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Prevalence of five human pathogens in host-seeking Ixodes scapularis and Ixodes pacificus by region, state, and county in the contiguous United States generated through national tick surveillance

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Abstract

The majority of vector-borne disease cases reported in the United States (U.S.) are caused by pathogens spread by the blacklegged tick, Ixodes scapularis. In recent decades, the geographic ranges of the tick and its associated human pathogens have expanded, putting an increasing number of communities at risk for tick-borne infections. In 2018, the U.S. Centers for Disease Control and Prevention (CDC) initiated a national tick surveillance program to monitor changes in the distribution and abundance of ticks and the presence and prevalence of human pathogens in them. We assessed the geographical representativeness of prevalence data submitted to CDC as part of the national tick surveillance effort. We describe county, state, and regional variation in the prevalence of five human pathogens (*Borrelia burgdorferi* sensu stricto (s.s.), *Borrelia* mayonii, Borrelia miyamotoi, Anaplasma phagocytophilum, and Babesia microti) in host-seeking I. scapularis and I. pacificus nymphs and adults. Although I. scapularis and I. pacificus are widely distributed in the eastern and western U.S., respectively, pathogen prevalence was estimated predominantly in ticks collected in the Northeast, Ohio Valley, and Upper Midwest regions,

Supplementary materials

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The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Disclaimers

The findings and conclusions in this report are those of the author(s) and do not necessarily represent the views of the Centers for Disease Control and Prevention.

CRediT authorship contribution statement

Erik Foster: Conceptualization, Data curation, Methodology, Visualization, Formal analysis, Writing – original draft, Writing – review & editing. **Sarah A. Maes:** Conceptualization, Methodology, Visualization, Formal analysis, Writing – review & editing. **Karen M. Holcomb:** Data curation, Methodology, Writing – review & editing. **Rebecca J. Eisen:** Conceptualization, Methodology, Visualization, Formal analysis, Writing – original draft, Writing – review & editing.

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where human Lyme disease cases are most commonly reported. Within these regions, we found that state and regional estimates of pathogen prevalence generally reached predictable and stable levels, but variation in prevalence estimates at the sub-state level was considerable. Borrelia burgdorferi s.s. was the most prevalent and widespread pathogen detected. Borrelia miyamotoi and A. phagocytophilum shared a similarly broad geographic range, but were consistently detected at much lower prevalence compared with B. burgdorferi s.s. Babesia microti was detected at similar prevalence to A. phagocytophilum, where both pathogens co-occurred, but was reported over a much more limited geographic range compared with A. phagocytophilum or B. burgdorferi s.s. Borrelia mayonii was identified at very low prevalence with a focal distribution within the Upper Midwest. National assessments of risk for tick-borne diseases need to be improved through collection and testing of ticks in currently under-represented regions, including the West, South, Southeast, and eastern Plains states.

Keywords

Tick surveillance; Lyme disease; Anaplasmosis; Hard tick relapsing fever; Babesiosis

1. Introduction

Ticks and tick-borne diseases pose an increasing threat to human health in the United States (U.S.), accounting for more than 75% of reported vector-borne infections (Rosenberg et al., 2018). The majority of tick-borne disease cases reported annually to the U. S. Centers for Disease Control and Prevention (CDC) are caused by pathogens spread by blacklegged ticks, Ixodes scapularis (Eisen and Eisen, 2018; NNDSS, 2023). The blacklegged tick is a vector of multiple pathogens, including the Lyme disease spirochetes Borrelia burgdorferi sensu stricto (s.s.) and *Borrelia mayonii, Borrelia miyamotoi* (hard tick relapsing fever), Anaplasma phagocytophilum (anaplasmosis), Ehrlichia muris eauclairensis (ehrlichiosis), Babesia microti (babesiosis), and Powassan virus lineage II [deer tick virus] (Powassan virus disease) (Eisen and Eisen, 2018; Fleshman et al., 2022). In the western U.S., the closely related western blacklegged tick, Ixodes pacificus, vectors a similar but more limited suite of pathogens, including B. burgdorferi s.s., B. miyamotoi, and A. phagocytophilum (Eisen et al., 2017; CDC, 2023). Although *I. scapularis* and *I. pacificus* are broadly distributed in the eastern U.S. and Pacific Coast states, respectively, the majority of infections associated with these ticks are limited to northern states in the eastern U.S. (NNDSS, 2023; Schwartz et al., 2020). The geographic range over which counties are classified as high incidence for Lyme diseases has expanded in recent decades (Kugeler et al., 2015) and this is likely related to changes in the distribution of ticks and their associated human pathogens (Eisen et al., 2016; Xu et al., 2020; Fleshman et al., 2021; Eisen and Eisen, 2023).

To monitor changes in risk for human exposure to ticks and tick-borne pathogens, CDC initiated a national tick surveillance program in 2018. The program aimed to describe the geographic distribution of medically important ticks and tick-borne pathogens, and to describe prevalence of infection in ticks and densities of host-seeking infected ticks (Eisen and Paddock, 2021). While documenting the distribution of medically important ticks is an important first step in defining risk for tick-borne diseases, understanding the distribution

of pathogens, their prevalence in ticks, and the likelihood of human-tick encounters (often measured as the density of host-seeking infected nymphs or adults) better informs estimates of risk for tick-borne disease case occurrence (Mather et al., 1996; Stafford et al., 1998; Diuk-Wasser et al., 2010, 2012; Pepin et al., 2012; Burtis et al., 2022).

Recent studies provided county scale updates on the distribution of I. scapularis and I. pacificus (Eisen et al., 2016; CDC ArboNET) and their associated human disease-causing pathogens (Fleshman et al., 2021, 2022; CDC ArboNET). Another previous study reported estimates of pathogen prevalence and co-infections in individual ticks at state and regional scales based on a limited set of ticks tested by CDC (2013–2019) using a standardized testing assay (Lehane et al., 2021). Here, we assessed the geographical representativeness of prevalence data submitted to CDC (2004–2022) as part of the national tick surveillance effort. We describe county, state, and regional variation in the prevalence of five human pathogens (B. burgdorferi s.s., B. mayonii, B. miyamotoi, A. phagocytophilum, Ba. microti) in host-seeking I. scapularis and I. pacificus nymphs and adults.

2. Methods

2.1. Prevalence datasets

We estimated the prevalence of B. burgdorferi s.s., B. mayonii, B. miyamotoi, A. phagocytophilum, and Ba. microti in host-seeking I. scapularis and I. pacificus at collection site, county, state, and regional geographic scales within the contiguous U.S. Data were derived from tick collection and testing records submitted to the ArboNET Tick Module through 2022. Collection and testing records in ArboNET are aggregated to the collection site by year, and spanned 2004 through 2022. The ArboNET Tick Module is a CDC database developed to accommodate reporting of tick surveillance data from public health agencies and their academic and other organizational partners. Standardized forms are used to generate comparable data across jurisdictions and at varying spatial scales. Records include site location, date of collection, tick species and life stage collected, collection methods, and tick-borne pathogen testing results.

CDC Division of Vector-Borne Diseases in Fort Collins, Colorado offers tick testing support for state health departments. From 2015 through 2022, ticks submitted to CDC for testing were screened individually for five known human pathogens (B. burgdorferi s.s., B. mayonii, B. miyamotoi, A. phagocytophilum, and Ba. microti) using a TaqMan testing algorithm described previously (Graham et al., 2018). Additional pathogen records for ticks tested by public health partners for one or more of the five pathogens could also be submitted to the ArboNET Tick Module. For these submissions, the ArboNET users confirmed that ticks were assayed individually using species specific molecular assays which met the minimum criteria for acceptability according to CDC Guidelines (CDC, 2018; Graham et al., 2018). All submissions contain data on collection location and date, allowing for error checking to remove duplicate entries, should these occur.

Pathogen prevalence values (no. pathogen positive ticks/no. individual ticks tested) were first calculated at the collection site level for records of host-seeking I. scapularis or I. pacificus ticks by life stage (nymph or adult) collected via tick dragging or flagging within

a single calendar year. We only included sites from which at least 25 ticks of a particular life stage were collected and submitted for testing within a single year. Although this limited the number of sampling sites included, by setting a lower limit of at least 25 ticks tested per life stage we reduce uncertainty in estimates attributable to small sample sizes. We used site level prevalence values by year and life stage to calculate annual countylevel average, minimum, and maximum prevalence values for each of the five pathogens. These annual county prevalence values for each pathogen and tick life stage were then averaged over the entire study period to generate a single average prevalence estimate, as well as minimum and maximum estimates for the county within the study period. State average prevalence values by life stage and pathogen were generated by averaging the average annual county prevalence estimates for all counties within that state. Minimum and maximum reported prevalence values represent the lowest and highest values observed at the site level, respectively. Regional average prevalence values were generated using the National Oceanic and Atmospheric Administration (NOAA) climate regions (Karl and Koss, 1984) (Figure S1) and are the average of all the county prevalence values within that region, and the corresponding minimum and maximum prevalence value from any field site within the region during the study period. States and regions were also assigned a geographic representativeness (GR) score, which is simply the proportion of counties within the state, or region where prevalence was estimated, relative to the total number of counties within that state or region.

2.2. Mapping

Tables containing county pathogen prevalence values for the five pathogens by life stage were joined in R statistical software (version 4.2.0, R Core Team, 2022) to a county-level GIS layer produced by the "usmap" package in R (Di Lorenzo, 2022) using Federal Information Processing Standards (FIPS) codes. For counties with an estimate, we plotted the average non-zero county-level prevalence for each pathogen and life stage by quartiles (i.e., lower 25%, middle 50%, and upper 25%). County, state, and NOAA climate region outlines were added for visualization. We added shading to counties for which each pathogen has previously been reported.

3. Results

3.1. Tick submissions and pathogen testing

The number of nymphal collection sites meeting study inclusion criteria for generating prevalence values ranged from 215 (B. mayonii) to 439 (B. burgdorferi s.s.) (Table 1). The number of adult collection sites ranged from 250 (B. mayonii) to 580 (A. phagocytophilum). Pathogen testing was most extensive for B. burgdorferi s.s. (27,314 nymph and 24,993) adult), A. phagocytophilum (20,969 nymph and 31,979 adult), and Ba. microti (20,174 nymph and 26,561 adult). Pathogen testing for B. mayonii was more limited, with the majority of sites yielding prevalence estimates situated in the Upper Midwest, whereas sampling for other pathogens was broadly distributed across the Northeast, Upper Midwest, Ohio River Valley and the Southeast. Western sites, predominated by collections in California, reported testing for B. burgdorferi s.s., B. miyamotoi, and A. phagocytophilum.

3.2. Geographic representativeness (GR) of prevalence estimates

The GR of prevalence estimates varied widely among states and regions (Table 1; Figs. 1–5) The GR for *B. burgdorferi* s.s., *A. phagocytophilum*, and *Ba. microti* was highest in the Northeast and Upper Midwest regions. In contrast, the Western region had the lowest GR of all regions in the study that reported prevalence estimates. Although pathogens have been recorded as present, no prevalence estimates were calculated for any counties or states within the Northern Rockies and Plains, Northwest, South, and Southwest regions of the U.S. due to either a lack of testing records or too few ticks tested at the collection site level within a single collection year (Figs. 1–5).

3.3. Prevalence estimates for five tick-borne pathogens in host-seeking nymphs and adults by pathogen

3.3.1. Borrelia burgdorferi s.s.—*Borrelia burgdorferi* s.s. was the most commonly reported pathogen present in host-seeking I. scapularis and I. pacificus adults and nymphs in all regions where prevalence estimates were calculated and was the pathogen with the greatest number of nymphs tested (Table 2). States with over 1000 nymphs tested included Connecticut, New York, Pennsylvania, Michigan, Minnesota, Wisconsin, and California, accounting for 84.19% ($N = 22,995$) of the 27,314 nymphs tested. Average state prevalence values ranged from 4.65% (range 0.00–22.00%) in I. pacificus nymphs in California to 36.46% (range 23.46–49.66%) in I. scapularis nymphs in Maine. Notably, variation within any state or region was considerable, as reflected by the ranges in prevalence values calculated at the site level (0.00–67.50%) (Supplemental Table 1). Regional prevalence averages ranged from 4.65% (range 0.00–22.00%) in the West region to 24.41% (range 2.60–50.00%) in the Northeast region (Table 2, Fig. 1).

Testing of adult *I. scapularis* for *B. burgdorferi* s.s. was greatest in Connecticut, New York, Pennsylvania, Vermont, Minnesota, and Indiana, accounting for 91.01% ($N = 22,747$) of the 24,993 adults tested (Table 3, Fig. 1). Notably, prevalence of B. burgdorferi s.s. was not estimated in adult ticks collected in the Northwest region. Prevalence of B. burgdorferi s.s. in adult ticks was generally higher than in nymphs in all states where prevalence estimates for both life stages were calculated, with average state prevalence values ranging from 0.00% in South Carolina (range 0.00–0.00%) to 69.84% in Maryland (range 58.82–80.85%). Regional prevalence averages ranged from 0.00% (range 0.00–0.00%) in the Southeast region to 56.34% (range 21.28–82.00%) in the Northeast region.

3.3.2. Borrelia mayonii—To date, *B. mayonii* has not been detected in *I. pacificus* and none were positive among ticks tested in this study (Table 2, Fig. 2). Prevalence of B. mayonii was the lowest of the five pathogens in host-seeking I. scapularis nymphs and adults, and was only reported in Michigan, Minnesota, and Wisconsin in the Upper Midwest region. The total number of nymphs tested for B. mayonii was highest in the Upper Midwest $(N = 4788)$. However, greater than 1000 nymphs were tested in the Northeast, Ohio Valley, and Southeast regions. Within the Upper Midwest region, state prevalence estimates in I. scapularis nymphs ranged from 0.04% (range 0.00–1.79%) in Michigan to 0.79% (range 0.00–14.29%) in Wisconsin.

Testing for *B. mayonii* in *I. scapularis* adults ranged from 199 individuals tested in the Southeast region to 7770 individuals tested in the Northeast region (Table 3, Fig. 2). All regions where prevalence for B. mayonii was calculated reported 0.00% (range $0.00-0.00\%$) except in the Upper Midwest where state average prevalence ranged from 0.22% (range 0.00–3.57% in Michigan) to 1.55% (range 0.00–5.83% in Minnesota).

3.3.3. Borrelia miyamotoi—*Borrelia miyamotoi* was identified at low prevalence in *I.* scapularis and I. pacificus nymphs in the Northeast, Upper Midwest, Ohio Valley, Southeast, and West regions (Table 2, Fig. 3). The number of nymphs tested varied by state and region but was highest in the Northeast region ($N = 6074$) closely followed by the Upper Midwest region ($N = 5132$). The number of nymphs tested was lowest in the Southeast region (N $= 1479$). Average state prevalence estimates ranged from 0.00% (range 0.00–0.00%) in Tennessee and West Virginia to 2.70% (range 2.70–2.70%) in the District of Columbia, with wide variation in infection prevalence at the site-and county-levels (range 0.00–13.95%) (Table 2, Supplemental Table 1, Fig. 3). Regional prevalence averages ranged from 0.57% (range 0.00–4.00%) in the Ohio Valley to 2.24% (range 0.00–8.39%) in the West (Table 2).

Testing effort for B. miyamotoi in adult I. scapularis was greater than for nymphs in the Northeast region ($N = 18,484$ adults vs. 6074 nymphs) and lower in the West region ($N =$ 1706 adults vs. 3141 nymphs) (Table 2,3). Average state-level prevalence of B. miyamotoi ranged from 0.00% (range 0.00–0.00% in Maryland, South Carolina, and Tennessee) to 3.00% (range 2.00–4.00% in Wisconsin) with wide variation at the site- and county-levels (range 0.00–15.38%) within a state (Table 3, Supplemental Table 1, Fig. 3). Regional prevalence averages ranged from 0.00% (range 0.00–0.00%) in the Southeast to 1.78% (range 0.00–7.00%) in the Upper Midwest (Table 3).

3.3.4. Anaplasma phagocytophilum—Testing effort for A. phagocytophilum in I. scapularis and I. pacificus nymphs was second only to B. burgdorferi s.s. (Table 1), with the Northeast ($N = 11,079$) and Upper Midwest ($N = 6723$) making up 84.90% of nymphs tested. The number of nymphs tested was lowest in the West region $(N = 159)$, represented only by the state of California. Average state prevalence of A. phagocytophilum in nymphs ranged from 0.00% (range 0.00–0.00%) in the District of Columbia and Tennessee to 9.43% (range 9.43–9.43%) in California with wide variation at the site- and county-levels (Table 2, Supplemental Table 1, Fig. 4). Regional prevalence averages for A. phagocytophilum in nymphs ranged from 1.90% (range 0.00–15.56%) in the Ohio Valley to 9.43% (range 9.43–9.43%) in the West (Table 2).

A total of 31,979 adult I. scapularis or I. pacificus were tested for A. phagocytophilum, which was the highest number tested per pathogen in the study (Table 1). Testing effort was greatest in the Northeast ($N = 22,266$) and Upper Midwest ($N = 5107$) representing 85.60% of adults tested. The number of adults tested was lowest in the Southeast region $(N = 199)$, represented only by the state of South Carolina. State-level average prevalence of A. phagocytophilum in adult ticks ranged from 0.00% (range 0.00–0.00%) in South Carolina and Tennessee to 12.53% (range 2.17–22.64%) in Maine, with wide variation in prevalence at the site- and county-levels (range 0.00–46.00%) (Table 3, Supplemental Table 1, Fig. 4). Regional prevalence averages in adults ranged from 0.00% (range 0.00–0.00%)

in the Southeast, represented only by South Carolina, to 10.91% in the Northeast (range 0.00–46.00%) (Table 3).

3.3.5. Babesia microti—Testing for *Ba. microti* in *I. scapularis* nymphs was reported from the Northeast, Ohio Valley, Southeast, and Upper Midwest regions (Table 1). However, Ba. microti was identified in I. scapularis nymphs only in the Northeast and Upper Midwest regions (Table 2, Fig. 5). To date, Ba. microti has not been identified in I. pacificus ticks in the U.S., and testing data for Ba. microti in I. pacificus were not reported in ArboNET. Testing was highest in the Northeast ($N = 10,505$) and Upper Midwest ($N =$ 6693), accounting for 85.24% of nymphs tested. Among regions where Ba. microti was previously reported in host-seeking I. scapularis nymphs, state average prevalence estimates ranged from 0.00% (range 0.00–0.00%) in the District of Columbia and Michigan, to 6.23% (range $0.00-32.00\%$) in New York. The regional prevalence averages in *I. scapularis* nymphs ranged from 0.00% (range 0.00–0.00%) in the Ohio Valley and Southeast to 4.56% (range 0.00–32.00%) in the Northeast (Table 2).

Babesia microti testing in I. scapularis adults was reported from the Northeast, Ohio Valley, Southeast, and Upper Midwest regions. In addition to the Northeast and Upper Midwest, Ba. microti was identified in *I. scapularis* adults in the Ohio Valley, including Illinois and Indiana (Table 3, Fig. 5). Testing was highest in the Northeast ($N = 18,619$) and Upper Midwest ($N = 5079$), accounting for 89.22% of adults tested. Among the regions where *Ba*. microti was previously reported in host-seeking *I. scapularis* adults, state average prevalence estimates ranged from 0.00% (range 0.00–0.00%) in Maryland, Ohio, and Tennessee, to 15.09% (range 4.76–35.14%) in Connecticut. Regional prevalence averages ranged from 0.00% (range 0.00–0.00%) in the Southeast, to 5.39% (range 0.00–36.00%) in the Northeast (Table 3).

4. Discussion

Understanding the distribution and geographic variation in the prevalence of pathogens in human-biting ticks aids in assessing the risk of tick-borne infections. While many previous studies have reported pathogen prevalence in Ixodes species ticks at local or state spatial scales in the U.S., few have described regional or national trends (Diuk-Wasser et al., 2012; Pepin et al., 2012; Crowder et al., 2014; Nieto et al., 2018; Lehane et al., 2021; Porter et al., 2021). The state and regional average prevalence values reported here expand upon those presented by Lehane et al. (2021) by encompassing a broader geographic coverage and highlighting the observed variability in prevalence estimates at the sub-state and sub-county spatial scales. Geographic representativeness of the data varied across the U.S. and to some extent is reflective of areas with high incidence of tick-borne diseases where public health agencies engage in tick surveillance to document and understand public risk for acquiring infections. Although Ixodes ticks are established across many counties in the western, southern, and southeastern U.S. (Eisen et al., 2016), pathogen prevalence was seldomly estimated within those regions. Lack of prevalence data is due to either limited participation in national tick surveillance efforts in those regions, or low densities of *Ixodes* species ticks resulting in volumes of ticks submitted for testing being below the inclusion criteria for our study. The average prevalence estimates at all geographic scales (county, state, and region)

may not represent the variability in tick-borne disease risk that is reflected in the range in values observed at the site level across each spatial scale.

Among regions where infection prevalence was estimated (predominantly the Northeast, Ohio Valley, and Upper Midwest), we found that average state and regional estimates of pathogen prevalence generally reached predictable and stable levels that were similar to previous reports (Prusinski et al., 2014; Johnson et al., 2017a, 2018; Lehane et al., 2021; Foley et al., 2023). Borrelia burgdorferi s.s. was the most prevalent and widespread pathogen detected. Borrelia miyamotoi and A. phagocytophilum shared a similarly broad geographic range, but were consistently detected at much lower prevalence compared with B. burgdorferi s.s. The reported prevalence of A. phagocytophilum (combining human and non-human active variants) was similar to the prevalence of Babesia microti in locations where these pathogens cooccurred, but Ba. microti was reported over a more limited geographic range compared with B. burgdorferi s.s., A. phagocytophilum or B. miyamotoi. The currently more limited geographic distribution of Ba. microti in areas of cooccurrence with B. burgdorferi s.s. appears consistent with previous studies showing Ba. microti establishment in I. scapularis populations typically lags B. burgdorferi s.s. (Diuk-Wasser et al., 2014, 2016). Within these broadly consistent regional trends, the reported range in prevalence values among collection sites within counties, states, and climate regions was broad. Variation may be attributable to ecological and host diversity among sampling sites, local abundance of vector ticks, duration of time the pathogen has been established in the area, or stochasticity related to small sample sizes (Mather et al., 1989; LoGiudice et al., 2003; Hamer et al., 2014; Prusinski et al., 2014; Foster et al., 2022).

A recent review depicted the broad geographical range of B. burgdorferi s.s. and other pathogens in host-seeking *I. scapularis* across northern tier states in the eastern U.S. and in I. pacificus throughout the tick's range in California and parts of Oregon and Washington (Fleshman et al., 2022). The reported ranges of the pathogens were more limited than the ranges of the vectors. However, in counties where pathogen records were lacking, it was unclear if absence was attributable to limited or lack of efforts to detect the pathogens, low prevalence, or if pathogens were truly absent. Here, we report pathogen prevalence within sites adhering to a standardized minimum sampling effort: at least 25 nymphs or adults tested. Counties from which we had sufficient numbers of ticks tested to estimate pathogen prevalence represented only a fraction of each pathogen's known range, with the exception of B. mayonii, where the range in counties in which ticks were tested expanded well beyond the reported range of the pathogen. For example, prevalence for B. burgdorferi s.s. in host-seeking *I. scapularis* or *I. pacificus* nymphs was calculated in only 193 of 528 (36.55%) counties where the pathogen has been reported present in these species, and in only 199 counties (37.69%) for adult ticks. Prevalence estimates were concentrated geographically in the Northeast and Upper Midwest, where high incidence of human Lyme disease has been reported for several decades (Mead, 2022).

Consistent with state-scale studies, we report B. burgdorferi s.s. prevalence at an average of 16%–24% in nymphs and 37–56% of adults in the Upper Midwest and Northeast (Prusinski et al., 2014; Johnson et al., 2018). Although B. burgdorferi s.s. has been detected in host-seeking I. scapularis in the Southeastern region (Fleshman et al., 2021, 2022),

the geographic representativeness of prevalence estimates for the region is low; only 3% of counties tested nymphs and 1% tested adults. Prevalence estimates in nymphs were concentrated primarily in Virginia and North Carolina and adult estimates were from South Carolina. Nymphal collections are likely the result of focused tick surveillance in areas where B. burgdorferi-infected I. scapularis populations are present along the Appalachian range, and where human Lyme disease cases have increased in the past decade (Brinkerhoff et al., 2014; Lantos et al., 2015; NNDSS, 2023). This contrasts with adult I. scapularis collected in South Carolina, where *B. burgdorferi* s.s. was not detected. The lack of nymphal submissions from this region is not surprising, as I. scapularis nymphs in southern states seldom host-seek in a way that they are collected by drag sampling (Diuk-Wasser et al., 2010; Arsnoe et al., 2015). Variation in infection prevalence within the Southeast region (e.g., comparison of Virginia and South Carolina) may be explained by differences in population genetic structure between northern and southern variants of I. scapularis (Xu et al., 2020; Frederick et al., 2023), differences in environmental factors affecting survivability of ticks and host-seeking behavior, with northern variant ticks ascending vegetation more commonly (Ginsberg et al., 2017; Arsnoe et al., 2019), and host and environmental factors contributing to differences in infection rates in host-seeking ticks (Kurtenbach et al., 2006; De Jesus et al., 2021). Notably, enhanced sampling and testing effort is needed in the Southeast region to better define the prevalence of pathogens in *I. scapularis* across the region.

Within nearly all counties where sufficient numbers of ticks were submitted to assess the prevalence of B. burgdorferi s.s., the prevalence rates of other pathogens were also calculated. Despite wide-spread testing, B. mayonii was detected in less than 1% of ticks submitted from Minnesota, Wisconsin and Michigan in the Upper Midwest and was not detected in any other regions. This fairly extensive testing effort supports the notion that this spirochete is rarely detected in host-seeking $I.$ scapularis and its range is currently limited to the Upper Midwest (Pritt et al., 2016; Fleshman et al., 2021, 2022; Lehane et al., 2021). Additionally, in areas where B. mayonii was detected, adult tick prevalence was higher than nymphal prevalence, indicating a potentially similar transmission cycle to B. burgdorferi s.s., where immature ticks have two opportunities to become infected from small mammal hosts (Johnson et al., 2017b; Siy et al., 2021). By contrast, B. miyamotoi was widespread, detected in each region tested, but occurred at low prevalence in nymphs and adults. This finding is consistent with previous reports at the national scale (Crowder et al., 2014; Nieto et al., 2018; Lehane et al., 2021; Porter et al., 2021). The widespread distribution may be explained by the transovarial route of transmission fostering a close association between the tick and pathogen that may be independent of the distribution of potential reservoir hosts (Scoles et al., 2001; Rollend et al., 2013; Lynn et al., 2018, 2022). However, low prevalence in ticks may be related to inefficient horizontal transmission from hosts to feeding ticks, or inefficient transstadial maintenance of infection (Lynn et al., 2019, 2022).

Anaplasma phagocytophilum was distributed similarly to B. burgdorferi s.s. in the Northeastern region but is less represented in total number of counties reported in all other regions. Additionally, A. phagocytophilum was consistently detected at lower prevalence, at rates comparable to Ba. microti, in all regions. The lower prevalence of A. phagocytophilum is consistent with previous state and regional studies (Prusinski et al., 2014; Diuk-Wasser et

al., 2016; Johnson et al., 2018; Lehane et al., 2021). This is likely the result of a relatively short-lived bacteremia in small-mammal hosts of I. scapularis such as white-footed mice (Peromyscus leucopus) (Telford et al., 1996; Stafford et al., 1999; Levin and Ross, 2004). Notably, in this study we do not differentiate between the human active variant that is known to cause anaplasmosis in humans and other variants (including the deer associated variant 1) which do not cause human disease (Massung et al., 2002; Liveris et al., 2021). Studies have shown co-circulation of these strains in some areas, but a predominance of one or the other in other localities (Courtney et al., 2003; Prusinski et al., 2023).

Babesia microti and B. burgdorferi s.s. are maintained in similar enzootic cycles involving P. leucopus and I. scapularis, resulting in frequent co-infections in I. scapularis (Diuk-Wasser et al., 2016). However, prevalence of Ba. microti is typically substantially lower than B. burgdorferi s.s. in *I. scapularis* nymphs, due to poor acquisition rates of larvae feeding on Ba. microti-infected P. leucopus and poor transstadial transmission from larvae to nymphs (Mather et al., 1990; Dunn et al., 2014). Establishment of Ba. microti normally lags B. burgdorferi s.s. (Hamer et al., 2014; Diuk-Wasser et al., 2016), a trend reflected in our data where *Ba. microti* was lacking in many counties and prevalence appears to decrease along sites radiating out from historical *I. scapularis* foci in the coastal Northeast and along the Wisconsin-Minnesota border in the Upper Midwest (Eisen and Eisen, 2023).

Although not all tick-borne diseases are nationally notifiable in the U.S., the distribution of reported cases aligns roughly with prevalence patterns in ticks reported here. For example, most high-incidence Lyme disease counties are in the Northeast and Upper Midwest regions corresponding with counties with moderately high to high prevalence of B. burgdorferi s.s. in tested ticks; incidence remains low in the South and Southeast regions where pathogen prevalence was low in tested ticks (Schwartz et al., 2017, 2020). While human anaplasmosis is reported broadly in the eastern U.S., most cases are reported from ten states in the Northeast and Upper Midwest regions, including Connecticut, Maine, Massachusetts, Minnesota, New Hampshire, New York, Pennsylvania, Rhode Island, Vermont, and Wisconsin (NNDSS, 2023). Prevalence patterns in ticks follow these broad trends. However, we did not differentiate between human pathogenic and nonpathogenic variants of A. phagocytophilum, therefore our maps may overestimate the risk of human anaplasmosis. Additionally, since human disease cases are reported by county of patient residence, and not necessarily county of exposure to an infected tick, interpretation of associations between tick prevalence and disease incidence must take this limitation into account.

An aim of the current study was to describe large scale trends in pathogen prevalence data currently available through national efforts and to highlight gaps in U.S. national estimates. Interpretation of state and regional estimates should consider these gaps, as many areas of the U.S. have limited surveillance data reported to ArboNET. Tick surveillance activities conducted by public health agencies typically target areas where people may be exposed to ticks and tick-borne pathogens in their communities with the aim of describing broad patterns in tick presence, density, and tick-borne pathogen prevalence typically at the county level. This conforms to the geographic scale of traditional epidemiological surveillance that measures the incidence of tick-borne disease cases at the county and

state scales and allows agencies to compare tick surveillance data to epidemiologic data of locally reported tick-borne disease cases. However, infection prevalence estimates generated from these non-random tick collection events may not be representative of all areas within a county, which may vary widely even within short distances. We sought to highlight sub-county scale variation by providing minimum and maximum prevalence values at the site level throughout the period of the study. Additionally, interpreting trends based exclusively on average values over such a long time period may be confounded by a lack of consistent sampling in the same locations. This may result in lower average prevalence values for areas where pathogens are recently emerging and previous prevalence estimates were zero or exceedingly low. However, these emerging high values should be reflected in the reported maximum prevalence values. Additionally, because our data inclusion criteria required at least 25 ticks tested per site within a calendar year, estimates for low-prevalence pathogens such as *B. mayonii and B. miyamotoi* may not be as reliable as using higher tick testing thresholds. Raising the threshold, however, would bias prevalence estimates to areas with well-established tick populations, potentially overlooking areas where I. scapularis or *I. pacificus* and associated pathogens are emerging. Risk assessments will be improved through widespread use of more specific assays (Hojgaard et al., 2022) and more expansive testing of ticks, particularly from the West, eastern Plains states, South, and Southeast regions where vector ticks have become established, but pathogen testing was infrequent resulting in under-representation of these areas in our surveillance effort. In addition to expanding collection and testing data, analyzing tick population densities in combination with prevalence metrics and investigating temporal trends will improve disease risk assessments at the county, state, and regional levels.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Data availability

CDC data sharing agreement does not allow sharing of tick surveillance data at the subcounty level. Data presented here in aggregate.

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Average nymphal prevalence ○ Not Detected ○ 2.22 - 12.39 ● 12.40 - 25.64 ● 25.65 - 50.00 per county (%) - B. burgdorferi s.s.

Average adult prevalence ○ Not Detected ○ 2.00 - 44.22 ● 44.23 - 60.10 ● 60.11 - 82.00 per county (%) - B. burgdorferi s.s.

Fig. 1.

Average prevalence of B. burgdorferi s.s. in host-seeking I. scapularis and I. pacificus (A) nymphs and (B) adults. County estimates indicated by colored circles at the centroid and categorized as not detected (white) or with prevalence in the lower \ll 25%; light), interquartile (25–75%; medium), or upper (> 75%; dark) quartile ranges. Documented presence of *I. scapularis* (eastern U.S.) and *I. pacificus* (western U.S.) populations (CDC, 2023) indicated by light gray, and counties where B . burgdorferi s.s. has been reported in host-seeking Ixodes ticks (CDC, 2023) are shaded dark gray.

A **County Status Tick Present** Pathogen Present No Records

Average nymphal prevalence ○ Not Detected ○ 0.37 - 0.78 ● 0.79 - 1.32 ● 1.33 - 3.70 per county (%) - B. mayonii

Average adult prevalence ○ Not Detected ○ 0.52 - 0.97 ● 0.98 - 2.01 ● 2.02 - 2.63 per county (%) - B. mayonii

Fig. 2.

B

Average prevalence of B. mayonii in host-seeking I. scapularis and I. pacificus (A) nymphs and (B) adults. County estimates indicated by colored circles at the centroid and categorized as not detected (white) or with prevalence in the lower $\langle \langle 25\% ; \text{light} \rangle$, interquartile (25–75%; medium), or upper (> 75%; dark) quartile ranges. Documented presence of I. scapularis (eastern U.S.) and *I. pacificus* (western U.S.) populations (CDC, 2023) indicated by light gray, and counties where B. burgdorferi s.s. has been reported in host-seeking Ixodes ticks (CDC, 2023) are shaded dark gray.

Average nymphal prevalence ○ Not Detected ○ 0.65 - 1.36 ● 1.37 - 2.69 ● 2.70 - 6.98 per county (%) - B. miyamotoi

Average adult prevalence ○ Not Detected ○ 0.23 - 1.52 ● 1.53 - 3.34 ● 3.35 - 15.38 per county (%) - B. miyamotoi

Fig. 3.

Average prevalence of B. miyamotoi in host-seeking I. scapularis and I. pacificus (A) nymphs and (B) adults. County estimates indicated by colored circles at the centroid and categorized as not detected (white) or with prevalence in the lower $\left($ < 25%; light), interquartile (25–75%; medium), or upper (> 75%; dark) quartile ranges. Documented presence of *I. scapularis* (eastern U.S.) and *I. pacificus* (western U.S.) populations (CDC, 2023) indicated by light gray, and counties where B . burgdorferi s.s. has been reported in host-seeking Ixodes ticks (CDC, 2023) are shaded dark gray.

Average nymphal prevalence ○ Not Detected ○ 0.98 - 3.40 ● 3.41 - 7.99 ● 8.00 - 26.00 per county (%) - A. phagocytophilum

Average adult prevalence ○ Not Detected ○ 0.26 - 5.99 ● 6.00 - 14.42 ● 14.43 - 33.00 per county (%) - A. phagocytophilum

Fig. 4.

B

Average prevalence of A. phagocytophilum in host-seeking I. scapularis and I. pacificus (A) nymphs and (B) adults. County estimates indicated by colored circles at the centroid and categorized as not detected (white) or with prevalence in the lower \ll 25%; light), interquartile (25–75%; medium), or upper (> 75%; dark) quartile ranges. Documented presence of *I. scapularis* (eastern U.S.) and *I. pacificus* (western U.S.) populations (CDC, 2023) indicated by light gray, and counties where B . burgdorferi s.s. has been reported in host-seeking Ixodes ticks (CDC, 2023) are shaded dark gray.

Average nymphal prevalence ○ Not Detected ○ 0.67 - 3.74 ● 3.75 - 8.06 ● 8.07 - 32.00 per county (%) - Ba. microti

Average adult prevalence ○ Not Detected ○ 0.50 - 3.99 ● 4.00 - 11.63 ● 11.64 - 26.00 per county (%) - Ba. microti

Fig. 5.

B

Average prevalence of Ba. microti in host-seeking I. scapularis and I. pacificus (A) nymphs and (B) adults. County estimates indicated by colored circles at the centroid and categorized as not detected (white) or with prevalence in the lower \ll 25%; light), interquartile (25–75%; medium), or upper (> 75%; dark) quartile ranges. Documented presence of I. scapularis (eastern U.S.) and *I. pacificus* (western U.S.) populations (CDC, 2023) indicated

by light gray, and counties where B. burgdorferi s.s. has been reported in host-seeking Ixodes ticks (CDC, 2023) are shaded dark gray.

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Table 1

Regional testing profiles for five tick-borne pathogens in host-seeking I. scapularis and I. pacificus generated through active tick surveillance in the Regional testing profiles for five tick-borne pathogens in host-seeking I. scapularis and I. pacificus generated through active tick surveillance in the contiguous U.S.

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were generated in the Northern Rockies and Plains, Northwest, South, and Southwest regions due to lack of tick surveillance records reported to ArboNET, or reported records not meeting study inclusion criteria. Washington D.C., represented by a single county is included in the Northeast region. criteria. Washington D.C., represented by a single county is included in the Northeast region. ∞

County-level presence of pathogens in host-seeking *I. scapularis* and *I. pacificus* ticks published in Fleshman et al. (2022) and includes additional data uploaded to CDC ArboNET from public health County-level presence of pathogens in host-seeking I. scapularis and I. pacificus ticks published in Fleshman et al. (2022) and includes additional data uploaded to CDC ArboNET from public health jurisdictions through December 31, 2022 (data available at https://www.cdc.gov/ticks/surveillance/TickbomePathogens.html). Regional percent representation is the ratio of counties where pathogen jurisdictions through December 31, 2022 (data available at <https://www.cdc.gov/ticks/surveillance/TickbornePathogens.html>). Regional percent representation is the ratio of counties where pathogen reported present in host-seeking ticks to the total counties within the region. reported present in host-seeking ticks to the total counties within the region.

Annual prevalence calculated at collection sites when 25 host-seeking Ixodes spp. ticks were collected within a calendar year and assayed for specific pathogen. Annual prevalence calculated at collection sites when ≥ 25 host-seeking Ixodes spp. ticks were collected within a calendar year and assayed for specific pathogen.

 $d_{\text{Country} \text{ prevalence}}$ is the average of all annual collection site prevalence estimates within a county throughout the study period (2004–2022). County prevalence is the average of all annual collection site prevalence estimates within a county throughout the study period (2004–2022).

 To identify tick-borne pathogens in I. scapularis and I. pacificus, ticks were tested individually using species specific molecular assays which met the minimum criteria for acceptability according to CDC To identify tick-borne pathogens in I. scapularis and I. pacificus, ticks were tested individually using species specific molecular assays which met the minimum criteria for acceptability according to CDC Guidelines: "Surveillance for *Ixodes scapularis* and pathogens found in this tick species in the United States" (2018). https://www.cdc.gov/ticks/resources/TickSurveillance_Iscapularis-P.pdf. Guidelines: "Surveillance for *Ixodes scapularis* and pathogens found in this tick species in the United States" (2018). https://www.cdc.gov/ticks/resources/TickSurveillance_Iscapularis-P.pdf.

Species-specific molecular assays for Anaplasma phagocytophilum did not discriminate between human- and non-human variants. Species-specific molecular assays for Anaplasma phagocytophilum did not discriminate between human- and non-human variants.

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Table 2

Regional and state prevalence estimates for five pathogens in host-seeking Ixodes scapularis and Ixodes pacificus nymphs reported through national tick Regional and state prevalence estimates for five pathogens in host-seeking Ixodes scapularis and Ixodes pacificus nymphs reported through national tick a surveillance in the contiguous U.S.

Ticks Tick Borne Dis. Author manuscript; available in PMC 2024 November 01.

pacificus nymphs, ticks were tested individually using species specific molecular assays which met the minimum criteria for acceptability acording to CDC Guidelines: "Surveillance for Ixodes scapularis pacificus nymphs, ticks were tested individually using species specific molecular assays which met the minimum criteria for acceptability according to CDC Guidelines: "Surveillance for Ixodes scapularis Regions correspond to U.S. Climate Regions defined by the U.S. National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information. No prevalence estimates Control and Prevention (CDC) ArboNET Tick Module, and from studies where CDC was the tick-bome pathogen resting agency (2004-2022). To identify tick-borne pathogens in *I. scapularis* and *I.* Control and Prevention (CDC) ArboNET Tick Module, and from studies where CDC was the tick-borne pathogen testing agency (2004–2022). To identify tick-borne pathogens in I. scapularis and I. and pathogens found in this tick species in the United States" (2018). https://www.cdc.gov/ticks/resources/TickSurveillance_Jscapularis-P.pdf. and pathogens found in this tick species in the United States" (2018). https://www.cdc.gov/ticks/resources/TickSurveillance_Iscapularis-P.pdf.

Host seeking Ixodes scapularis and Ixodes pacificus collected by public health agencies and academic partners. Cumulative prevalence values generated from data submitted to the U.S. Centers for Disease

were generated in the Northern Rockies and Plains, Northwest, South, and Southwest regions due to lack surveillance records reported to ArboNET or reported records not meeting study inclusion were generated in the Northern Rockies and Plains, Northwest, South, and Southwest regions due to lack of tick surveillance records reported to ArboNET or reported records not meeting study inclusion Regions correspond to U.S. Climate Regions defined by the U.S. National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information. No prevalence estimates criteria. Washington D.C., represented by a single county is included in the Northeast region. criteria. Washington D.C., represented by a single county is included in the Northeast region.

Minimum and maximum values represent the lowest and highest values recorded at the site level within the state and region. Minimum and maximum values represent the lowest and highest values recorded at the site level within the state and region.

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 d species-specific molecular assays for *Anaplasma phagocytophilum* did not discriminate between human active and non-human active variants. Species-specific molecular assays for Anaplasma phagocytophilum did not discriminate between human active and non-human active variants. **Author Manuscript**

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Regional and state prevalence estimates for five pathogens in host-seeking Ixodes scapularis and Ixodes pacificus adults reported through national tick Regional and state prevalence estimates for five pathogens in host-seeking Ixodes scapularis and Ixodes pacificus adults reported through national tick a . surveillance in the contiguous U.S.

Host seeking *Ixodes scapularis* and *Ixodes pacificus* collected by public health agencies and academic partners. Cumulative prevalence values generated from data submitted to the U.S. Centers for Disease Host seeking Ixodes scapularis and Ixodes pacificus collected by public health agencies and academic partners. Cumulative prevalence values generated from data submitted to the U.S. Centers for Disease pacificus nymphs, ticks were tested individually using species specific molecular assays which met the minimum criteria for acceptability according to CDC Guidelines: "Surveillance for *Ixodes scapularis* pacificus nymphs, ticks were tested individually using species specific molecular assays which met the minimum criteria for acceptability according to CDC Guidelines: "Surveillance for Ixodes scapularis Control and Prevention (CDC) ArboNET Tick Module, and from studies where CDC was the tick-bome pathogen testing agency (2004-2022). To identify tick-borne pathogens in *I. scapularis* and *I.* Control and Prevention (CDC) ArboNET Tick Module, and from studies where CDC was the tick-borne pathogen testing agency (2004–2022). To identify tick-borne pathogens in I. scapularis and I. and pathogens found in this tick species in the United States" (2018). https://www.cdc.gov/ticks/resources/TickSurveillance_Iscapularis-P.pdf. and pathogens found in this tick species in the United States" (2018). https://www.cdc.gov/ticks/resources/TickSurveillance_Iscapularis-P.pdf.

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Minimum and maximum values represent the lowest and highest values recorded at the site level within the state and region. Minimum and maximum values represent the lowest and highest values recorded at the site level within the state and region.

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