that was sterilized between uses with a glass bead sterilizer (Germinator 500). Due to size, larval ticks were pooled into groups of ten. Half of each tick was kept as a voucher and housed in Axygen (8 x 12, racked) 1.1 ML mini tubes in 80% ethanol at 20° C. The other half was used for pathogen analyses. DNA was extracted from each tick by placing the half in Qiagen (10 x 96, racked) 1.2 ML collection microtubules containing 180 ul tissue lysis buffer ATL and 20 µl of Proteinase K (Qiagen, Hilden, Germany) and a sterile stainless-steel bead. Beads were sterilized with 0.4 M HCL for 10 minutes and washed with sterilized deionized water. Ticks were then pulverized for five minutes using a Qiagen Tissue Lyser II stopping halfway to flip tube plates to ensure homogeneity. Plates were then incubated overnight at 56°C in a Fisher Scientific Isotemp 210 hot water bath. Next a QIAamp 96 DNA kit was used for purification and extraction of total tick DNA following instructions from the manufacturer using a Qiagen 96-well QIAcube HT.

***Anaplasma* and *Ehrlichia* detection.**

Nested PCR was used to amplify the *groEL* gene to detect the presence of *Anaplasma* and *Ehrlichia* species (Tabara et al. 2007). Although these methods were originally used for *Ehrlichia* detection they can also be used to detect *Anaplasma* (Tabara et al. 2007). The primary reaction consisted of a 10 µl total reaction which contained 2 µl extracted DNA, 1 µl of 10 µM forward: Gro607F 5' GAA GAT GCW GTW GGW TGT ACK GC and reverse: Gro1294R 5'AGM GCT TCW CCT TCW ACR TCY TC primers, 1µl of nuclease free water, and 5 µl of DreamTaq Hot Start Clear PCR Master Mix (2x) (Thermo Scientific, Waltham, MA). Afterwards samples were run at cycle conditions: 95° C for 15 min followed by 40 cycles (for the primary) or 35 cycles (for the nested) of 95° C for 30 s, 58° C for 30 s, 72° C for 30 s, and a final extension at 72° C for 3 min. After completion, the nested PCR was performed using a 20 ul total reaction which contained 2 µl extracted DNA, 1 ul of 10 µM forward: Gro677F 5'ATT ACT CAG AGT GCT TCT CAR TG and reverse primers: Gr01121R 5'TGC ATA CCR TCA GTY TTT TCA AC (Tabara et al. 2007), 6 ul of nuclease free water, and 10 ul of DreamTaq Hot Start Clear PCR Master Mix (2x) (Thermo Scientific, Waltham, MA). Samples were then run at conditions 95° C for 15 min followed by 35 cycles of 95° C for 30 s, 58° C for 30 s, 72° C for 30 s and a final extension at 72° C for 3 min. All reactions were run inside a Veriti 96 Well Thermal Cycler (Applied Biosystems, Grand Island, New York USA). Both reactions had a negative control (PCR mix with no DNA) and a positive control (*A. americanum* tick positive with *E. chaffeensis*). All products were then visualized with gel electrophoresis using a 2% agarose gel that was stained with ethidium bromide and run for 1 hour at 100 volts using a Biorad PowerPac 200 electrophoresis power supply, Fisher brand large gel electrophoresis system, and 1X TAE

electrophoresis buffer. Finally, the gels were viewed on an Analytik Jena UVP Transilluminator for the presence of a band indicating a positive sample (detection of *groEL* gene).

***Theileria orientalis* detection.**

Real-time PCR was used for amplification of *T. orientalis* MPSP gene for all extracted tick DNA using an Applied Biosystems QuantStudio 6 Flex. A 20 µl reaction was used, combining three total plates, with 10 µl of TaqMan Universal Master Mix 2.0 (Thermo Fisher Scientific, Waltham, MA), 0.6 µl (1.8 µl total) was used for both forward: 5'-GCAAACAAGGATTTGCACGC-3' and reverse: 5'-TGTGAGACTCAATGCGCCTAGA-3' primers, 0.2 ul (0.6 µl total) universal probe 5'-NED-TCGACAAGTTCTCACCAC-MGB-NFQ-3', and 6 µl of DNA (2 µl per plate). Conditions for QPCR were 10 min at 95 °C followed by 45 cycles of 15s at 95 °C and 1 min at 60 °C (Dinkel et al. 2021). Cycle threshold (CT) values less than 35 were not considered. Positive controls were taken from *T. orientalis* positive blood stabilate from bovine and negative controls were a combination of water, PCR master mix with no template DNA.

Samples that were real-time PCR positive for *T. orientalis* were confirmed using conventional PCR. A total reaction of 10 µl was used for the first reaction which comprised of 5 µl DreamTaq Hot Start Clear PCR Master Mix (2x) (Thermo Scientific, Waltham, MA), 0.5 µl of 10 µM forward: (5'-GCA AAC AAG GAT TTG CAC GC-3') and reverse: (5'-TGT GAG ACT CAA TGC GCCTAG A-3') primers (Dinkel et al. 2021), 3 µl of DNA, and 1 µl nuclease free water. The secondary reaction was a 20 µl total reaction comprised of 10 µl DreamTaq Hot Start Clear PCR Master Mix (2x) (Thermo Scientific, Waltham, MA), 1 µl of 10 µM forward: (5'-GCA AAC AAG GAT TTG CAC GC-3') and reverse: (5'-TGT GAG ACT CAA TGC GCCTAG A-3') primers (Dinkel et al. 2021), 2 µl of DNA, and 6 µl nuclease free water. Both

reactions were run in a thermocycler at conditions: 5 min at 95 °C followed by 35 cycles of 15 s at 95 °C, 5 s at 57 °C and 1 min at 68 °C (Dinkel et al. 2021). All assays included a negative control (PCR mix with no DNA) and a positive control (*T. cervi*). All samples were then run via gel electrophoresis using a 1.5% agarose gel that was stained with ethidium bromide and run for 1 hour 100 volts and gels were viewed on a transilluminator.

Sequencing for pathogen identification.

All PCR positive samples (20 µl of our amplified product) were cleaned using 6 µl of Exo-SAP-IT (Thermo Fisher Scientific, Waltham, MA) in a thermocycler (37 °C for 15 minutes followed by 80 °C for 15 minutes) to remove excess dNTPs and residual single-stranded primers and DNA. Samples were then sent to Eurofins Genomics (Louisville, Kentucky USA) for bidirectional Sanger sequencing and then bidirectionally aligned in Bioedit to create a single consensus sequence which was blasted in GenBank to determine species similarities. Due to high similarities in sequence reads (>95%) we determined that tree construction was unnecessary.

Spatial prevalence

Prevalence was calculated by dividing the total number of pathogen positive ticks by the total number screened in each county. In addition, the average prevalence between years was calculated by taking the mean percent prevalence between 2019, 2020, 2021, and 2022 for when ticks were collected. Data for canine serum *Ehrlichia* prevalence by Tennessee county was retrieved from the Companion Animal Parasite Council (CAPC) website (<https://capcvet.org/>). Map modeling and visualizations were conducted in ArcGIS pro (version 3.0).

Results

Overall, 10,311 total ticks representing six species were collected from 633 companion and 681 livestock hosts through our statewide tick surveillance. Descriptive statistics including the mean,

standard deviation, and total number of ticks collected from mammal hosts are presented in (Table 3.1). A total of ticks 2,573 (~25%) were screened from 534 companion animals and 230 livestock hosts.

Baseline pathogen presence in ticks

Up to seven specimens of each tick species were randomly selected from each host to be screened for *Anaplasma*, *Ehrlichia*, and *Theileria*. These ticks were composed of *D. variabilis* (total tick species screened per host species/total number of ticks screened) (62.40%), *A. maculatum* (1.32%), *H. longicornis* (2.50%), and (33.79%) *A. americanum* on 489 common dogs (*Canis lupus familiaris*). Additionally, 20 *A. americanum*, 57 *D. variabilis*, and one *A. maculatum* were present on 102 different common dogs (20.3%) that were *groEL*-positive. Tick species *D. variabilis* 25/558 (4.48%), *A. maculatum* (28.85%), *H. longicornis* (17.56%), and *A. americanum* (49.10%) were found on 215 domesticated cattle (*Bos taurus*). Overall, there were 18 *A. americanum*, ten *A. maculatum*, two *H. longicornis*, and one *groEL*-positive *D. variabilis* present on 26 cattle (12.09%) and there were 15 *Theileria*-positive *H. longicornis* ticks on eight bovine hosts (3.72%). Ticks *D. variabilis* (49.48%), *H. longicornis* (3.07%), and *A. americanum* (47.42%) were found on 50 domesticated felines (*Felis catus*) which had two *groEL*-positive *A. americanum* ticks present on two of these hosts (3.91%). *D. variabilis* (50.00%), *A. maculatum* (33.33%), and *A. americanum* (16.67%) ticks were found on five domestic pigs (*Sus scrofa domesticus*); *D. variabilis* (25.00%), *A. maculatum* (12.50%), and *A. americanum* (62.50%) were found on five domestic goats (*Capra aegagrus hircus*); and *D. variabilis* (12.50%), and *A. americanum* (87.50%) were found on seven domesticated horses (*Equus ferus caballus*).

More ticks were *groEL*-positive (8.20%) than *MPSP*-positive (0.58%) (Table 3.2). Only 15 *H. longicornis* ticks collected from bovine were *T. orientalis* Ikeda positive with qPCR and

all 15 were nymphs. Of the 973 *A. americanum*, 18 (6.56%) from cattle, 120 (18.37%) from dogs, and 2 (4.34%) from cats were *groEL*-positive. Fifty-six of the 1,203 *D. variabilis* were *groEL*-positive including 57 from dogs and 1 from a cow. Only 11 (5.91%) of the 186 *A. maculatum* were *groEL*-positive including 10 from cattle and 1 from a dog. Two *H. longicornis* were both *groEL* positive and *MPSP* positive. The only two pathogen positive ticks from felines were *A. americanum* (4.34% total prevalence). None of the ticks collected from pigs, horses, or goats were PCR positive for either gene. Although most of the pathogen-positive ticks came from hosts with just one positive tick (92 total hosts), there were 42 total hosts that had multiple pathogen positive ticks present with from two to eight positive ticks feeding at once in this study.

All of the *MPSP* qPCR-positive *H. longicornis* samples were sequenced and were identified as *T. orientalis* genotype Ikeda positive (>98% GenBank#MG758109). Due to costs, we did not sequence ticks from same host and used 1 plate. We sequenced 94 of the 120 *groEL*-positive ticks from different hosts and most of the *groEL* sequences were *Ehrlichia* species. We amplified *Ehrlichia chaffeensis* (>95% similarity GenBank#OL907292, OM960692, and KJ907753) from five *A. americanum* females collected from one cow, one cat, and three dogs. We also amplified *Ehrlichia chaffeensis* from one *D. variabilis* female collected from one dog. *Ehrlichia ewingii* (>96%% similarity GenBank#KJ907744, OM960693, and MN313356) was the most commonly amplified *Ehrlichia*. Fifty-six different dogs had pathogen-positive ticks and included 34 *A. americanum*, 21 *D. variabilis*, and one *A. maculatum*. Ten bovine-collected ticks (eight *A. maculatum*, one *D. variabilis*, and one *A. americanum*) and one feline-collected tick with an *A. americanum* female also had *E. ewingii* positive ticks. An additional *A. maculatum* collected from a cow had a sequence 97% similar to *E. muris* (GenBank#MW008558). Sequences from one *A. americanum* collected from a dog was similar to Panola Mountain

Ehrlichia (100% similarity GenBank# OM960694) and two *A. americanum* nymphs collected from a dog and cow were similar to *A. phagocytophilum* (99% similarity GenBank# MG570466). Coinfection, finding more than one pathogen with a single tick species, did occur in this dataset. Specifically, one female *A. americanum* collected from a dog was coinfecting with *E. ewingii* and *E. chaffeensis* and one *H. longicornis* nymph collected from a cow was coinfecting with *T. orientalis* Ikeda and *groEL*.

Spatial prevalence

Likely due to proximity to the University of Tennessee (Knox County, TN), the highest proportion of collected ticks were in eastern and middle Tennessee counties (**Figure 3.1**). The 95 Tennessee counties are divided into three grand regions and counties in those regions with submitted ticks, but no detected pathogens included Middle (Giles, Williamson, Davidson) and East (Anderson, Carter, Cocke, Dickson, Franklin, Grainger, Greene, Hawkins, Jefferson, Johnson, Rhea, Robertson, Sullivan, Sumner, and Washington). *Haemaphysalis longicornis* were primarily collected in eastern counties but included one middle Tennessee county. *Amblyomma americanum* and *Dermacentor variabilis* were the most cosmopolitan and abundant tick species in the state. *Amblyomma maculatum* were mostly collected from the southern regions of the state. Only *H. longicornis* collected from Union County were *Theileria* positive (3.50%).

The highest prevalence of *groEL* in Tennessee occurred in Western and Middle Tennessee counties, whereas *Theileria* was most prevalent in eastern Tennessee (**Figure 3.2**). As expected, *groEL* prevalence varied by county and was likely due to differences in collection effort by individual shelters. Eight counties reported a 1-5% *groEL* prevalence (Dyer, Fayette, Cheatham, Bradley, Blount, Claiborne, Union, and Hamblen) and ticks were found to have *A. phagocytophilum* and *E. ewingii*; five counties reported a 6-10% prevalence (Maury, Marshall,

Lincoln, Roane, Loudon, Monroe, and McMinn) with *E. muris* and *E. ewingii* in ticks; four counties reported 11-15% prevalence (Wilson, Putnam, White, and Hamilton) and ticks were reported with *E. chaffeensis* and *E. ewingii*; three counties reported 16-20% prevalence (Shelby, Bedford, and Cumberland) with ticks infected with Panola Mountain *ehrlichia* and *E. ewingii*. Fentress and Coffee counties, in the Middle region of the state, had the highest *groEL* prevalence (21-25%) with ticks infected with *E. ewingii*.

When possible, we compared our *groEL* prevalence data from canine-collected ticks to CAPC canine serum tests (68 counties) and found counties with higher prevalence for *Ehrlichia* canines serum samples also had the highest *groEL* prevalence in ticks (**Table 3.3, Figure 3.3**). Companion Animal Parasite Council data reported higher *Ehrlichia* prevalence in western and less in eastern regions, and our cattle-collected ticks positive with *groEL* had the highest pathogen prevalence in middle TN counties (**Table 3.4**).

Discussion

This study aimed to identify the current tickborne pathogen (TBP) prevalence in ticks collected from companion and livestock hosts throughout the state of Tennessee. These results indicated an increased prevalence of *groEL*-associated pathogens and the first detection of *Theileria orientalis* Ikeda. Additionally, this study documented an increase in the diversity of *Ehrlichia* species encompassing a greater geographic range in Tennessee than was previously reported even though we only screened ~25% of the potential ticks (Pompo et al. 2016). Other studies that detected *groEL*-associated pathogens in field or host collected ticks in the state were conducted more than five years ago; a surveillance of the current status of TBP statewide is needed (Cohen et al. 2010; Pompo et al. 2016, Trout Fryxell et al. 2017). This study is the first comprehensive survey in Tennessee to screen companion and livestock ticks for TBP and

Ehrlichia species detected are associated with ehrlichiosis. Thus, passive surveillance to detect TBP in ticks on hosts with close human associations use a One Health approach to decrease pathogen transmission.

The increased pathogen prevalence found in *A. americanum* could be due to its generalist feeding strategies between life stages, whereas *D. variabilis* immatures are more specialized to hosts (Koch 1981, Zimmerman et al. 1988, Kollars et al. 2000). Here, we built on Tennessee's foundational understanding, adding that *Ehrlichia*-positive ticks (*A. americanum*, *A. maculatum*, *D. variabilis*, and *H. longicornis*) are found in more areas and these ticks include specimens from livestock and companion animals (Cohen et al. 2010). Based on our findings, 8 of 100 ticks in the state of Tennessee may be *groEL*-positive and the risk increases based on host, tick species, and life stage.

Previous studies that screened ticks for tick-borne pathogens throughout Tennessee found *Ehrlichia* prevalent in western and middle regions of the state (Cohen et al. 2010); however, passive surveillance in this study showed the pathogen is present throughout the state. These results suggest a geographic expansion of *Ehrlichia* over time. Previously, only three of 512 (0.59%) bovine-collected *groEL*-positive ticks were confirmed in western Tennessee (Pompo et al. 2016). Our study found the prevalence of *groEL* in ticks on cows was greatest in Middle Tennessee compared to eastern and western regions of the state, suggesting a possible increase in the geographic prevalence of TBP throughout the state. Collections of *A. maculatum* from bovine hosts documented the presence of *Rickettsia* but not *Anaplasma* or *Ehrlichia* (Theuret 2017); thus, this study confirmed *groEL* in *A. maculatum* from cattle and canines. Previously, 11% of East Tennessee dogs were seroreactive against *E. canis* antigens (Seaman et al. 2004), which supports our finding of an increase in *Ehrlichia* and *Anaplasma* pathogens prevalence in eastern

Tennessee. This suggests an increase in *Ehrlichia* and *Anaplasma* prevalence compared to previous studies. The most common *Ehrlichia* species identified in this study were *E. ewingii* and *E. chaffeensis* that are known to cause human ehrlichiosis which is prevalent in Tennessee (Heitman et al. 2016). Also, *E. ewingii* is known to cause canine ehrlichiosis and dogs may serve as a reservoir that amplifies the bacteria and allows naïve ticks to acquire the pathogen and transmit it to other susceptible dogs (Starkey et al. 2015). Similarly, our results documented dogs to be the predominant carriers of pathogen-positive ticks that also cause human ehrlichiosis. This is a serious concern because of the close relationship companion animals have with human hosts; for example, dog-owners who sleep with their dog are at a greater risk of contracting a tick-borne disease than owners who do not (Paul et al. 2010). We also found Panola Mountain *Ehrlichia* in an *A. americanum* nymph in Cumberland County which supports finding by Harmon et al. (2015) that reported the first detection of the pathogen in Tennessee. These findings reiterate the need for widespread screening for TBPs in this county to identify environments and hosts at risk of encountering this pathogen. This also represents the first report of *E. muris* in Tennessee, found in *A. maculatum* on a cow host in middle Tennessee. This finding is concerning due to the ability of this pathogen to cause disease in human hosts (Johnson et al. 2015). Mays et al. (2014) found *A. phagocytophilum* in an *Ixodes scapularis* tick that previously fed on deer in western Tennessee (Fayette and Hardeman Counties). Our results also found this pathogen in *A. americanum* nymphs collected in Fayette and Union Counties. These results not only signify a larger geographic distribution of the pathogen but also the potential for higher incidence of human disease in these areas. Previously, *D. variabilis* ticks screened for *Ehrlichia* throughout the state all showed negative results (Cohen et al. 2010). However, this study found a 4% prevalence of *groEL* in dogs and cows screened throughout the state. This suggests an increased

prevalence of *groEL* associated pathogens in a greater variety of tick species which could increase the risk of humans encountering a pathogen.

This study confirmed the presence of the harmful bovine pathogen, *T. orientalis* Ikeda, in Tennessee *H. longicornis* ticks. There is an urgent need for on-farm and host management and surveillance of ticks throughout the state to help prevent the spread to additional sites. We discovered *T. orientalis* Ikeda in *H. longicornis* ticks feeding on cattle in eastern Tennessee. However, most *H. longicornis* that cofed with *Theileria*-positive ticks tested negative. Although the only other published account of *T. orientalis* Ikeda in the US was reported in Albemarle County, Virginia (Oakes et al. 2019) other sources have reported the pathogen in West Virginia and New York (Agriculture 2020; CUAHDC 2022). We found coinfection of cattle-collected *H. longicornis* positive with *T. orientalis* Ikeda and *groEL*. Previously, Oakes et al. (2022) reported coinfections of *A. marginale* and *T. orientalis* in bovine serum samples from Virginia. Results from this study suggest an association of *Theileria* and *groEL*, but their relationship and interactions need to be further addressed. Specifically, ticks infected with both pathogens may have acquired them from the host during blood feeding. Studies investigating the role of coinfecting ticks, ticks with multiple pathogens, could help explain changes in vectorial capacity and/or transmission rates. Spread of the pathogen to East TN may be due to producers traveling south to sell cattle at Tennessee markets. Movement of livestock in the US is not extensively monitored which could enhance the dispersal of *H. longicornis* into new regions (Raghavan, Barker, et al. 2019). Swisher and Pesapane (2022) noted that 30% of states require regulations for ectoparasites and only 20% of states required TBD screening when importing animals across state boundaries. In Tennessee, there are no current restrictions for movement of livestock on roadways due to *H. longicornis* or *Theileriosis* (Agriculture 2022). These findings emphasize the

need for more comprehensive monitoring and/or management for ticks and their associated pathogens on animals across state lines.

Statewide passive surveillance of ticks and their associated pathogens is an important tool to monitor tick distributions across geographic regions. Results from this study will be used to help prevent new cases of BA and canine ehrlichiosis and prevent the establishment of bovine theileriosis. In high-risk regions, tick control methods could be important for reducing tick abundance and associated problems. For example, the methods outlined in Butler and Trout Fryxell (2023) (unpublished) used cost-effective integrated pest management practices to reduce the number of *H. longicornis* on farms. In addition, Butler et al. (2021) confirmed on-animal control options in the US for effectively killing *H. longicornis* nymphs. This study identified an increase in prevalence and geographic distribution of *groEL* in ticks collected from companion and livestock hosts throughout TN and justified the importance of routine surveillance of TBP in widespread regions of the state. Reducing pathogen exposure risk in canines and managing this tick species could be important for reducing human ehrlichiosis incidence.

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Appendix

Table 3.1. Descriptive statistics of the mean $\pm$ standard error of the mean and (total number of ticks) collected from companion and livestock animals in Tennessee 2019-2022. The total number of hosts searched for ticks is in parenthesis under host scientific name.

Tick Species	Life Stage	Common dog <i>Canis lupus familiaris</i> (571)	Domestic cat <i>Felis catus</i> (62)	Domestic cattle <i>Bos taurus</i> (658)	Domestic pig <i>Sus scrofa domestica</i> (5)	Domestic goat <i>Capra aegagrus hircus</i> (6)	Domestic horse <i>Equus caballus</i> (12)	Total (1,312)
<i>Dermacentor variabilis</i>	Female	1.67 $\pm$ 0.150 (959)	0.48 $\pm$ 0.123 (30)	0.02 $\pm$ 0.007 (18)	0.60 $\pm$ 0.244 (3)	(0)	(0)	1,010
	Male	1.57 $\pm$ 0.169 (902)	0.25 $\pm$ 0.064 (16)	0.01 $\pm$ 0.004 (8)	(0)	0.33 $\pm$ 0.210 (2)	0.16 $\pm$ 0.112 (2)	930
	Total	3.26 $\pm$ 0.299 (1862)	0.74 $\pm$ 0.148 (46)	0.04 $\pm$ 0.008 (27)	0.60 $\pm$ 0.244 (3)	0.33 $\pm$ 0.210 (2)	0.16 $\pm$ 0.112 (2)	1,942
<i>Amblyomma maculatum</i>	Female	0.02 $\pm$ 0.009 (14)	(0)	0.13 $\pm$ 0.033 (89)	0.40 $\pm$ 0.400 (2)	(0)	(0)	105
	Male	0.02 $\pm$ 0.009 (14)	(0)	0.28 $\pm$ 0.057 (185)	(0)	0.16 $\pm$ 0.166 (1)	(0)	200
	Total	0.04 $\pm$ 0.015 (28)	(0)	0.41 $\pm$ 0.085 (274)	0.40 $\pm$ 0.400 (2)	0.16 $\pm$ 0.166 (1)	(0)	305

Table 3.1 continued

Tick Species	Life Stage	Common dog <i>Canis lupus familiaris</i> (571)	Domestic cat <i>Felis catus</i> (62)	Domestic cattle <i>Bos taurus</i> (658)	Domestic pig <i>Sus scrofa domesticus</i> (5)	Domestic goat <i>Capra aegagrus hircus</i> (6)	Domestic horse <i>Equus caballus</i> (12)	Total (1,312)
<i>Haemaphysalis longicornis</i>	Female	0.04±0.126 (25)	(0)	0.05±0.039 (33)	(0)	(0)	(0)	58
	Nymph	0.04±0.032 (26)	0.11±0.080 (7)	0.12±0.064 (82)	(0)	(0)	(0)	115
	Larvae	0.04±0.042 (24)	0.30±0.306 (19)	0.00±0.001 (1)	(0)	(0)	(0)	44
	Total	0.13±0.075 (75)	0.41±0.373 (26)	0.17±0.068 (116)	(0)	(0)	(0)	217
<i>Amblyomma americanum</i>	Female	0.99±0.126 (568)	0.38±0.120 (24)	0.28±0.039 (186)	0.20±0.200 (1)	1.00±0.683 (6)	3.08±2.641 (37)	822
	Male	0.65±0.111 (373)	0.09±0.044 (6)	0.16±0.037 (108)	(0)	0.33±0.210 (2)	5.08±4.461 (61)	550
	Nymph	0.56±0.255 (321)	0.08±0.041 (5)	0.05±0.012 (33)	(0)	1.00±0.516 (6)	0.16±0.112 (2)	367
	Larvae	0.27±0.173 (157)	0.59±0.402 (37)	(0)	(0)	(0)	(0)	194
	total	2.48±0.416 (1,418)	1.14±0.417 (71)	0.49±0.075 (328)	0.20±0.392 (1)	2.33±1.054 (14)	8.33±7.173 (100)	1,932

Table 3.1 continued

Tick Species	Life Stage	Common dog <i>Canis lupus familiaris</i> (571)	Domestic cat <i>Felis catus</i> (62)	Domestic cattle <i>Bos taurus</i> (658)	Domestic pig <i>Sus scrofa domesticus</i> (5)	Domestic goat <i>Capra aegagrus hircus</i> (6)	Domestic horse <i>Equus caballus</i> (12)	Total (1,312)
<i>Ixodes scapularis</i>	Female	0.43±0.070 (251)	0.38±0.106 (24)	0.02±0.006 (14)	(0)	(0)	1.08±0.398 (13)	302
	Male	0.07±0.026 (40)	0.03±0.022 (2)	(0)	(0)	(0)	0.08±0.083 (1)	43
	Total	0.51±0.088 (292)	0.41±0.118 (26)	0.01±0.006 (13)	(0)	(0)	1.16±0.440 (14)	345
<i>Rhipicephalus sanguineus</i>	Female	0.05±0.024 (31)	(0)	(0)	(0)	(0)	(0)	31
	Male	0.04±0.022 (26)	(0)	(0)	(0)	(0)	(0)	26
	Nymph	0.28±0.233 (161)	(0)	(0)	(0)	(0)	(0)	161
	Larvae	0.34±0.339 (197)	(0)	(0)	(0)	(0)	(0)	197
	Total	0.72±0.464 (415)	(0)	(0)	(0)	(0)	(0)	415
Total ticks		8,079	339	2,232	12	34	232	10,311

Table 3.2. Total prevalence of *Theileria* and *groEL* positive ticks on host species domestic cattle *Bos taurus*, common dog *Canis lupus familiaris*, and domestic *Felis catus* throughout the state of Tennessee 2019-2022.

Tick Life Stage	<i>groEL</i> positive / number screened (%)			<i>Theileria</i> positive / number screened (%)		
	<i>Bos taurus</i>	<i>Canis lupus familiaris</i>	<i>Felis catus</i>	<i>Bos taurus</i>	<i>Canis lupus familiaris</i>	<i>Felis catus</i>
<i>Amblyomma americanum</i>						
Female	9/166 (5.42%)	94/390 (24.10%)	2/25 (8.00%)	0/166 (0%)	0/390 (0%)	0/25 (0%)
Male	5/80 (6.25%)	18/165 (10.90%)	0/6 (0%)	0/80 (0%)	0/165 (0%)	0/6 (0%)
Nymph	4/28 (14.28%)	8/80 (10.00%)	0/4 (0%)	0/28 (0%)	0/80 (0%)	0/4 (0%)
Larvae	0/0 (0%)	0/3 (0%)	0/11 (0%)	0/0 0%	0/3 (0%)	0/11 (0%)
Total	18/ 274 (6.56%)	120/653 (18.37%)	2/46 (4.34%)	0/274 (0.00%)	0/653 (0%)	0/46 (0%)
<i>Haemaphysalis longicornis</i>						
Female	1/32 (3.12%)	0/18 (0.00%)	0/0 (0%)	0/32 (0.00%)	0/18 (0%)	0/0 (0%)
Nymph	1/66 (1.51%)	0/24 (0.00%)	0/3 (0.00%)	15/66 (22.72%)	0/24 (0%)	0/3 (0%)
Larvae	0/0 (0%)	0/5 (0.00%)	0/0 (0%)	0/0 (0%)	0/5 (0%)	0/0 (0%)
Total	2/98 (2.04%)	0/47 (0.00%)	0/3 (0.00%)	15/98 (15.30%)	0/47 (0%)	0/3 (0.0%)

Table 3.2 continued

Tick Life Stage	<i>groEL</i> positive / number screened (%)			<i>Theileria</i> positive / number screened (%)		
	<i>Bos taurus</i>	<i>Canis lupus familiaris</i>	<i>Felis catus</i>	<i>Bos taurus</i>	<i>Canis lupus familiaris</i>	<i>Felis catus</i>
<i>Amblyomma americanum</i>						
Female	5/70 (7.14%)	1/12 (8.33%)	0/0 (0%)	0/70 (0.00%)	0/12 (0%)	0/0 (0%)
Male	5/91 (5.49%)	0/13 (0%)	0/0 (0%)	0/91 (0.00%)	0/13 (0%)	0/0 (0%)
Total	10/161 (6.21%)	1/25 (4.00%)	0/0 (0%)	0/161 (0.00%)	0/25 (0%)	0/0 (0%)
<i>Dermacentor variabilis</i>						
Female	0/17 (0%)	38/762 (4.98%)	0/31 (0%)	0/17 (0%)	0/762 (0%)	0/31 (0%)
Male	1/8 (12.50%)	19/416 (4.56%)	0/17 (0%)	0/8 (0%)	0/416 (0%)	0/17 (0%)
Total	1/25 (4.00%)	57/1178 (4.83%)	0/48 (0%)	0/25 (0%)	0/1,178 (0%)	0/48 (0%)
Overall Total	31/558 (5.00%)	178/1903 (9.35%)	2/97 (2.06%)	15/558 (3.00%)	0/1903 (0%)	0/97 (0%)

Table 3.3. Period prevalence of *groEL* positive ticks on host species *Canis lupus familiaris* and *Ehrlichia* positive canine serum samples reported by the Companion Animal Parasite Council by county throughout the state of Tennessee 2019-2022.

County	Tick <i>groEL</i> prevalence from canines				CAPC canine serum <i>Ehrlichia</i> prevalence			
	2019	2020	2021	Average	2019	2020	2021	Average
Anderson	0/1 (0.00%)	0/4 (0.00%)		0.00%	80/879 (9.10%)	110/1126 (9.76%)	108/1527 (7.07%)	8.86%
Bedford	1/6 (6.25%)			6.25%	0/154 (0.00%)	1/97 (1.03%)	7/59 (11.86%)	4.29%
Blount	2/27 (7.40%)	0/8 (0.00%)		3.70%	44/1683 (2.61%)	89/3875 (2.29%)	108/4178 (2.58%)	2.49%
Bradley	2/38 (5.26%)			5.26%	82/1716 (4.77%)	87/1850 (4.70%)	102/2274 (4.48%)	4.65%
Carter	0/6 (0.00%)			0.00%	2/354 (0.56%)	2/81 (2.46%)	0/14 (0.00%)	1.00%
Claiborne	1/31 (3.22%)			3.22%	4/69 (5.79%)	17/282 (6.02%)	16/299 (5.35%)	5.72%
Cocke	0/76 (0.00%)			0.00%	0/383 (0.00%)	5/414 (1.20%)	9/432 (2.08%)	1.09%
Coffee	1/4 (25.00%)			25.00%	111/1401 (7.92%)	107/1554 (6.88%)	117/1806 (6.47%)	7.09%
Cumberland	2/26 (7.69%)	29/105 (27.61%)	3/14 (21.42%)	18.90%	380/2767 (13.73%)	445/3222 (13.81%)	357/3147 (11.34%)	12.96%

Table 3.3 continued

County	Tick <i>groEL</i> prevalence from canines				CAPC canine serum <i>Ehrlichia</i> prevalence			
	2019	2020	2021	Average	2019	2020	2021	Average
Dyer	1/55 (1.81%)			1.81%	0/19 (0.00%)	0/1 (0.00%)		0.00%
Fayette	1/15 (6.66%)			6.66%	26/214 (12.14%)	32/401 (7.98%)	32/289 (11.07%)	10.39%
Fentress	5/22 (22.72%)	1/2 (50.00%)		36.36%	66/245 (26.93%)	64/275 (23.27%)	97/378 (25.66%)	25.28%
Greene	0/1 (0.00%)	0/21 (0.00%)	0/7 (0.00%)	0.00%	4/164 (2.43%)	1/94 (1.06%)	7/202 (3.46%)	2.31%
Hamblen	1/55 (1.81%)	0/4 (0.00%)		0.91%	0/0 (0.00%)	0/37 (0.00%)	1/102 (0.98%)	0.32%
Hawkins	0/10 (0.00%)			0.00%	1/12 (8.33%)	0/7 (0.00%)	0/9 (0.00%)	2.77%
Jefferson	0/62 (0.00%)			0.00%		5/85 (5.88%)	6/199 (3.01%)	4.44%
Lincoln	1/8 (12.50%)			12.50%	8/44 (18.18%)	5/24 (20.83%)	9/45 (20.00%)	19.67%
Loudon	9/69 (13.04%)	6/95 (6.31%)	0/12 (0.00%)	6.45%	17/116 (14.65%)	20/245 (8.16%)	24/456 (5.26%)	9.35%
Maury	0/1 (0.00%)				129/1275 (10.11%)	125/1290 (9.68%)	101/1406 (7.18%)	8.99%
McMinn	1/8 (12.50%)	0/3 (0.00%)		6.25%	296/2654 (11.15%)	336/3347 (10.03%)	352/3970 (8.86%)	10.01%
Monroe	4/81 (4.93%)	7/61 (11.47%)		8.20%	25/325 (7.69%)	25/199 (12.56%)	35/460 (7.60%)	9.28%

Table 3.3 continued

County	Tick <i>groEL</i> prevalence from canines				CAPC canine serum <i>Ehrlichia</i> prevalence			
	2019	2020	2021	Average	2019	2020	2021	Average
Putnam	16/103 (15.53%)	21/134 (15.67%)	4/21 (19.04%)	16.74%	242/2890 (8.37%)	278/3211 (8.65%)	239/3336 (7.16%)	8.06%
Rhea	0/2 (0.00%)			0.00%	141/693 (20.34%)	164/782 (20.97%)	111/688 (16.13%)	19.14%
Roane	0/13 (0.00%)	2/38 (5.26%)		2.63%	52/255 (20.39%)	159/879 (18.08%)	156/1062 (14.68%)	17.71%
Shelby	5/31 (16.12%)			16.12%	330/6600 (5.00%)	385/8787 (4.38%)	399/11117 (3.58%)	4.32%
Sullivan	0/2 (0.00%)			0.00%	12/899 (1.33%)	23/1079 (2.13%)	25/1719 (1.45%)	1.63%
Union	14/226 (6.19%)	2/107 (1.86%)	2/16) (12.50%)	6.85%				
Washington	0/21 (0.00%)			0.00%	48/3570 (1.34%)	46/3765 (1.22%)	54/4328 (1.24%)	1.26%
White	4/14 (28.57%)	6/63 (9.52%)	4/27 (14.81%)	17.63%	7/36 (19.44%)	27/155 (17.41%)	64/321) (19.93%)	18.92%
Williamson	0/7 (0.00%)				1154/12200 (9.45%)	1491/17329 (8.60%)	1494/17830 (8.37%)	8.80%
Wilson	5/35 (14.28%)			14.28%	659/8423 (7.82%)	764/8959 (8.52%)	755/10122 (7.45%)	7.93%

Table 3.4. Prevalence of *groEL* positive ticks on *Bos taurus* by county throughout the state of Tennessee 2019-2022.

Region	County	Tick <i>groEL</i> prevalence from bovine				
		2019	2020	2021	2022	Average
East	Cheatham	1/18 (5.55%)		0/16 (0.00%)		6.05%
East	Cocke	0/26 (0.00%)				0.00%
East	Cumberland	0/23 (0.00%)				0.00%
East	Union		0/27 (0.00%)		2/49 (4.08%)	2.04%
East	Roane	4/14 (28.57%)				28.57%
Middle	Giles	0/6 (0.00%)				0.00%
Middle	Marshall	2/3 (66.66%)	3/43 (6.97%)			70.14%
Middle	Maury	7/140 (5.00%)		2/8 (25.00%)	1/6 (16.67%)	38.33%
Middle	Robertson	0/1 (0.00%)				0.00%
Middle	Wilson	1/19 (5.26%)		5/23 (21.73%)		13.49%
West	Fayette	2/96 (2.08%)				2.08%

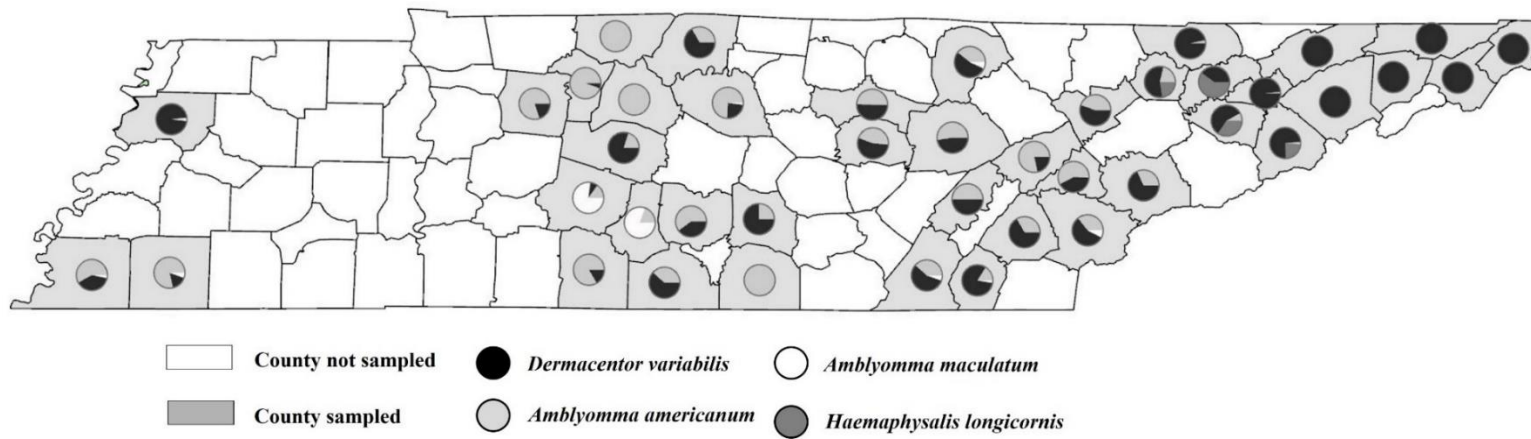


Figure 3.1. The proportion of ticks collected from companion and livestock animals throughout Tennessee 2019-2022.

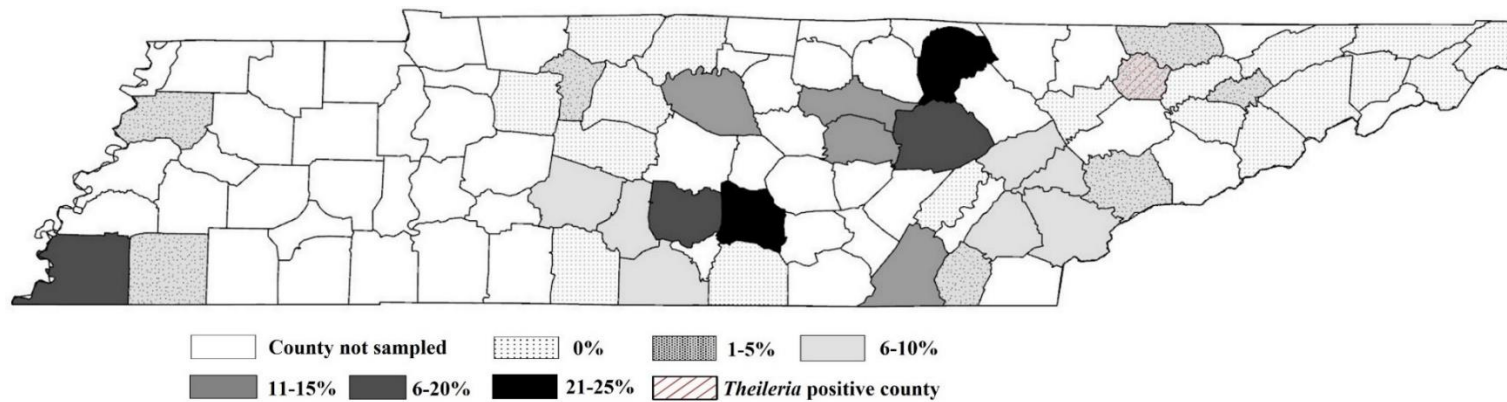


Figure 3.2. Total county prevalence for *groEL*-positive ticks collected from companion and livestock animals throughout Tennessee 2019-2022. County with *Theileria* positive ticks collected from bovine identified in red stripes.

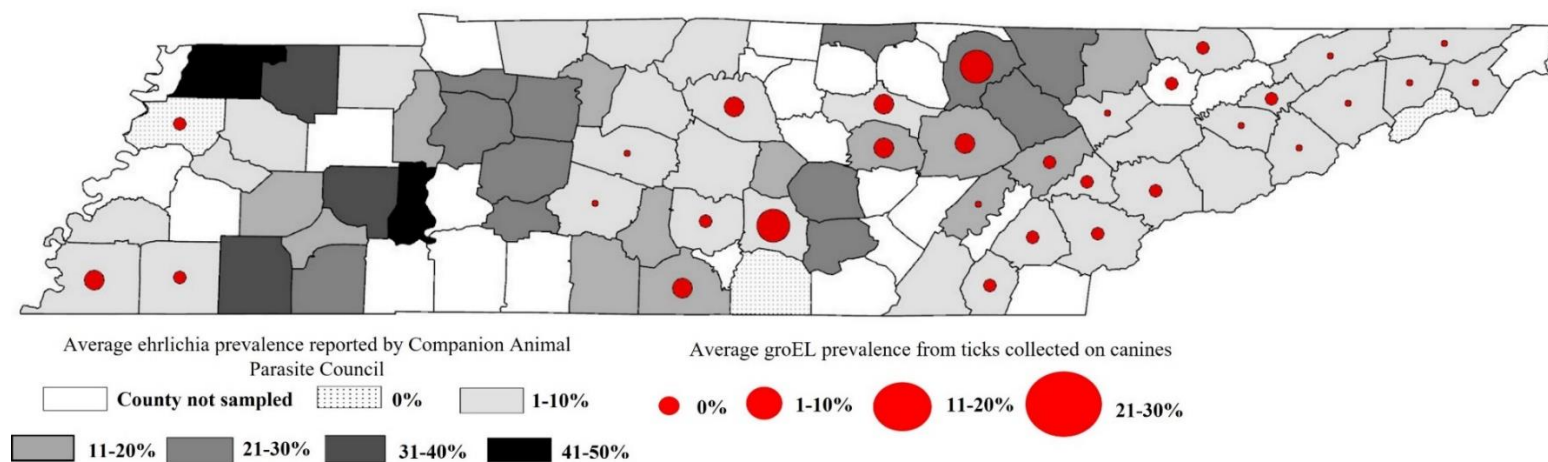


Figure 3.3. Average prevalence of *Ehrlichia* in canine serum samples reported from the Companion Animal Parasite Counsel and *groEL* screened from ticks collected on canines throughout Tennessee 2019-2022.

**CHAPTER IV: ECOLOGICAL RELATIONSHIPS OF *HAEMAPHYSALIS*
LONGICORNIS NEUMANN AT THE WILDLIFE-LIVESTOCK INTERFACE ON COW-
CALF FARMS IN EASTERN TENNESSEE**

Abstract

Haemaphysalis longicornis is a newly introduced tick species that parasitizes a variety of vertebrate hosts and transmits pathogens affecting humans and livestock in the United States (US); however, the role of this invasive tick species at the wildlife-livestock interface in newly invaded regions is not well understood. This study investigated how *H. longicornis* uses wildlife hosts and interacts with established tick species on hosts in farm settings. To do this, small and medium wildlife were sampled once a season for a year, using Sherman and Tomahawk traps, on three cattle farms in eastern Tennessee infested with *H. longicornis* from 2021-2022. We confirmed that host (species, sex X age, body region, weight X sex) and tick life histories (species and number of tick species simultaneously present) predicted the likelihood that *H. longicornis* would be present on a host. Ticks were less likely to be present on hosts when on-farm integrated pest management strategies were applied to reduce tick populations. Results from this study can be used to target host species characteristics for on-animal management of *H. longicornis*. Activity patterns for when established tick species are feeding simultaneously on hosts can also be used to predict when *H. longicornis* will be present. Finally, reducing tick abundance in the environment can be important for on-animal control.

Introduction

The introduction of exotic and invasive vector species into the United States (US) is not only a concern for their negative ecological and economic effects (Marbuah et al. 2014; Bradshaw et al. 2016), but also for potential health impacts (Juliano and Philip Lounibos 2005; Lounibos 2002). Several tick species of great concern due to their potential negative impact on the livestock industry have invaded the US, including the red sheep tick *Haemaphysalis punctata* Tufts and Diuk-Wasser (2021), cattle fever ticks, *Rhipicephalus (Boophilus) annulatus* (Say) and *Rhipicephalus (Boophilus) microplus* (Canestrini) Lohmeyer et al. (2011), and the Asian longhorned tick *H. longicornis* (Beard et al. 2018). The recent introduction of *H. longicornis*, into the US is a considerable public health interest due to its ability to transmit a variety of pathogens that impact humans and other animal hosts (Thompson et al. 2020). Although *H. longicornis* is not known to use humans as a preferred host (Ronai et al. 2020), it is able to harbor and transmit pathogens which negatively affects humans (Zhuang et al. 2018; Stanley et al. 2020). Additionally, *H. longicornis* readily cofeeds with native ticks on a variety of companion and livestock species which could indirectly have negative implications for human health due to their close associations (Price et al. 2022).

Reports in the US found *H. longicornis* parasitizing hosts which included a wide array of mammal and bird species (Beard et al. 2018; White et al. 2020; Tufts et al. 2021; Pandey et al. 2022). Although this tick has been widely reported on companion (Duncan et al. 2020; Fryxell et al. 2021) and livestock (Rainey et al. 2018; Dinkel et al. 2021; Trout Fryxell et al. 2021) hosts, its role in the transmission of pathogens from wildlife in the US is likely underreported. Previous studies surveying *H. longicornis* on wildlife hosts found white-tailed deer (*Odocoileus virginiana*), raccoon (*Procyon lotor*), and Virginia opossum (*Didelphis virginiana*) to be heavily

infested with this tick species (Thompson et al. 2021, 2022). Recently, *Theileria orientalis* Ikeda genotype was found in bovine serum and host-seeking *H. longicornis* ticks in Virginia US (Thompson et al. 2020; Dinkel et al. 2021). Although medically important arthropods have been characterized on *Theileria*-positive farms Hammer et al. (2015), host communities which could support *H. longicornis* and its associated pathogens at the wildlife-livestock interface are less studied. Thompson et al. (2020) found *T. cervi* in tick specimens on white-tailed deer on a *T. orientalis* Ikeda-positive farm; however, medium and small wildlife mammals were not sampled.

Cofeeding between *H. longicornis* and other native tick species on companion and wildlife hosts in the US have been reported (Tufts et al. 2019; Tufts et al. 2021). Cofeeding ticks are able to obtain pathogens from one another; thus, *H. longicornis* may obtain pathogens from native tick species or vice versa. For example, Bourbon virus and *Anaplasma phagocytophilum* acquired from native co-feeding ticks were found in *H. longicornis* (Cumbie et al. 2022, Price et al. 2022). Trout Fryxell et al. (2023) (in review) found *H. longicornis* follows similar phenological patterns to native tick species and these species were often found questing together in similar habitats. It is possible that native species could be interacting with *H. longicornis* in the environment as well as on hosts. Knowing how exotic and native tick species select host species is important for pathogen transmission.

The purpose of the present study was to identify predictors for *H. longicornis* presence on hosts, at the wildlife-livestock interface, which can be targeted for on-host tick control. Specifically, we tested if host and native tick species life histories and farm management regimes predicted the presence of *H. longicornis* on hosts.

Methods

Mammal handling and tick collection

All wildlife were handled following guidelines of the American Society of Mammalogists (Sikes and Gannon 2011) and identified to species using taxonomic key outlined in (Schwartz, C. W. and Schwartz 2016). Methods for handling small and medium-sized wildlife were approved by the University of Tennessee, Knoxville (IACUC #2774-0620). Species, sex, age (subadult and adult), weight (g), and external morphological measurements (mm) were taken on each wildlife host. Small mammals were trapped using (2" x 2.5" x 6.5") Sherman live traps (Tallahassee, FL) baited with rolled oats and black oil sunflower seeds. Medium-size mammals were trapped using medium (16.5" x 5.75" x 5.75") and large (32" x 10" x 12") tomahawk live traps (Hazelhurst, WI) baited with sardines and marshmallows. In 2020-2021, 42 Sherman live traps, 14 medium-sized tomahawk, and 10 large tomahawk traps were run for two-week intervals in each season as determined by equinox and solstice. There was a total of 7,920 trap nights. Medium-sized mammals were immobilized with 50 mg/ml ketamine and 100 mg/ml xylazine before a reversal 5 mg/ml atipamezole was used following (Kreeger and Anemo 2018). Raccoons were sedated with 20 mg/kg ketamine and 4 mg/kg xylazine and reversed with 0.375 mg/kg atipamezole. Opossums were sedated with 10 mg/kg ketamine and 2 mg/kg xylazine, but a reversal was not used. Small mammals (rodents and squirrels) were sedated in an enclosed plastic box with cotton balls of ethanol and monitored for sedation every five seconds or until the animal became drowsy. Ticks were removed from trapped mammal hosts with forceps and stored in 80% ethanol, all ticks were identified to species and life stage using taxonomic keys (Yunker, et al., 1986; Durden, 1996; Keirans and Durden 1998; Egizi et al. 2019).

Site selection

Mammals were trapped in forested and edge habitats on three farms (Farm 1, Farm 2, Farm 3) in eastern Tennessee. Farms each consisted of upland hardwoods surrounded by fields of fescue in eastern Tennessee. Each farm had an established population of *H. longicornis* on site and a herd of beef cattle. Producer led IPM strategies were conducted on site at each farm and outlined in Butler and Trout Fryxell (2023) (in review). These on-farm management strategies consisted of chemical control in the form of an on-animal acaricide for cattle, cultural control in the form of bushhogging, and mechanical control by removing ticks from the environment using a corduroy drag. Here Farm 1 opted to bushhog their pasture once monthly during the growing season, used an on-animal acaricide, and frequently removed ticks from the environment by mechanical control using a corduroy drag; Farm 2 bushhogged their property once a year, did not use an on animal acaricide, and moderately removed ticks from the environment by mechanical control; and Farm 3 bushhogged their pastures once yearly, used an on-animal acaricide, and scarcely removed ticks from the environment by using mechanical control. Overall, Farm 1 was reported to have a 90% reduction, Farm 2 did not have a reduction, and Farm 3 had a 68% reduction in tick presence.

Statistical modeling

All analyses were performed in Statistical Analysis Software (SAS, ver. 9.4, Cary, North Carolina) with two-tailed hypotheses ($\alpha = 0.05$) using generalized linear models (PROC GLIMMIX). The presence or absence of *H. longicornis* on a host was used as a binary response for each individual model. We created a “host model” with host sex, age (juvenile or adult), mammal type (small or medium), host weight (g), and the farm location as categorical fixed effects. For the host model the host was the unit of observation. Additionally, a separate dataset

“tick model” was constructed with the presence or absence of native tick species (*A. americanum*, *D. variabilis*, and *I. scapularis*), the body region where ticks were found, and the farm location as categorical variables and the total number of tick species collected from each host as continuous variables as fixed effects. The unit of observation in the “tick model” was each individual tick, to model body region where ticks were found, and therefore each individual host was used as a random effect in the “tick model” to compensate for multiple observations on a single host.

Results

In total, 6,042 ticks were collected from 331 wildlife hosts comprised of 11 different species on farms in eastern Tennessee (**Tables 4.1, 4.2, and 4.3**). Farm 1 had 800 (13.24%) ticks on 90 mammal hosts (**Table 1**), Farm 2 had 4,031 ticks (66.72%) on 120 mammal hosts (**Table 4.2**), and Farm 3 had 1,211 (20.04%) ticks on 121 wildlife hosts (**Table 4.3**). Overall, 40 northern short-tailed shrews (*Blarina brevicauda*), six southern flying squirrels (*Glaucomys volans*), one eastern woodrat (*Neotoma floridana*), and two eastern gray squirrels (*Sciurus carolinensis*) were collected with zero ticks present. There were 67 Virginia opossums with 843 ticks (mean $\pm$ standard error of the mean) (12.97 ± 4.597), 17 woodland voles (*Microtus pinetorum*) with four ticks (0.24 ± 0.182), six golden mice (*Ochrotomys nuttalli*) with five ticks (0.83 ± 0.833), seven cotton deermice (*Peromyscus gossypinus*) with five ticks (0.71 ± 0.285), 74 white-footed deermice (*Peromyscus leucopus*) with 21 ticks (0.25 ± 0.074), 36 North American deermice (*Peromyscus maniculatus*) with 38 ticks (1.06 ± 0.344), 31 raccoons with 5,096 ticks (164.38 ± 53.357), and 44 eastern chipmunks (*Tamias striatus*) with 28 ticks present (0.64 ± 0.386).

Statistical analysis

Our host model indicated *H. longicornis* was more likely to be present on medium-size mammals (e.g., racoon and opossum) compared to small mammals (e.g., eastern chipmunk) ($F_{1, 5744} = 52.05$; $P < 0.0001$). Interactions between host sex and age were associated with *H. longicornis* presence on a host ($F_{1, 5744} = 49.45$; $P < 0.0001$). Although ticks were more likely to be present on adult males compared to any other group, juvenile females had a higher likelihood of being tick positive compared to adult females and juvenile males. *Haemaphysalis longicornis* was more likely to be present on host's leg regions ($F_{7, 5744} = 39.51$; $P < 0.0001$) compared to the ventral, neck, foot, face, ear, dorsal, or posterior regions. In addition, interactions between host size and sex were associated with the likelihood of *H. longicornis* being present ($F_{1, 5744} = 49.81$; $P < 0.0001$). Although there was no association for female hosts, the likelihood for a male host to have a tick present decreased as the host's weight increased. Increases in host weight decreased the likelihood of *H. longicornis* presence on hosts with a greater diversity of tick species ($F_{4, 5744} = 26.55$; $P < 0.0001$). Finally, *H. longicornis* was less likely to be present on hosts on Farm 1 ($F_{1, 5744} = 39.61$; $P < 0.0001$) compared to Farms 2 and 3. Farm 1 used management strategies which ultimately reduced the number of ticks present in the environment by 90%.

Our tick model indicated that the likelihood *H. longicornis* presence increased along with the number of tick species present on a host ($F_{1, 321} = 29.72$; $P < 0.0001$). In addition, the abundance of established Tennessee tick species *A. americanum* ($F_{1, 321} = 5.16$; $P = 0.0238$), *D. variabilis* ($F_{1, 321} = 8.07$; $P = 0.0048$), or *I. scapularis* ($F_{1, 321} = 8.56$; $P = 0.0037$), predicted *H. longicornis* presence on a host. When any one of those native tick species was feeding on a host, *H. longicornis* was less likely to also be present.

Discussion

There is a need to better understand endemic tick species ecology because of their effects on livestock, but the invasion of *H. longicornis* makes the need more urgent (Dinkel et al. 2021). Discerning interactions between invasive and established tick species are imperative for understanding tick community structure on hosts. This investigation successfully isolated wildlife and established tick species associated with the presence of *H. longicornis* which can be targeted for tick control. Although ixodid tick species only spend 10% of their total life cycle on hosts compared to the environment (Needham 1991), knowing which host characteristics are associated with tick attachment allows us to develop important tools for reducing large abundances at a single time. In this study, we were able to identify host traits associated with *H. longicornis* presence that can be targeted for their control. For example, we found that adult male hosts were more likely to have ticks compared to any other sex and age group. This could be due to adult male hosts having larger home ranges in search of females (Krasnov et al. 2005). Juvenile female hosts had a lower likelihood of *H. longicornis* presence compared to adult females, but a higher likelihood compared to juvenile male hosts. Butler et al. (2020) found a similar result in which subadult females were more likely to have a higher abundance of ticks compared to male subadults; this could be from increased grooming from mothers on male over female offspring (Bemis et al. 2014). Ticks were also less likely to be present on male hosts as their body weight increased. Host weight can be an indication of poor health and can have detrimental immune effects (Ritz and Gardner 2006). As host weight increased, the abundance of tick species cofeeding decreased; additionally, as host weight increased, the likelihood of *H. longicornis* presence was reduced. Esser et al. (2016) found tick species diversity increased as

host weight increased for adult ticks but not for immature life stages; our result could be because most ticks collected were larvae and nymphs.

Here we identified wildlife host characteristics that can be evaluated as targets for on-farm tick control. Ticks were more likely to be present on medium-sized hosts compared to small mammals. Raccoons had the highest abundance of *H. longicornis* and the greatest number of co-feeding tick species (five species total). The next most heavily parasitized mammal after the raccoon was the Virginia opossum. In previous studies in Tennessee, >90% of the ticks were collected from these two species and raccoons similarly had the highest tick species diversity (Kollars 1993). The high abundances of *H. longicornis* on these two species is concerning because they serve as reservoir hosts for some *Anaplasma* and *Rickettsia* species (Levin et al. 2002; Boostrom et al. 2002). Although the lowest number of *H. longicornis* was found infesting eastern chipmunks, they can serve as a potential reservoir host for some tickborne pathogens (McLean et al. 1993, Keesing et al. 2014; Siy et al. 2021). Despite collecting *I. scapularis* and *D. variabilis* from rodents, we did not find *H. longicornis* on rodents. Although *H. longicornis* is known to occasionally feed on rodents, they are not the primary host of this tick species and are not a major concern for transmission of rodent associated pathogens such as *B. burgdorferi* (Breuner et al. 2020, Ronai et al. 2020). Overall, we identified wildlife hosts, raccoons and opossums, with the highest likelihood of having invasive ticks present at the wildlife-livestock interface, which can be isolated for tick management in large abundances. Baiting regime focused on these hosts species could be evaluated for acaricide applications to target *H. longicornis* on farm settings. Additionally, these two species are also likely to take advantage of livestock operations, by exploiting feed and watering systems, and come into frequent contact with cattle (Atwood et al. 2009; Beatty et al. 2016).

Different tick species are known to parasitize certain regions of hosts' bodies, including the neck, head, ear, head, tail, legs, scrotum, and rump (Koch 1982; Hart et al. 2022). The inclination to parasitize different body regions could be a result of attraction to pheromones or host excessive heat, humidity, or protection from grooming (Hair et al. 1975, Cardé and Baker 1984, Shaw et al. 2003, Carr and Salgado 2019). *Haemaphysalis longicornis* were more likely to be present on the host's leg compared to any other body region. Similar to our findings, Jang et al. (2016) noted the primary attachment sites for *H. longicornis* were the extremities, abdomen, and inguinal region. These preferences may also be related to competition with other tick species (Andrews et al. 1982) or based on density dependence in available feeding space (Anderson et al. 2013). Since this tick species is readily found on the extremities on wildlife hosts, these regions can be targeted for tick control with an acaricide application.

Haemaphysalis longicornis ticks were more likely to be present on a host as the number of tick species increased; we found one to five tick species co-feeding on hosts. Competition between tick species is often the result of limited shared resources (Mirrahimi et al. 2014). In this study, *H. longicornis* presence was predicted to occur when a greater number of tick species were present, suggesting a neutral relationship. In addition, *H. longicornis* was less likely to be present whenever it occurred alone with either tick species *A. americanum*, *I. scapularis*, or *D. variabilis*. Co-feeding ticks are able to transmit pathogens to one another (Randolph et al. 1996). Although a diverse TBP community infesting hosts and tick vectors could promote competition between pathogens which ultimately reduces their abundance (Genne et al. 2018), tick-pathogen community structure is less studied for *H. longicornis* in the US. Presently, we identified established tick characteristics which can be used to identify the presence of an *H. longicornis* on wildlife hosts. The increased likelihood for *H. longicornis* to be present feeding on a host when

multiple tick species are also present at the same time is a concern because the transmission risk is unknown for the cofeeding behavior.

Importantly, we observed significant farm effects on the host level; specifically, ticks were less likely to be present on Farm 1 compared to Farms 2 or 3. The management decisions used by the producers effectively reduced *H. longicornis* populations from the environment on Farms 1 and 3. However, Farm 1 had a 90% reduction, compared to 68% reduction on Farm 3, in tick presence with a combined integrated pest management (IPM) strategy (Butler and Trout Fryxell unpublished). Lower *H. longicornis* tick abundance on Farm 1 resulted in lower *H. longicornis* infestations on wildlife hosts in the areas around the farm. Understanding interactions between the environment, hosts, tick population dynamics, and human exposure is important for creating a tick IPM strategy (Stafford et al. 2017). We documented that mechanical, cultural, and on-animal chemical control can reduce *H. longicornis* in the environment in a farm setting.

We identified life histories of different host and tick species which can be targeted for control of an invasive tick at the wildlife-livestock interface. Future studies may investigate on-host management regimes in the field to reduce *H. longicornis*. These could include baiting regimes to target medium size hosts (raccoons and opossum), or behaviors associated with these hosts during periods such as mating season using attractants; however, this approach needs to be evaluated. These medium size hosts could also be targeted by directing management toward farm practices that allow access to livestock food. The likelihood *H. longicornis* was present on a host was associated with the presence of multiple species feeding at the same. Tick control that can target a greater number of tick species may help simultaneously reduce both invasive and established tick species. Identifying activity periods for when established tick species are feeding

simultaneously could be important for future *H. longicornis* management. Subsequent research could focus on how semiochemicals on hosts affect tick-feeding strategies. This study identified host and tick life histories which were associated with *H. longicornis* at the wildlife-livestock interface. In addition, previous research including producer led IPM strategies in the environment were identified that reduced the likelihood ticks would be present on wildlife hosts. Although we recommend evaluation before culling animals, future studies should investigate *H. longicornis* management by targeting these variables to reduce tick presence.

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Appendix

Table 4.1. Total abundance of ticks by species and life stage collected on wildlife hosts at Farm 1 in eastern Tennessee (2019-2021). Host common and scientific name followed by the total number collected in parentheses. The mean $\pm$ standard error of the mean followed by the total number of ticks collected in parentheses.

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (22)	White-footed deer mouse <i>Peromyscus leucopus</i> (26)	North American deer mouse <i>Peromyscus maniculatus</i> (13)	Golden mouse <i>Ochrotomys nuttali</i> (6)
<i>Haemaphysalis longicornis</i> larva	0.12 ± 0.125 (1)	0.09 $\pm$ 0.065 (2)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> nymph	(0)	0.19 ± 0.111 (4)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> female	(0)	(0)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> total	0.12 ± 0.125 (1)	0.28 ± 0.122 (6)	(0)	(0)	(0)
<i>Amblyomma americanum</i> larva	78.37 ± 34.510 (627)	0.85 ± 0.670 (18)	(0)	(0)	(0)
<i>Amblyomma americanum</i> nymph	6.00 ± 2.052 (48)	0.04 ± 0.047 (1)	(0)	(0)	(0)

Table 4.1 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (22)	White- footed deer mouse <i>Peromyscus leucopus</i> (26)	North American deer mouse <i>Peromyscus maniculatus</i> (13)	Golden mouse <i>Ochrotomys nuttalli</i> (6)
<i>Amblyomma americanum</i> male	(0)	0.04 ± 0.047 (1)	(0)	(0)	(0)
<i>Amblyomma americanum</i> female	(0)	(0)	(0)	(0)	(0)
<i>Amblyomma americanum</i> total	84.37 ± 35.526 (675)	0.95 ± 0.674 (20)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> larva	(0)	0.09 ± 0.065 (2)	0.03 ± 0.038 (1)	0.07 ± 0.076 (1)	0.33 ± 0.333 (2)
<i>Dermacentor variabilis</i> nymph	(0)	(0)	(0)	(0)	0.16 ± 0.166 (1)
<i>Dermacentor variabilis</i> male	1.25 ± 0.839 (10)	0.52 ± 0.235 (11)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> female	0.62 ± 0.323 (5)	0.33 ± 0.105 (7)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> total	1.87 ± 0.833 (15)	0.95 ± 0.280 (20)	0.03 ± 0.038 (1)	0.07 ± 0.076 (1)	0.50 ± 0.500 (3)

Table 4.1 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (22)	White-footed deer mouse <i>Peromyscus leucopus</i> (26)	North American deer mouse <i>Peromyscus maniculatus</i> (13)	Golden mouse <i>Ochrotomys nuttali</i> (6)
<i>Ixodes scapularis</i> larva	0.12 ±0.125 (1)	0.23 ±0.095 (5)	0.11 ±0.084 (4)	0.92 ±0.771 (12)	(0)
<i>Ixodes scapularis</i> nymph	(0)	0.47 ±0.190 (10)	0.07 ±0.053 (2)	(0)	0.33 ±0.333 (2)
<i>Ixodes scapularis</i> male	(0)	(0)	(0)	(0)	(0)
<i>Ixodes scapularis</i> female	(0)	0.09 ±0.065 (2)	(0)	(0)	(0)
<i>Ixodes scapularis</i> total	0.12 ± 0.125 (1)	0.80 ± 0.190 (17)	0.19 ± 0.096 (6)	0.92 ± 0.771 (12)	0.33 ± 0.333 (2)
<i>Ixodes cookei</i> larva	0.37 ±0.263 (3)	0.04 ± 0.047 (1)	(0)	(0)	(0)
<i>Ixodes cookei</i> nymph	0.12 ±0.125 (1)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> male	(0)	(0)	(0)	(0)	(0)

Table 4.1 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (22)	White- footed deer mouse <i>Peromyscus leucopus</i> (26)	North American deer mouse <i>Peromyscus maniculatus</i> (13)	Golden mouse <i>Ochrotomys nuttali</i> (6)
<i>Ixodes cookei</i> female	(0)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> total	0.50 ± 0.377 (4)	0.04 ± 0.047 (1)	(0)	(0)	(0)
<i>Ixodes texanus</i> larva	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> nymph	0.50 ±0.377 (4)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> male	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> female	1.12 ±0.666 (9)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> total	1.62 ±0.730 (13)	(0)	(0)	(0)	(0)
Total ticks	88.62 ±35.163 (709)	3.04 ±0.967 (64)	0.23 ±0.100 (9)	1.00 ±0.767 (13)	0.83 ±0.833 (5)

Table 4.2. Total abundance of ticks by species and life stage collected on wildlife hosts at Farm 2 in eastern Tennessee (2019-2021). Host common and scientific name followed by the total number collected in parentheses. Host common and scientific name followed by the total number collected in parentheses. The mean $\pm$ standard error of the mean followed by the total number of ticks collected in parentheses.

Tick species and life stage	Raccoon <i>Procyon lotor</i> (15)	Virginia opossum <i>Didelphis virginiana</i> (30)	Eastern chipmunk <i>Tamias striatus</i> (8)	North American deer mouse <i>Peromyscus maniculatus</i> (9)	Cotton deer mouse <i>Peromyscus gossypinus</i> (7)
<i>Haemaphysalis longicornis</i> larva	4.46 ± 1.956 (67)	8.80 ± 4.772 (264)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> nymph	4.80 ± 1.387 (72)	0.96 ± 0.393 (29)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> female	0.06 ± 0.066 (1)	0.36 ± 0.273 (11)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> total	9.33 ± 2.349 (140)	10.13 ± 5.349 (304)	(0)	(0)	(0)
<i>Amblyomma americanum</i> larva	21.20 ± 12.314 (318)	0.10 ± 0.100 (3)	(0)	(0)	(0)
<i>Amblyomma americanum</i> nymph	10.40 ± 3.006 (156)	0.06 ± 0.046 (1)	(0)	(0)	(0)

Table 4.2 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (15)	Virginia opossum <i>Didelphis virginiana</i> (30)	Eastern chipmunk <i>Tamias striatus</i> (8)	North American deer mouse <i>Peromyscus maniculatus</i> (9)	Cotton deer mouse <i>Peromyscus gossypinus</i> (7)
<i>Amblyomma americanum</i> female	(0)	(0)	(0)	(0)	(0)
<i>Amblyomma americanum</i> total	31.80 ±12.857 (477)	0.16 ±0.136 (4)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> larva	(0)	(0)	(0)	(0)	0.14 ±0.142 (1)
<i>Dermacentor variabilis</i> nymph	(0)	(0)	(0)	0.11 ±0.111 (1)	(0)
<i>Dermacentor variabilis</i> male	3.20 ±1.618 (48)	1.13 ±0.456 (34)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> female	2.66 ±1.382 (40)	0.93 ±0.342 (28)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> total	5.86 ±2.940 (88)	2.06 ±0.771 (62)	(0)	0.11 ±0.111 (1)	0.142 ±0.142 (1)
<i>Ixodes scapularis</i> larva	4.20 ±1.310 (63)	0.56 ±0.370 (17)	0.12 ±0.125 (1)	0.44 ±0.242 (4)	0.57 ±0.297 (4)

Table 4.2 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (15)	Virginia opossum <i>Didelphis virginiana</i> (30)	Eastern chipmunk <i>Tamias striatus</i> (8)	North American deer mouse <i>Peromyscus maniculatus</i> (9)	Cotton deer mouse <i>Peromyscus gossypinus</i> (7)
<i>Ixodes scapularis</i> nymph	0.46± 0.215 (7)	(0)	0.12± 0.125 (1)	(0)	(0)
<i>Ixodes scapularis</i> male	(0)	(0)	(0)	(0)	(0)
<i>Ixodes scapularis</i> female	(0)	(0)	(0)	(0)	(0)
<i>Ixodes scapularis</i> total	4.66 ±1.416 (70)	0.56 ±0.370 (17)	0.25 ±0.163 (2)	0.44 ±0.242 (4)	0.57 ±0.297 (4)
<i>Ixodes cookei</i> larva	0.66 ±0.287 (10)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> nymph	0.80 ±0.527 (12)	0.03 ±0.033 (1)	(0)	(0)	(0)
<i>Ixodes cookei</i> male	(0)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> female	0.13 ±0.090 (2)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> total	1.60 ±0.803 (24)	0.03 ±0.033 (1)	(0)	(0)	(0)

Table 4.2 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (15)	Virginia opossum <i>Didelphis virginiana</i> (30)	Eastern chipmunk <i>Tamias striatus</i> (8)	North American deer mouse <i>Peromyscus maniculatus</i> (9)	Cotton deer mouse <i>Peromyscus gossypinus</i> (7)
<i>Ixodes texanus</i> male	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> female	0.06 ±0.066 (1)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> total	0.60 ±0.600 (1)	(0)	(0)	(0)	(0)
Total ticks	53.86 ±16.049 (808)	12.96 ±6.006 (389)	0.25 ±0.163 (2)	0.55 ±0.242 (5)	0.71 ±0.285 (5)

Table 4.3. Total abundance of ticks by species and life stage collected on wildlife hosts at Farm 3 in eastern Tennessee (2019-2021). Host common and scientific name followed by the total number collected in parentheses. Host common and scientific name followed by the total number collected in parentheses. The mean $\pm$ standard error of the mean followed by the total number of ticks collected in parentheses.

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (15)	Eastern chipmunk <i>Tamias striatus</i> (30)	White-footed deer mouse <i>Peromyscus leucopus</i> (29)	North American deer mouse <i>Peromyscus maniculatus</i> (14)	Woodland vole <i>Microtus pinetorum</i> (7)
<i>Haemaphysalis longicornis</i> larva	285.25 $\pm$ 121.908 (2282)	23.78 $\pm$ 16.303 (333)	0.03 $\pm$ 0.033 (1)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> nymph	3.62 $\pm$ 0.419 (29)	2.07 $\pm$ 0.892 (29)	0.16 $\pm$ 0.136 (5)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> female	0.12 $\pm$ 0.125 (1)	(0)	(0)	(0)	(0)	(0)
<i>Haemaphysalis longicornis</i> total	289.00 $\pm$ 121.894 (2312)	25.85 $\pm$ 16.704 (362)	0.20 $\pm$ 0.147 (6)	(0)	(0)	(0)
<i>Amblyomma americanum</i> larva	130.62 $\pm$ 63.881 (1045)	(0)	0.20 $\pm$ 0.200 (6)	(0)	(0)	(0)
<i>Amblyomma americanum</i> nymph	12.00 $\pm$ 1.908 (96)	0.14 $\pm$ 0.097 (2)	0.23 $\pm$ 0.233 (7)	(0)	(0)	(0)

Table 4.3 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (15)	Eastern chipmunk <i>Tamias striatus</i> (30)	White- footed deer mouse <i>Peromyscus leucopus</i> (29)	North American deer mouse <i>Peromyscus maniculatus</i> (14)	Woodland vole <i>Microtus pinetorum</i> (7)
<i>Amblyomma americanum</i> male	(0)	(0)	(0)	(0)	(0)	(0)
<i>Amblyomma americanum</i> female	(0)	(0)	(0)	(0)	(0)	(0)
<i>Amblyomma americanum</i> total	142.62 ±64.135 (1141)	0.14 ±0.097 (2)	0.43 ±4.333 (13)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> larva	(0)	(0)	0.06 ±0.046 (2)	0.27 ±0.120 (8)	1.42 ±0.521 (20)	0.57 ±0.428 (4)
<i>Dermacentor variabilis</i> nymph	(0)	(0)	(0)	0.13 ±0.095 (4)	(0)	(0)
<i>Dermacentor variabilis</i> male	10.25 ±5.080 (82)	1.07 ±0.997 (15)	0.06 ±0.066 (2)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> female	4.62 ±2.711 (37)	0.42 ±0.358 (6)	(0)	(0)	(0)	(0)
<i>Dermacentor variabilis</i> total	14.87 ±7.640 (119)	1.50 ±1.349 (21)	0.13 ±0.079 (4)	0.41 ±0.160 (12)	1.42 ±0.521 (20)	0.57 ±0.428 (4)

Table 4.3 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (15)	Eastern chipmunk <i>Tamias striatus</i> (30)	White- footed deer mouse <i>Peromyscus leucopus</i> (29)	North American deer mouse <i>Peromyscus maniculatus</i> (14)	Woodland vole <i>Microtus pinetorum</i> (7)
<i>Ixodes scapularis</i> nymph	0.12 ±0.125 (1)	0.28 ±0.163 (4)	0.06 ±0.046 (2)	(0)	(0)	(0)
<i>Ixodes scapularis</i> male	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes scapularis</i> female	(0)	0.07 ±0.071 (1)	(0)	(0)	(0)	(0)
<i>Ixodes scapularis</i> total	0.12 ±0.125 (1)	0.35 ±0.169 (5)	0.10 ±0.055 (3)	(0)	(0)	(0)
<i>Ixodes cookei</i> larva	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> nymph	0.75 ±0.750 (6)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> male	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> female	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes cookei</i> total	0.75 ±0.750 (6)	(0)	(0)	(0)	(0)	(0)

Table 4.3 continued

Tick species and life stage	Raccoon <i>Procyon lotor</i> (8)	Virginia opossum <i>Didelphis virginiana</i> (15)	Eastern chipmunk <i>Tamias striatus</i> (30)	White- footed deer mouse <i>Peromyscus leucopus</i> (29)	North American deer mouse <i>Peromyscus maniculatus</i> (14)	Woodland vole <i>Microtus pinetorum</i> (7)
<i>Ixodes texanus</i> larva	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> nymph	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> male	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> female	(0)	(0)	(0)	(0)	(0)	(0)
<i>Ixodes texanus</i> total	(0)	(0)	(0)	(0)	(0)	(0)
Total ticks	447.37 ±171.891 (3579)	27.85 ±16.733 (390)	0.86 ±0.562 (26)	0.41 ±0.160 (12)	1.42 ±0.521 (20)	0.57 ±0.428 (4)



Figure 4.1. Ticks infesting a sedated raccoon's paw on a farm in eastern Tennessee.

VITA

Rebecca A. Butler is from western Tennessee where she obtained Bachelor and Master of Science degrees in biology at The University of Memphis, Memphis Tennessee under the direction of Dr. Michael Kennedy. She then went on to obtain a PhD in the Department of Entomology, Plant Pathology, and Nematology at the University of Tennessee, Knoxville under the direction of Dr. Rebecca Trout Fryxell.