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Review

Effect of Vegetation on the Abundance of Tick Vectors in the Northeastern United States: A Review of the Literature

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Abstract

Tick-borne illnesses have been on the rise in the United States, with reported cases up sharply in the past two decades. In this literature review, we synthesize the available research on the relationship between vegetation and tick abundance for four tick species in the northeastern United States that are of potential medical importance to humans. The blacklegged tick (*Ixodes scapularis*) (Say; Acari: Ixodidae) is found to be positively associated with closed canopy forests and dense vegetation thickets, and negatively associated with open canopy environments, such as grasslands or old agricultural fields. The American dog tick (*Dermacentor variabilis*) (Say; Acari: Ixodidae) has little habitat overlap with *I. scapularis*, with abundance highest in grasses and open-canopy fields. The lone star tick (*Amblyomma americanum*) (Linnaeus; Acari: Ixodidae) is a habitat generalist without consistent associations with particular types of vegetation. The habitat associations of the recently introduced Asian longhorned tick (*Haemaphysalis longicornis*) (Neumann; Acari: Ixodidae) in the northeastern United States, and in other regions where it has invaded, are still unknown, although based on studies in its native range, it is likely to be found in grasslands and open-canopy habitats.

Key words: *Ixodes scapularis*, *Amblyomma americanum*, *Dermacentor variabilis*, *Haemaphysalis longicornis*

Tick abundance has been increasing in the United States over the past century, due to multiple factors including reforestation, changing wildlife populations, and climate change (Eisen et al. 2016, Diuk-Wasser et al. 2020). As tick populations expand, tick-borne illnesses have been on the rise, as demonstrated by reported cases more than doubling from 2004 to 2018 (Beard et al. 2019). Three tick species are recognized to present the greatest risk to humans within the northeastern United States (Centers for Disease Control and Prevention 2018). The blacklegged tick (*Ixodes scapularis*) (Say; Acari: Ixodidae) can transmit etiologic agents of Lyme disease, anaplasmosis, ehrlichiosis, babesiosis, and other illnesses (Eisen et al. 2017). The lone star tick (*Amblyomma americanum*) (Linnaeus; Acari: Ixodidae) is known to transmit the agents of multiple illnesses, and exposure to its saliva is likely the cause of alpha-gal syndrome, symptoms of which include an allergy to mammalian meat (Crispell et al. 2019). The American dog tick (*Dermacentor variabilis*) (Say; Acari: Ixodidae) can harbor the agents of Rocky Mountain spotted fever and tularemia (Eisen et al. 2017).

Additionally, the Asian longhorned tick (*Haemaphysalis longicornis*) (Neumann; Acari: Ixodidae) is an invasive tick that has been rapidly spreading in the eastern United States (Beard et al.

2018, Egizi et al. 2020, Maestas et al. 2020, Tufts et al. 2021). In Asia, *H. longicornis* has been shown to transmit the agent of severe fever with thrombocytopenia syndrome (SFTS), as well as the pathogens that cause ehrlichiosis, babesiosis, and anaplasmosis (Lee et al. 2005, Zhuang et al. 2018, Kobayashi et al. 2020). To date, no human pathogen has been reported to have been transmitted by this vector in the United States; however, the presence of *Borrelia burgdorferi*, the causative agent of Lyme disease, has been documented in an adult *H. longicornis* in southeastern Pennsylvania (Price et al. 2021). Furthermore, it has been shown to be of veterinary concern in the United States, suspected of causing death in large mammals via exsanguination in North Carolina, and of vectoring *Theileria orientalis*, a parasite that causes disease in cattle in Virginia (Oakes et al. 2019, Tufts et al. 2021).

With four species of ticks of concern in the northeastern United States, a thorough understanding of the factors that influence tick habitat for each species is needed. Ixodid ticks may spend up to 98% of their lives off-host (Lubelczyk et al. 2004, Anderson and Magnarelli 2008). While off-host, ticks can survive many months or even years without feeding due to their low resting metabolism

(Lighton and Fielden 1995). During these long periods between host contacts, their ability to survive depends on the availability of suitable habitat that allows them to avoid desiccation, drowning, predators, and pathogens (Stein et al. 2008).

Both developing and host-seeking ticks are vulnerable to desiccation (Gray et al. 2016). When ticks emerge from the soil or leaf litter to quest in exposed environments, they balance a risk/return tradeoff, putting themselves at greater risk of desiccation in exchange for the potential reward of finding a host (McClure and Diuk-Wasser 2019). Different tick species display different tolerances to desiccation, and therefore, the soil environment and structure and composition of vegetation are expected to play key roles in determining the presence and abundance of these tick species in species-specific ways.

The soil environment has been shown to affect tick survival, with soil texture, slope aspect, and hydrology all found to affect habitat quality (Burtis et al. 2019). Soil composition, including features such as the ratio of organic to inorganic matter, affects the distribution of ticks (Burtis et al. 2019). Humidity levels within the soil, influenced by snowpack, precipitation, wind speed, solar exposure, and vegetation cover, also play a role in tick distribution patterns (Burtis et al. 2019).

A challenge in assessing the role vegetation plays in tick distribution patterns is that different methods are used to collect ticks and assess tick densities (Rulison et al. 2013). In 'dragging' studies, a white corduroy cloth, typically 1 m² in size, is slowly pulled over vegetation and the ground, and then examined for ticks at regular time or distance intervals (Ostfeld et al. 1995, Rulison et al. 2013). 'Flagging' uses smaller cloths mounted on poles that can be swept in and under vegetation (Ginsberg and Ewing 1989), and hybrid techniques combine aspects of the two methods (Carroll and Schmidtmann 1992, Rulison et al. 2013). Alternate techniques to collect questing ticks include a 'walking survey', where a researcher walks through vegetation and then examines his or her clothing after a set time or distance, or 'CO$_2$ trapping' where CO$_2$ is released as an attractant with responding ticks collected on an adhesive surface or on a white cloth (Ginsberg and Ewing 1989, Falco and Fish 1992, Mays et al. 2016).

Another method to assess tick densities is sampling ticks that are feeding on vertebrate hosts. An advantage of this technique is that collection of ticks from host animals is unaffected by factors, such as dragging speed and differing vegetation structure (Estrada-Peña et al. 2013). However, flag/drag sampling collects ticks that are actively questing in an area, so more accurately measures exposure risk to humans than ticks collected from hosts (Ginsberg and Ewing 1989). Flag/drag sampling has been found to collect different information than host sampling (Ginsberg et al. 2020).

With multiple species of ticks being assessed using multiple methods, it can be challenging for researchers, land managers, and public health officials to assess the risk of tick encounters in different types of vegetation and forest types. Here, we synthesize research on the composition of vegetation and tick abundance for each of the four tick species that has significant actual or potential human health implications in the northeastern United States (*Ixodes scapularis*, *Amblyomma americanum*, *Dermacentor variabilis*, and *Haemaphysalis longicornis*).

Ixodes scapularis: Forest Dweller

Ixodes scapularis is primarily a forest-dwelling species, with at least ten studies finding higher population densities in forests than in grasslands or other open canopy habitats, and none finding the reverse (Table 1). Contrary to popular admonitions to avoid grassy areas to prevent Lyme disease, the literature reveals *I. scapularis* abundance to be typically quite low in grassy and other open canopy habitats (Duffy et al. 1994, Ginsberg and Zhioua 1996, Guerra et al. 2002). Ferrell and Brinkerhoff (2018) looked at multiple land cover variables across 13 sites in Virginia and found that the proportion of forested area was the best single predictor of *I. scapularis* nymph densities. Talbot et al. (2019) found the same studying 33 sites near Ottawa, Canada. At least six studies have found canopy cover percentage to be a predictor of *I. scapularis* abundance, with Ginsberg et al. (2020) reporting that canopy cover was the best predictor of tick densities in drag samples among several vegetation variables. Eight different studies found a positive association between *I. scapularis* and dense shrub vegetation (Schulze et al. 2002, Clow et al. 2017; Table 1).

Densities of *I. scapularis* have been found to be higher in deciduous than coniferous forests in at least six studies (Lindsay et al. 1999, Elias et al. 2006; Table 1). Lubelczyk et al. (2004) found *I. scapularis* density decreased as hemlock saplings (*Tsuga canadensis)* increased. Leaf litter in coniferous forests has a different seasonal pattern of

Table 1. Findings of selected *Ixodes scapularis* habitat association studies

Author	Year	Location	Deciduous forest	Leaf litter	Canopy	Shrubs	Pines	Grasslands
Ginsberg and Ewing	1989	NY	+			+		−
Duffy et al.	1994	NY	+					−
Ostfeld et al.	1995	NY	+					−
Ginsberg and Zhioua	1996	NY	+				−	
Lindsay et al.	1999	Ontario	+				−	
Guerra et al.	2002	WI, IL	+				−	−
Schulze et al.	2002	NJ	+	+		+		
Lubelczyk et al.	2004	ME	+	+	+	+	−	
Jordan and Schulze	2005	NJ	+	+		+		
Schulze and Jordan	2005	NJ		+			−	
Elias et al.	2006	ME	+	+	+	+	−	
Prusinski et al.	2006	NY				+		
Werden et al.	2014	Ontario			+			
Adalsteinsson et al.	2016	DE		+		+		
Clow et al.	2017	Ontario				+		
Talbot et al.	2019	Ontario			+			
Ginsberg et al.	2020	MA, WI	+		+			

+/−, indicate statistically significant positive or negative association with tick density.

deposition and is often associated with lower pH soils than deciduous forests (Dickinson 2012), perhaps leading to lower survival rates for *I. scapularis*. Consistently, leaf litter depth has been repeatedly found to be positively associated with *I. scapularis* abundance (Table 1). Ticks spend significant time waiting for a host in all three postembryonic stages of a tick's life cycle, and a deep layer of leaf litter enables them to stay hydrated (Lindsay et al. 1999). This may be particularly important for *I. scapularis*, which has been found to be more sensitive to desiccation than other sympatric species of ticks (Ginsberg and Zhioua 1996). The importance of leaf litter to *I. scapularis* has been confirmed experimentally. Removal of leaf litter has been found to dramatically reduce the abundance of both nymphs and larvae (Wilson 1986, Schulze et al. 1995), and the artificial accumulation of leaf litter due to leaf blowing has been shown to increase *I. scapularis* densities (Jordan and Schulze 2020).

Acorn production may be a factor in explaining why deciduous forests have been found to have greater *I. scapularis* densities than coniferous forests. Ostfeld et al. (1995) found that *I. scapularis* nymphal abundance was higher in oak-dominated patches the year after a mast year, but higher abundance of nymphs occurred in maple-dominated patches after nonmast years. They postulated that deer typically spend more time in maple-dominated patches but shift their space-use to oak-dominated patches when acorn production is high, altering the distribution of *I. scapularis* adults. A separate study in Virginia is consistent with this theory, finding that white-tailed deer (*Odocoileus virginianus*) (Zimmerman; Artiodactyla: Cervidae) spend approximately 40% of their time in oak patches in mast years, versus less than 5% of their time there in nonmast years (McShea and Schwede 1993).

Lubelczyk et al. (2004) found *I. scapularis* presence to be positively associated with plant species that create thickets and/or grow in moist soils, specifically Japanese barberry (*Berberis thunbergii*), winterberry holly (*Ilex verticillata*), honeysuckle species (*Lonicera* spp.), and ferns (*Osmunda* spp. and *Onoclea* spp.). Elias et al. (2006) found approximately twice the number of *I. scapularis* adults and nymphs in plots dominated by 'exotic-invasive' shrubs in the coastal region of Maine, such as oriental bittersweet (*Celastrus orbiculatus*), compared with plots dominated by native shrubs, such as highbush blueberry (*Vaccinium corymbosum*). They found that patches dominated by exotic-invasives have higher stem densities than native-dominated patches and are more resistant to deer browsing than most native species. However, invasive patches had higher deer pellet counts, indicating that the deer favor the dense invasive shrubs for cover. The authors surmise that the denser mats of exotic-invasive vegetation create a perfect storm for high *I. scapularis* abundance: protected microhabitat for white-footed mice (*Peromyscus leucopus*) (Rafinesque; Rodentia: Cricetidae), the predominant host for the

larvae and nymph stages in the studied region, along with high deer usage, the predominant host for the adult stage, combined with humid microhabitat to prevent desiccation, while all life stages host-seek. Japanese barberry, considered an exotic-invasive in the United States, was confirmed to support higher densities of larval ticks in a Connecticut study by Williams et al. (2009), who further found that barberry removal reduced *I. scapularis* tick abundance for up to 9 yr, with managed barberry stands averaging 55% fewer adult *I. scapularis* than intact barberry stands (Williams et al. 2017).

Adalsteinsson et al. (2016) studied the relationship of another exotic-invasive, multiflora rose (*Rosa multiflora*), with *I. scapularis* abundance at a fine spatial scale. They placed CO_2 traps directly in multiflora rose thickets, with paired traps placed in other vegetation 25 m away. CO_2 trapping is not considered an ideal methodology for assessing *I. scapularis* due to their low mobility, but drag/flag methods may be ineffective in areas of dense vegetation (Ginsberg and Ewing 1989, Falco and Fish 1991). Within sites, Adalsteinsson et al. trapped 2.3 times more nymphs in stands of multiflora rose versus in other vegetation although, when comparing across different sites, they found more nymphs in sites entirely absent of multiflora rose stands. Their results demonstrate how habitat associations of *I. scapularis* can be scale dependent. Table 2 summarizes specific plant species that have been found to be positively associated with *I. scapularis*.

Amblyomma americanum: Habitat Generalist

Habitat associations of *A. americanum* are still unclear. Trout Fryxell et al. (2015) failed to find any vegetation or habitat variables that predicted *A. americanum* nymph or adult abundance in Tennessee. They reported finding both adults and nymphs in moist bottomland deciduous forest, xeric upland deciduous forest, coniferous forest, and grasslands, with no significant trends. Ferrell and Brinkerhoff (2018) were similarly unable to identify any environmental variables that predicted *A. americanum* densities across 13 sites in central Virginia. An earlier Oklahoma study found no differences in survival of *A. americanum* between oak-hickory forests versus pine forests in years with normal rainfall, although the species had better survival in moist bottomland oak-hickory forests during drought years (Koch 1984). Schulze and Jordan (2005) found no consistent differences in *A. americanum* abundance between pine and mixed hardwood forests in central New Jersey.

Some studies did, however, find habitat associations between *A. americanum* and vegetation. A study in New Jersey found that *A. americanum* nymphs were most frequently encountered in open canopy conditions with less dense shrub layers and significantly reduced layers of litter and duff (Schulze et al. 2002). Stein et al. (2008) showed similar results in a Virginia forest, finding

Table 2. Plant species positively associated with *Ixodes scapularis*

Author	Year	Location	Species	Common name
Ostfeld et al.	1995	NY	*Quercus* spp.	Oaks
Lubelczyk et al.	2004	ME	*Berberis thunbergii*	Japanese barberry
			Ilex verticillata	Winterberry holly
			Lonicera spp.	Honeysuckles
			Osmunda spp.	Cinnamon fern
			Onoclea spp.	Sensitive fern
Elias et al.	2006	ME	*Berberis thunbergii*	Japanese barberry
			Lonicera spp.	Honeysuckles
			Celastrus orbiculatus	Asian bittersweet
Williams et al.	2009	CT	*Berberis thunbergii*	Japanese barberry
Adalsteinsson et al.	2016	DE	*Rosa multiflora*	Multiflora rose

that *A. americanum* nymphs and adults were negatively associated with high-density vegetation. On the other hand, Gilliam et al. (2018) found that *A. americanum* density decreased as bare ground increased and that larvae were associated with leaf litter depth and greater herbaceous and shrub cover. Koch and Burg (2006) concluded that *A. americanum* nymphs and male adults require shelter from the sun, finding that nymphs were approximately three times more likely to be found in shade than sun. However, they surprisingly found the reverse was true for adult females, which were three times more likely to be found in open-canopy sun. The authors speculate that adult females, being larger than males, are better able to tolerate warm and dry conditions and that there may be host-seeking benefits of host seeking in open areas.

Amblyomma americanum is able to survive in dryer conditions than *I. scapularis*. *Amblyomma* ticks have a waxy cuticle that reduces water loss, allowing them to live in harsher habitats than *I. scapularis* (Trout Fryxell et al. 2015). Ginsberg and Zhioua (1996) found that *A. americanum* nymphs were hardier than *I. scapularis* nymphs, showing greater survival rates in both forests and grasslands. As deer ambulate through diverse patches of vegetation, both *A. americanum* and *I. scapularis* adult ticks likely drop off in many different habitat types. However, the *A. americanum* nymphs and adults can survive in xeric habitats where *I. scapularis* cannot, such as in sandy pitch pine forests and open canopy conditions (Schulze and Jordan 2005).

In addition to tolerating xeric conditions, *A. americanum* differ from *I. scapularis* in their questing behaviors. Whereas *I. scapularis* uses an ambush strategy, *A. americanum* actively hunts, moving toward carbon dioxide and possibly vibrations (Schulze et al. 2005). *Amblyomma americanum* can move faster than *I. scapularis* (Carroll and Kramer 2001) and have been recorded moving as much as 22.8 m in 7 d, as opposed to a maximum recorded horizontal movement of only 1.6 meters in 6 d for *I. scapularis* (Wilson et al. 1972, Falco and Fish 1991). The greater movement ability of *A. americanum* may have the effect of distributing the ticks further from areas that host animals frequent, and therefore may add another source of stochasticity to their locations.

Although exotic-invasive plants have been shown to harbor high densities of *I. scapularis* (Lubelczyk et al. 2004, Elias et al. 2006), the evidence for associations between invasives and *A. americanum* is mixed. Allan et al. (2010) found higher abundances of both nymphal and adult *A. americanum* in plots with significant presence of invasive Amur honeysuckle (*Lonicera maackii*). As with *I. scapularis*, white-tailed deer are also a primary host for the adult stage of *A. americanum*, and deer use honeysuckle thickets for year-round food, thermal protection, and protective cover (Allan et al. 2010). In contrast, another study found that a widespread invasive plant in the northeastern United States may decrease the abundance of *A. americanum*. Civitello et al. (2008) performed a survival experiment and found increased mortality of *A. americanum* in Japanese stiltgrass (*Microstigeum vimineum*) versus in plots of varied native ground vegetation. Japanese stiltgrass is an invasive that often forms dense monocultures and crowds out native vegetation but grows to a shorter height than many of the natives it displaces (Civitello et al. 2008). The authors surmised that the increased mortality was due to decreased vegetation height and increased temperatures, resulting in habitat that is suboptimal for the tick species. Overall, a review of the literature shows that compared with *I. scapularis*, *A. americanum* are habitat generalists, surviving in a variety of vegetation types, including grasslands and xeric environments where *I. scapularis* would rarely be found.

Dermacentor variabilis: Field Dwellers

The adult stage of *D. variabilis* is the primary concern from a human health perspective, because nymphs and larvae have rarely been found on humans (Stafford 2004). The immature stages are primarily nidicolous, questing within host burrows and are typically found on ground-inhabiting species such as the meadow vole (*Microtus pennsylvanicus*) (Bishopp and Smith 1938, Campbell 1979). The preferred habitat of *D. variabilis* adults was described by Bishopp and Smith (1938), 'the ticks are most numerous in areas covered with grass or underbrush, occurring less frequently in forests …'. Since then, studies have confirmed Bishopp and Smith's early findings. Sonenshine and Stout (1968) found grass-dominated abandoned fields carried large numbers of adult *D. variabilis*, but that nymphs were mostly found in herbaceous plants close to deciduous forest. Dodds et al. (1969) found the highest densities of adults among fields with grasses and sedges. They also found high densities along trail edges with shrubby vegetation, but found very few in wooded areas with a well-developed canopy. Ten years later, a study in Nova Scotia found that densities of *D. variabilis* were highest in abandoned farmland covered primarily in graminoid species such as Kentucky bluegrass (*Poa pratensis*) and sheep fescue (*Festuca ovina*), and lower in forested areas (Campbell and MacKay 1979).

More recent studies confirmed earlier findings: Stein et al. (2008) reported a negative association between *D. variabilis* and high-density vegetation, and Trout Fryxell et al. (2015) found *D. variabilis* primarily in open areas, clustered in agricultural areas with defined edges. *Dermacentor variabilis* are tolerant of xeric conditions (Trout Fryxell 2015) and long-lived, with Yunik et al. (2015) finding that 20% of unfed *D. variabilis* adults survived through two Canadian winters. In one study, unfed adult *D. variabilis* were documented to live as long as 1,053 d (Stafford 2004).

Campbell and MacKay (1979) noted that the mammalian species present in an area likely affect the distribution and vegetation associations of *D. variabilis*. Whereas white-tailed deer serve as the primary host of both *I. scapularis* and *A. americanum* adults in the northeastern United States (Spielman et al. 1985, Rand et al. 2003, Kollars et al. 2000a, Paddock and Yabsley 2007), adult *D. variabilis* feed primarily on medium-sized mammals such as raccoons (*Procyon lotor*), porcupines (*Erethizon dorsatum*), and Virginia opossums (*Didelphis virginiana*) (Dodds et al. 1969, Campbell 1979, Zimmerman et al. 1988, Kollars et al. 2000b, Tufts et al. 2021). Differences in seasonal space usage patterns of these mammalian hosts, combined with increased survival rates in xeric conditions, may explain the different habitat associations of *D. variabilis* adults versus the deer-hosted *I. scapularis* and *A. americanum*.

Haemaphysalis longicornis: Still an Unknown

The invasive Asian longhorned tick, *Haemaphysalis longicornis*, was detected in the United States for the first time in late 2017 in New Jersey (Rainey et al. 2018). It has since been confirmed in 15 states and is now considered established in the United States (Hutcheson et al. 2019, Namgyal et al. 2020). Its habitat associations in the United States are not yet well characterized in the literature. Tufts et al. (2019) reported finding *H. longicornis* ticks in 17 sites on Staten Island, NY, in 2017 and 2018, 13 of which were classified as forest, and 4 of which were classified as grassland. They also reported finding *H. longicornis* in maintained lawns and tall grass on residential properties (Tufts et al. 2019). In Westchester County, NY, *H. longicornis* nymphs and adult females have been collected in tall grasses adjacent to woods as well as in well-maintained mowed lawn grass in full sun and shade (Piedmonte et al. 2020, Wormser et al.

2020). Maestas et al. (2020) collected *H. longicornis* larvae and nymphs in grasses along a hiking trail and in upland forest habitat in Delaware, and also reported collection of an adult female in wetland vegetation within intertidal marsh.

Established populations of *H. longicornis* in the United States are likely of east Asian origin (Egizi et al. 2020). Habitat studies in its native range have shown higher densities of *H. longicornis* in grassland and shrub vegetation than in coniferous and deciduous forests (Coburn et al. 2016, Jung et al. 2019, Kim et al. 2020). Multiple studies that did not explicitly examine habitat associations revealed that *H. longicornis* can be found in grasses: for example, Kamio et al. (1990) collected large numbers of all three life stages of *H. longicornis* in Japan from open cow pasture where the dominant plant was *Pleioblastus chino*, a mid-sized bamboo, while Lee et al. (2005), collected large numbers of *H. longicornis* nymphs and larvae by dragging 'grass vegetation' in nine provinces of Korea. In Australia, Sutherst and Bourne (1991) collected *H. longicornis* from maintained fields of *Pennisetum clandestinum*, a drought-tolerant lawn grass. On the other hand, Zheng et al. (2012) found high densities in shrub habitat and negligible numbers in grasslands and closed canopy forest in northern China.

Although comparisons with its native habitats may be informative, the habitat associations of *H. longicornis* may differ in the United States, where it parasitizes different hosts, with different seasonal and space use patterns than the hosts of its native range. In South Korea, Kim et al. (2013) found that mice and other small mammals did not act as hosts for *H. longicornis*, whereas several Asian studies have reported deer species to be common hosts for all three stages, including the water deer (*Hydropotes inermis*), the Siberian roe deer (*Capreolus pygargus*), and the sika deer (*Cervus nippon*) (Kim et al. 2011, Tsukada et al. 2014).

In the United States, host associations are consistent with findings in the native range; Tufts et al. (2019) reported finding no *H. longicornis* on avian hosts or mice in Staten Island, NY, but found all three life stages on white-tailed deer. Beard et al. (2018) reported that in addition to white-tailed deer, hosts in the eastern United States included domestic animals including dogs (*Canis lupus*), cows (*Bos taurus*), and sheep (*Ovis aries*), and wild mammals including coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), and groundhogs (*Marmota monax*). Ronai et al. (2019) conducted a laboratory study and found that *H. longicornis* larvae showed negative selection toward white-footed mice (*Peromyscus leucopus*). Tufts et al. (2021) sampled medium-sized mammals and found *H. longicornis* in the highest proportions on raccoons (*Procyon lotor*), opossums (*Didelphis virginiana*), and white-tailed deer. Despite these observations of the most common associations, it should be noted that *H. longicornis* has been collected from 35 mammalian species within the United States (United States Department of Agriculture 2021). Further research is required to determine whether the different mammalian hosts and the different vegetation of the United States will alter its habitat associations.

Conclusion

The literature indicates that *I. scapularis* is positively associated with closed canopy forests and dense vegetation thickets, and negatively associated with open canopy environments, such as grasslands or old agricultural fields. *Amblyomma americanum* is more of a habitat generalist, with no consistent associations found. *Dermacentor variabilis* has little habitat overlap with *I. scapularis*, with abundance highest in grasses and open canopy fields. The habitat associations of *H. longicornis* in the United States are still unknown; although based on studies in the Eastern Hemisphere, it is likely to be most abundant in grasslands and open-canopy habitats.

Beyond these broad characterizations, researchers to date have been unable to forecast fine-scale locations of ticks based on vegetation characteristics or composition. Killilea et al. (2008) noted that the factors that influence tick densities at a fine scale are poorly understood. They raised the possibility that at too fine a scale, stochastic factors may overwhelm deterministic ones, making patterns impossible to detect. Schulze et al. (2002) examined the distribution of *I. scapularis* and *A. americanum* on a single 1-ha site, setting up 100 microplots of 1 m^2 each. They found a nonrandom distribution, concluding that although sympatric, *I. scapularis* and *A. americanum* 'appear to use subtly different habitat patches'. Host movement patterns would also be critical in determining tick distributions at a small spatial scale (Diuk-Wasser et al. 2020). Future studies should increase the number of sampling plots and reduce their plot size to account for microhabitat differences within sites, even if the sites appear uniform. Further research is needed to understand the link between vegetation composition and tick densities. Larger data sets of fine-scale tick densities over longer time periods may overcome the stochastic factors and provide land managers and public health officials with a better answer to the question: where are the ticks?

Acknowledgments

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