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Forest-associated habitat variables influence human–tick encounters in the southeastern United States

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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 the US Department of Agriculture Forest Inventory and Analysis (FIA) program, we identified environmental variables associated with tick encounters by forestry personnel. Ticks were identified by species and life stage, and site-specific variables were associated with each tick using FIA forest inventory datasets and generalized linear models with negative binomial distributions. Of the 55 FIA variables available, we identified biotic and abiotic environmental variables associated with *Amblyomma americanum* L. (carbon in litter material and standing dead tree aboveground dry biomass), *Dermacentor variabilis* Say (seedling species unevenness and elevation), and *Ixodes scapularis* L. (carbon in dead woody material and seedling species unevenness). We propose conducting future treatment–control studies using these forestry-related environmental variables to test their ability to alter tick abundance at sites. Land management decisions not only affect common flora and fauna, but changes to these habitats can also alter 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.

Key words: Amblyomma americanum, *Dermacentor variabilis*, *Ixodes scapularis*, forestry variables, forestry

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 (US). In the southeastern US, lone star ticks (*Amblyomma americanum* L.), American dog ticks (*Dermacentor variabilis* Say), and blacklegged ticks (*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 species cause the majority of vector-borne diseases in the US (Beard et al. 2021, Eisen and Paddock 2021). Specifically, they are responsible for tick-associated illnesses caused by bacteria (e.g., *Anaplasma*, *Borrelia*, *Ehrlichia*, *Francisella*, and *Rickettsia*), viruses (e.g., Heartland, Bourbon, and 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, Costero and 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 of up to 10.8 per 100,000 persons from 2008 to 2015, Rocky Mountain spotted fever incidence of >30 cases total over the entire 2000–2007 period, and an incidence rate of human granulocytic anaplasmosis of up to 75 per million persons per year from 2008 to 2012 (Openshaw et al. 2010, Dahlgren et al. 2015, Schwartz et al. 2017).

The US Centers for Disease Control and Prevention (CDC) now report expanding ranges of these important species. Expanded distributions and increased abundances of *A. americanum* in 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). *Dermacentor variabilis* is historically common in the central and southeastern US, and up until a recent species differentiation (Lado et al. 2021), it was also thought to reside in the western US. 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, Eisen and Eisen 2016, 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 the tick abundance of common southeastern tick species at a site with habitats common throughout the southeastern US, but few variables were identified to explain tick distributions. The authors noted that the 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, US Department of Agriculture (USDA), knowing the program inventories sites throughout the southeastern U.S.. Forestry crews encounter ticks at sites where they classify variables. Here, we used those tick encounters and environmental variables classified at the time of encounter. Our goal was to describe habitat suitability and identify environmental variables associated with increased tick encounters. Specifically, we used tick encounter data to analyze associations between tick abundance and environmental variables assessed during encounters.

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 5 yr (2017–2021) in the southeastern United States. Ultimately, ticks were submitted from crews in Kentucky, Tennessee, Florida, Alabama, Arkansas, Georgia, South Carolina, and Louisiana (Table 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, magnifying forceps, and 80% ethanol-filled vials. While on or traveling to/from FIA plots, crews encountered ticks and placed all collected ticks into a single vial labeled with the date, crew identifier, plot identifier, number of foresters present on the day of collection, and GPS coordinates of the plots. Submitted ticks were then identified by species and life stages using taxonomic keys (Yunker et al. 1986, Durden 1996, Keirans and Durden 1998).

We included data 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 tick of one species was submitted and the other species were not, then that site was recorded as a 0 for the absent species. In other words, if a crew sent a single *A. americanum* nymph from a site, then *D. variabilis* and *I. scapularis* were recorded as 0 for that same site. Collections in 2020 and 2021 were limited due to the Covid-19 pandemic.

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 one plot per 2,428 ha (Reams et al. 2005). Depending on the state, each forest plot is assigned to one of five, seven, or ten spatially balanced panels, and 1 panel of plots is measured every year, so that each state is completely inventoried once every 5–10 yr on an ongoing basis. Inventory data for this study were collected on a 5-yr cycle for most states, except for Alabama and Louisiana, which are on a 7-yr cycle.

Each forest inventory plot is a cluster of four points (subplots) arranged where one point is central and the other three points 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 (Supplementary Table 1). 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 2.5–12.7 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 (Supplementary Table 1). Additional forest characteristics (e.g., live tree density) were derived from the tree-level metrics

Table 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	*Amblyomma americanum*	*Dermacentor variabilis*	*Ixodes scapularis*
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	1,094 (151 sites)	88 (52 sites)	39 (30 sites)

and summarized for each plot condition on a per 0.40 ha (1-acre) basis (Supplementary Table 1). In total, 54 environmental variables describing physical geography and forest stand structure were selected as possible predictors of tick abundance (Supplementary Table 1). 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 2-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. Correlated variables (PROC CORR) (>70%), which contributed to model overfitting or dispersion, were removed from further consideration (Supplementary Table 1). 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 the number of *A. americanum* ticks encountered at each plot and environmental variables. Due to excessive zero counts for *D. variabilis* and *I. scapularis*, zero-inflated models (PROC GENMOD) with negative binomial distributions were used for each tick species separately. A stepwise regression was used for the iterative removal of nonsignificant terms to find the most parsimonious model. For plots with multiple condition classes (~30 instances), environmental variables were taken from the first forest condition encountered on the plot. This was done to account for categorical variables that could not be averaged or aggregated across condition classes to a single plot-level value. Finally, because there were differences in the number of foresters in each crew size and the amount of time that foresters spent at each plot was not recorded, 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; Fig. 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 (Supplementary Table 1). 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 caused a decrease in tick abundance (Table 2 and Fig. 2a and b). 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 2 and Fig. 2c). Elevation ($P = 0.038$) was significantly associated with *D. variabilis* abundance, in which tick numbers increased as the variables increased (Table 2 and Fig. 2d). 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 2 and Fig. 2e and f).

Discussion

The chances of a tick surviving to find its next host depend on the environment where it either molts to the next life stage or hatches from an egg to find its initial 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 United States. Our study not only identified where ticks are encountered but also provided 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 where the 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, fine woody debris (diameter < 7.6 cm), and fine 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 that 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 with humans (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 understory vegetation (Stokland 2001).

There was a decrease in *D. variabilis* abundance as seedling species unevenness increased. That is to say, *D. variabilis* encounters decreased as more and more of the total seedling count became concentrated in a single species. Plantation forestry operations typically have fewer tree species and, as a result, fewer wildlife species (Stephens and Wagner 2007). Habitats with high seedling unevenness could include areas such as timber plantations, which are numerous in the southeastern US (Miller et al. 2003, 2009). Fewer wildlife species could cause a decrease in *D. variabilis* populations. Previously, the study by Trout Fryxell et al. (2015) found no relationship between *D. variabilis* and habitat type diversity in the Southeast, whereas this study did. Because *D. variabilis* parasitize a variety of host types (small, medium, and large mammals) throughout different life stages (Kollars and Kengluecha 2001, Foster et al. 2003, Butler et al. 2020), and because 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 m mean sea level. Butler et al. (in review) found *D. variabilis* to be absent from areas with

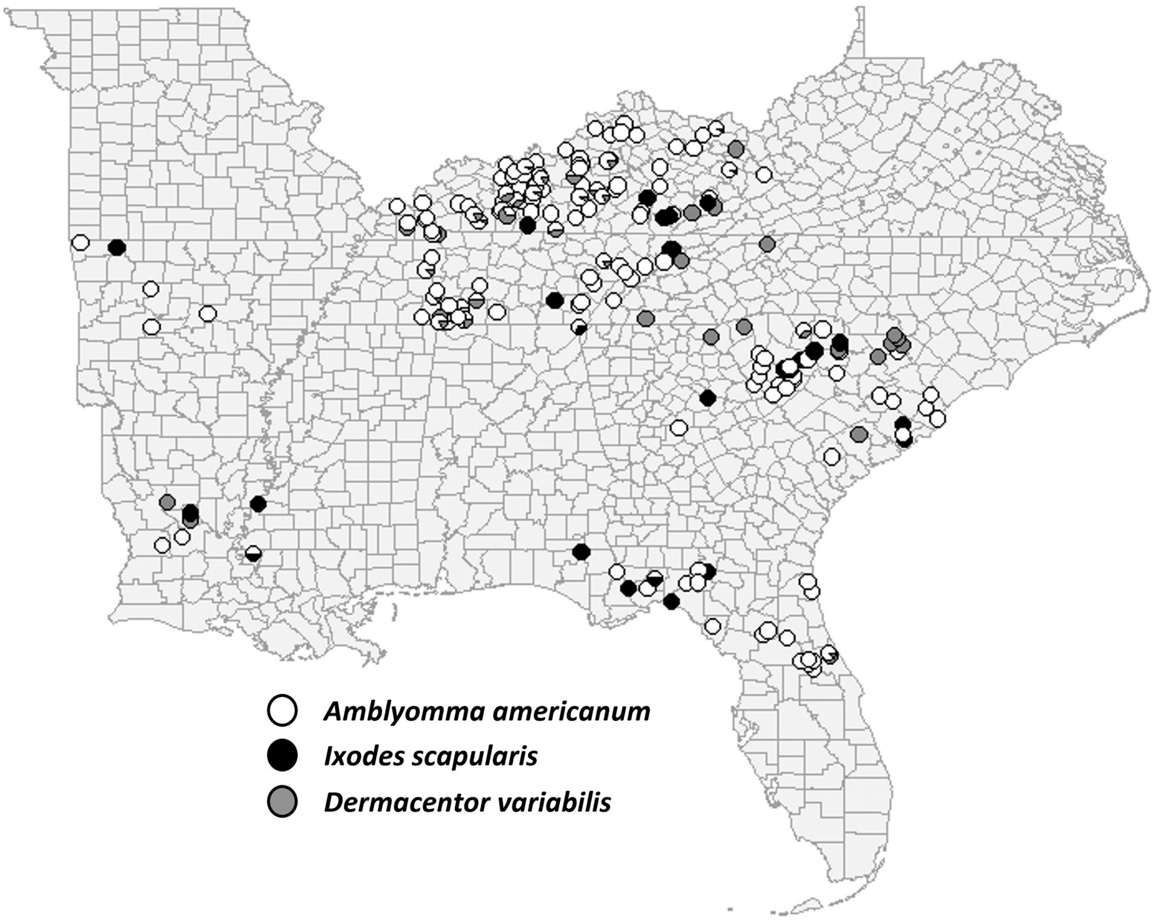

Fig. 1. Approximate location of sites where *Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis* were collected by Forestry Inventory Analysis foresters in the southeastern United States 2017–2021.

Table 2. Site-specific variables were significantly associated with each tick species (*Amblyomma americanum*, *Dermacentor variabilis*, and *Ixodes scapularis*) from the southeastern United States. A generalized linear model was used for *A. americanum*, and zero-inflated models were used for *D. variabilis* and *I. scapularis*

Tick species	Variables	Estimate	Standard error	Degrees of freedom	Regression model results
Amblyomma americanum	Standing dead tree aboveground dry biomass	−1.3565	0.4531	1, 183	$T = -2.99$; $F = 8.96$; $P = 0.0031$
	Carbon in litter material	−1.1479	0.5812	1, 183	$T = -1.98$; $F = 3.90$; $P = 0.0498$
Dermacentor variabilis	Elevation	0.0034	0.0016	1	$\chi^2 = 4.30$; $P = 0.038$
	Seedling species unevenness	−2.2719	0.9891	1	$\chi^2 = 5.28$; $P = 0.0216$
Ixodes scapularis	Seedling species unevenness	1.7515	0.8105	1	$\chi^2 = 4.67$; $P = 0.0307$
	Carbon in down dead woody material	3.6489	0.6774	1	$\chi^2 = 29.02$; $P < 0.0001$

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. That is, tick abundance increased as stumps and their associated root system and coarse woody material (diameter ≥ 7.6 cm) on the forest floor increased. This variable aligns with the larval and nympal 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 because rodents feed on invertebrates (Hamilton 1941), and coarse woody debris is associated with increased vertebrate diversity; rodents are also primary hosts for immature *I. scapularis* (Wolff and Hurlbutt 1982, Buskirk and Ostfeld 1995). Additionally, down-woody material is the foundation for carbon in down dead, and therefore, our results indicate areas with increased coarse

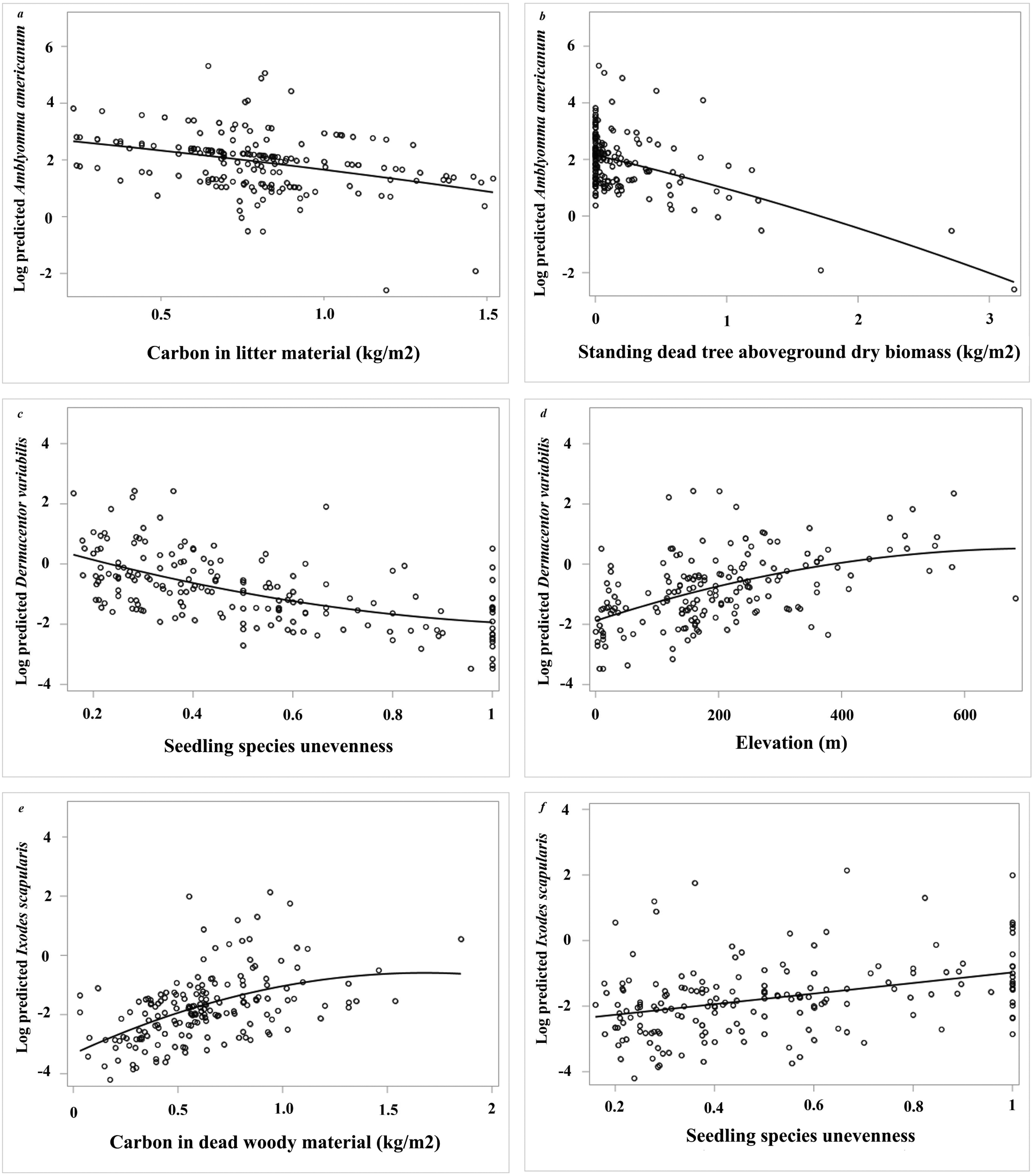

Fig. 2. Relationships between environmental variables associated with the abundance of *Amblyomma americanum* (a and b), *Dermacentor variabilis* (c and d), and *Ixodes scapularis* (e and f) on Forestry Inventory Analysis foresters in the southeastern United States (2017–2021).

woody material likely serve as a refuge for tick-infested hosts (Riffell et al. 2011). Thus, because mammal activity patterns at the forest stand level have the ability to impact *I. scapularis* tick populations (Coyle et al. 2013) increasing coarse woody material could augment mammal activity consequently increasing tick abundance. *Ixodes scapularis* abundance increased with an increase in seedling species unevenness. Unevenness in plant communities often results from the 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 increased white-tailed deer movement. Increases in tick numbers in these areas could be due to the 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 that 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, which leads to more questions about burning to reduce tick and mammal habitats to subsequently lower *I. scapularis* 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 that controlled burns can reduce the abundance of ticks and the prevalence of tick-borne 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 in 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* requires a higher relative humidity for survivability, burn treatments could be important for reducing this tick abundance by altering the 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 to environmental conditions (Cawson et al. 2020) reducing soil evaporation (Ogée et al. 2001). In addition, moist soils are associated with a more diverse and abundant array of microbial biomass (Baldrian et al. 2010), whereas dry soils are associated with a decrease in microbial biomass (Sardans and Peñuelas 2005). Previous studies have shown 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 of 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 controlled 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 tick-borne disease, or limited time to perform tick checks. Unbalanced tick collections also affected data collection geographically in which most collections were 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's *I* values indicated that there were no correlations (>70%) among locations 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 that 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 at 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). The effects of environmental variables associated with tick abundance that were not included in our full models should also be explored for their ability to manage or predict tick abundance. 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 select control strategies that 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 the management of forestry-related environmental variables and their effects on tick populations.

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Author Contributions

R. Butler (Data curation [Equal], Formal analysis [Equal], Investigation [Equal], Methodology [Equal], Visualization [Equal], Writing – original draft [Equal]), KaDonna Randolph (Data curation [Equal], Formal analysis [Equal], Methodology [Equal], Resources

[Equal], Visualization [Equal], Writing – original draft [Equal], Writing – review & editing [Equal]), James Vogt (Conceptualization [Equal], Funding acquisition [Equal], Resources [Equal], Supervision [Equal], Writing – review & editing [Equal]), Dave Paulsen (Data curation [Equal], Methodology [Equal], Writing – review & editing [Equal]), and Rebecca Trout Fryxell (Conceptualization [Equal], Data curation [Equal], Funding acquisition [Equal], Investigation [Equal], Project administration [Equal], Resources [Equal], Supervision [Equal], Writing – original draft [Equal], Writing – review & editing [Equal])

Supplementary Material

Supplementary material is available at *Environmental Entomology* online.

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