**Title:**

**Authors:**

**Author Affiliations:**

**Corresponding Author:**

**Abstract:**

**Keywords:**

**Highlights:**

**Graphical Abstract:**

**Introduction:**

*Anaplasma phagocytophilum* is a tick-borne, intraerythrocytic bacterium capable of causing anaplasmosis in humans and animals (Bakken 1994; Chen et al. 1994; Dumler et al. 2001; Rikihisa 1991). In the United States, *A. phagocytophilum*-infection is primarily a concern for humans and is spread by the ticks *Ixodes scapularis* in the east and *I. pacificus* in the west (Eisen et al., 2016). Anaplasmosis has been the second most frequently reported tick-borne disease in the United States, where nearly 40,000 cases were reported between 2004 and 2016 (Rosenberg et al., 2018). Notably, *A. phagocytophilum* is considered a host-generalist, however, analysis and characterization of its genetic variants over the last two decades indicate that specific genetic variants have varying host competences (Dugat et al., 2014; Stuen et al., 2013). Further, the distribution of *A. phagocytophilum* genetic variants differ across spatial scales and are likely maintained in nature through different epidemiological and ecological cycles (Stuen et al., 2013). In the United States, cases of anaplasmosis are not endemic nation-wide, and their heterogeneity is partly attributable to the distribution of genetic variants of *A. phagocytophilum* (Massung et al., 2002; Teglas and Foley, 2006).

Within the United States, New York State (NYS) holds a particularly high burden of anaplasmosis, and incidence has increased in the last two decades (Dahlgren et al., 2015; O’Connor et al., 2021; Rosenberg et al., 2018; Russell et al., 2021). Recent tick-borne disease (TBD) research in NYS has identified an area of increased risk for anaplasmosis which grew in total area from 2010 – 2018, likely attributable to the geographic delineation and spatial expansion of two primary *A. phagocytophilum* variants, the pathogenic “human-active” variant (Ap-ha) and the non-pathogenic “Variant-1” (Ap-V1) (Massung et al., 2002; Robert F. Massung et al., 2003; Massung et al., 2005; Prusinski et al., 2023; Russell et al., 2021). Despite being present within the same sub-national boundary, each genetic variant exhibits a distinct epidemiological cycle; the white-footed mouse (*Peromyscus leucopus*) is the natural reservoir of Ap-ha, and the white-tailed deer (*Odocoileus virginianus*) is the natural reservoir of Ap-V1 (Massung et al., 2002). Previous research has shown that each variant is unable to infect the other’s primary host, adding another layer of separation between these epidemiological cycles (Massung et al., 2005; Robert F. Massung et al., 2003). As Ap-ha *A. phagocytophilum* expands into locations with historically low incidence of anaplasmosis, understanding how the epidemiological cycles of both genetic variants will impact anaplasmosis risk will remain an important topic for scientific research and public health mitigation efforts.

One framework used to describe the establishment and spread of *I. scapularis* and its pathogens is the pathogen-vector-host system (Killilea et al., 2008). As much of tick-borne disease research focuses on Lyme disease, the pathogen-vector-host system has historically been used to describe how *Borrelia burgdorferi* (the causative agent of Lyme disease) is spread between its primary reservoir hosts (white-footed mice) and how *I. scapularis* uses reproductive-stage hosts (white-tailed deer) to aid in reproductive success (Mather et al., 1989; Piesman and Spielman, 1979). Notably, white-tailed deer are poor reservoirs for *B. burgdorferi*, which has prompted continued debate about the mammal’s role in spreading the pathogen (Telford et al., 1988). Two competing hypotheses are the dilution-effect and the amplification-effect (Ogden and Tsao, 2009). The dilution effect suggests that increasing biodiversity decreases the relative number of pathogen-competent hosts available to harbor a pathogen, thus decreasing pathogen-prevalence (Norman et al., 1999; Richard S. Ostfeld and Keesing, 2000; Richard S Ostfeld and Keesing, 2000). Meanwhile, the amplification-effect suggests that increasing biodiversity increases the reproductive success of *I. scapularis*, allowing for pathogens to spread more easily (Huang et al., 2019; Ogden and Tsao, 2009). The exact role of white-tailed deer in the spread of *B. burgdorferi* as it pertains to dilution or amplification remains unclear, partly because of the inability to separate white-tailed deer hosts from the downstream results in the pathogen-vector-host system, i.e., *B. burgdorferi* prevalence and *I. scapularis* density. The epidemiological cycles of Ap-ha and Ap-V1 *A.* phagocytophilum may provide insight into the role of white-tailed deer as dilution or amplification hosts given the pathogen’s differing natural reservoirs (Figure 1).

The dilution and amplification effect hypotheses are invariably related to the phenomenon of forest fragmentation. It is often assumed that as forest fragmentation increases, biodiversity within smaller, less connected forest patches will decrease (Diuk-Wasser et al., 2021). The result of decreasing biodiversity within fragmented forests leaves white-footed mice as the primary mammal by which *I. scapularis* can feed, resulting in an increase in both tick density and pathogen prevalence (Nupp and Swihart, 1998). Conversely, the relationship between forest fragmentation, white-tailed deer, and entomological risk remains difficult to disentangle. The preference of white-tailed deer towards edge habitat is well described (Alverson et al., 1988; Kremsater and Bunnell, 1992; Leopold, 1933; Miyashita et al., 2008). This behavioral preference, combined with the assumed relative increase in white-footed mice abundance in fragmented landscapes, suggests that fragmented landscapes result in increased entomological risk. Previous research has linked forest fragmentation to entomological risk; however, other research indicates that the connectivity of fragmented forests also plays a role in the propagation of tick populations and thus, tick-borne disease risk (Allan et al., 2003; Brownstein et al., 2005; Keesing et al., 2023, 2023; Tran and Waller, 2013; VanAcker et al., 2019). It appears the relationship between white-tailed deer density and forest fragmentation and land cover type can be modulated by several factors. Studies in New York City have indicated white-tailed deer are more likely to use natural land cover, while forest connectivity was positively related to nymphal *I. scapularis* prevalence (VanAcker et al., 2023, 2019). Conversely, studies in wildlife preserves, suburban, and rural areas may present conflicting evidence on the relationship between deer presence and natural land cover (Harveson et al., 2007; Hinton et al., 2022; Maurer et al., 2022, 2022; Peterson et al., 2005; Urbanek and Nielsen, 2013). In NYS, the Adirondack park is a mountainous region of nearly 25,000 km2 and consists of large connected forests but generally low estimates of deer density, tick-borne pathogen prevalence and tick-borne disease (Foley et al., 2023; Hinton et al., 2022; Hurst and Porter, 2008; Khatchikian et al., 2015, 2012; O’Connor et al., 2024; Prusinski et al., 2023, 2014; Russell et al., 2021). The effect modification of urbanization on the relationship between connectivity and white-tailed deer density is described in O’Connor et al. (in review), where geographically weighted regression models indicate positive relationships between deer density and connectivity in some regions of NYS, and negative relationships in others. Together, these results describe a scale-dependent and complex relationship between white-tailed deer, forest fragmentation, and land use.

To better define the role of white-tailed deer in the pathogen-vector-host system, this paper investigates the following:

1.) The role of white-tailed deer as they pertain to the dilution and amplification effects, or more specifically, how white-tailed deer impact entomological risk for pathogens which they are not a reservoir for, despite increasing *I. scapularis* density and reproductive success.

2.) How the relationship between white-tailed deer functional connectivity and pathogen prevalence is modulated by land cover and spatial scale.

An improved understanding of these systems can help entomologists, tick-borne disease researchers, forest managers and landscape planners in preventing tick-borne disease and the proliferation of *I. scapularis* populations in the future.

**Material and Methods:**

*Tick sampling*

Host-seeking nymphal and adult ticks were sampled at 834 unique sites between 2007 and 2024 using standardized flagging and dragging surveys as previously described (Prusinski et al., 2014). Briefly, sampling sites were selected according to habitat suitability of nymphal and adult *I. scapularis*, specifically, northern hardwood forests with accessible trails and forest edge. Nymphal *I. scapularis* were targeted at sites via dragging surveys on trails with leaf-litter during summer months (May – September) while adult *I. scapularis* were targeted at sites via flagging surveys on low-lying vegetation during spring (April – May) and fall months (October – December). The GPS coordinates of each sampling site were recorded at initial visit and were used for all data analysis. Field-collected ticks, including targeted *I. scapularis* and any bycatch tick species, were immediately placed in 99.5% ethanol. Ethanol tubes containing field-collected ticks were stored on cold packs in an insulated cooler until being transferred to a refrigerator at 4°C. Field-collected ticks were then identified to species and developmental-stage by dichotomous key under a dissecting microscope (Model SMZ1000, Nikon, Tokyo, Japan) (Keirans et al., 1996; Keirans and Clifford, 1978). Nymphal and adult *I. scapularis* were then stored in 1.5 ml Eppendorf tubes containing 99.5% ethanol and stored at -20°C until DNA extraction.

*Pathogen testing*

A maximum of 50 individual nymphal and adult *I. scapularis* per sampling site

automated total genomic DNA extraction via Qiagen QIAcube HT using the QIAamp 96 kit (Qiagen USA, Germantown, MD) according to manufacturer protocols. Extracted DNA was tested for the presence of (target genee) *A. phagocytophilum* (*msp2*), *Babesia microti* (Prioplasmida: Babesiidae) (*18s rDNA*), *B. burgdorferi* (*16S rDNA*), and *B. miyamotoi* (Spirochaetales: Spirochaetaceae) (*16s rDNA)* using a quadplex real-time PCR assay as previously described (Piedmonte et al., 2018). All samples testing positive for *A. phagocytophilum* were then tested using a custom Taqman® SNP genotyping PCR assay to differentiate between the Ap-ha and Ap-V1 variants of *A. phagocytophilum* as described by (Prusinski et al., 2023).

*Data cleaning and visualization*

Results of tick sampling and pathogen testing were summarized for each year, developmental stage, and collection site for both Ap-ha and Ap-v1 *A. phagocytophilum* using R version 4.2.1 (R Core Team, 2022). Data cleaning and summarization was performed using the `dplyr` package in R (Wickham et al., 2023). Aspatial plots and figures were created using the `ggplot2` package in R (Wickham, 2016). Maps were generated using both the `tmap` and `tmaptools` packages in R (Tennekes, 2021, 2018).

*White-tailed deer functional connectivity modeling*

White-tailed deer functional connectivity was quantified using the patch-level sinuous connection reduction (SCR) index for each unique sampling site visited, and landscape-level SCR for wildlife management units (WMUs) in NYS. (O’Connor et. al., in-review). The SCR index is a connectivity metric that makes use of least-cost paths and can be calculated for organisms with a home-range. Least-cost paths are used to calculate the movement potential of an organism based on the level of resistance a landscape provides to the organism’s movement (Keeley et al., 2021; McRae, 2012, 2006; McRae et al., 2008; McRae and Beier, 2007). Recently, least-cost paths have been used to examine how white-tailed deer connectivity influences tick density and the prevalence of *B. burgdorferi* in nymphal ticks in New York City (VanAcker et al., 2019). In this study, the patch-level SCR index functions by assessing how connected sampling site’s forest patch is to surrounding forest patches within the home-range of the organism in-question. The connection of a sampling site to nearby patches is modulated by the effort required for an organism to move between the patches, which can be modeled as the irregularity of the least-cost path taken between the patches. Mathematically, the patch-level SCR index can be written as:

(Eq. 1)

where is the area of sampling site and is the area of patch , located within a buffer of distance from focal patch . is the area of the buffer around patch , with a buffer distance typically set to be equivalent to a species-specific home range, . is the reciprocal of the sinuosity of the least-cost path between patches and , written as:

(Eq. 2)

Where is the Euclidean distance between nodes and , and is the distance of the least-cost path between patches and . Meanwhile, indicates that if there is no least-cost path between patches and , will equal zero, rather than being undefined.

Similarly, the landscape-level SCR index assesses the functional connectivity of an entire landscape by incorporating all patches within the landscape. The landscape-level SCR index can be written as:

(Eq. 3)

where is the number of patches within the landscape (with area ) and is the number of patches within the species-specific home range. All other parameters are the same as the patch-level calculation.

*Sinuous connection reduction parameterization and computation*

Both the patch-level and landscape-level SCR index was calculated using parameters previously described, where wildlife management units (WMUs) in NYS were used as landscape polygons (O’Connor et al, in review). Both types of the SCR index were calculated to examine if the relationship between the prevalence of each *A. phagocytophilum* variant and white-tailed deer functional connectivity varied with spatial scale. The home-range of white-tailed deer used in Eq. 1 was parameterized as 1,675 meters (Williams et al., 2012). Notably, the home-range of white-tailed deer can vary due to a host of biotic and abiotic factors, however, the SCR index calculation aims to provide a static estimate of connectivity (Dechen Quinn et al., 2013; Tierson et al., 1985; Whitman et al., 2018). Land cover classifications were used to identify forest patches, and were gathered in the form of raster data from the National Land Cover Database (2019) Land Cover Dataset at 30-meter resolution using the ‘FedData’ package in R version 4.2.2. (Bocinsky, 2020; Dewitz, 2021; R Core Team, 2022). Land cover classes of “deciduous forest,” “evergreen forest”, and “mixed forest” were recategorized as a single forest class, and disjoint forest patches were then identified using the `landscapemetrics` package in R using rook’s adjacency rules (Hesselbarth et al., 2019). Both 30m and 60m forest patches were removed from the calculation to improve computation times and because patches of this size do not noticeably affect the values for SCR (O’Connor et al, in review). Collection sites were then matched to the WMU they reside in, and to the nearest forest patch with a patch area greater than or equal to the mean of all forest patches in the dataset. This process ensured that focal forest patches in the patch-level SCR index calculation matched the forested areas where collections took place, rather than small, disjointed patches present in the data. The resistance-raster used in the SCR index was calculated from land cover classifications, roadway data, and alpine region data at 30-meter resolution. Land cover classifications were gathered from the National Land Cover Database (2019) Land Cover Dataset, as described. NYS roadways were gathered as vector data from the 2020 NYS Roadway Inventory System Data via NYS ArcGIS Clearinghouse. Shapefiles for alpine regions in NYS were gathered from the Environmental Protection Agency’s Ecoregion shapefiles. WMU shapefiles were gathered from the NYS Department of Environmental Conservation (DEC). Roadway and alpine region vector data were resampled to raster data at 30-meter resolution to match the NLCD 2019 Land Cover Dataset. Resistance values for each data source were assigned according to values used in the literature (Girardet et al., 2015; Gurrutxaga et al., 2011; VanAcker et al., 2019). When values for the same land cover classification were different, an average was used. Resistance values were then summed to generate final resistance values. Resistance raster values, calculations and data sources are shown in Supplementary Table 1. All operations on raster data were performed using the “terra” package in R. Least-cost-paths between adjacency pairs were calculated from the resistance raster using the ‘leastcostpath’ package in R (Lewis, 2023). All calculations were performed using the University at Buffalo’s High Performance Computing Cluster.

*Statistical analysis*

Statistical modeling was performed to estimate the relationship between white-tailed deer functional connectivity and the pathogen prevalence of both Ap-ha and Ap-v1 *A. phagocytophilum* within field-collected *I. scapularis* populations in NYS. Separate models were built for all combinations of dependent variables of Ap-ha and Ap-v1 prevalence, independent variables of patch and landscape-level SCR, for each of the field collected nymphal and adult *I. scapularis* data, resulting in eight final models. Models were built using the following process: First, zero-inflated Poisson (ZIP) models with site-level random effects were built using the `glmmTMB` package in R (Brooks et al., 2017). ZIP models used counts of Ap-ha or Ap-v1 infected *I. scapularis* as the dependent variable, patch or landscape-level SCR as the independent variable, and a log-transformed count of the total number of ticks tested as an offset. The residuals of each model were tested for spatial autocorrelation using Moran’s I ( = 0.05) via the `moranfast` package in R (Cooper, 2020; Moran, 1950). If residual spatial autocorrelation was present, spatial models were built using ZIP generalized additive models (GAMs) with site-level random effects and a spline of the interaction between latitude and longitude values of collection sites. GAMs were built using the `mgcv` package in R (Wood, 2011). Final models were then selected by comparing AIC between aspatial and spatial models.

**Results:**

*Tick sampling and pathogen testing*

Of the 834 sampling sites visited, 487 had at least one tick collected and tested for *A. phagocytophilum* between November 2007 and April 2024. A total of 149,201 *I. scapularis* were collected at 3,412 unique sampling events at these sites, and 89,921 (60.3%) of those ticks were tested with the quadplex real-time PCR assay as described. Of the 89,921 tested ticks, 6,126 (6.81%) were positive for *A. phagocytophilum*, which comprised of 4,143 Ap-ha positive ticks, 1,773 Ap-v1 positive ticks, and 236 ticks of an undetermined *A. phagocytophilum* genotype. Full genotyping results broken down by nymphal and adult *I. scapularis* life stages are presented in Table 1. The prevalence of Ap-ha and Ap-v1 in tested nymphal and adult *I. scapularis* from 2007 to 2024 are shown in Figure 2. Collection site level average prevalence of each genotype in nymphal and adult *I. scapularis* are shown in Figure 3.

*Sinuous Connection Reduction index*

**Discussion:**

**Conclusion:**

**Author contributions:**

**Tables and Figures:**

A diagram of a disease risk

Description automatically generated

Figure 1: A simplified causal diagram depicting the role of white-tailed deer in the Lyme disease and Ap-ha/Ap-V1 *Anaplasma phagocytophilum* risk systems.

A graph of growth in different times

Description automatically generated with medium confidence

Figure 2: The prevalence of Ap-ha and Ap-v1 *A. phagocytophilum* in nymphal and adult *I. scapularis* populations for each sampling event from 2007 to 2024. If 50 or greater ticks were tested, true prevalence is shown. If fewer than 50 ticks were tested, the prevalence was weighted by dividing the total positive ticks by 50 and multiplying this number by the true prevalence. Red and blue lines depict smoothed prevalences using a Generalized Additive Model.

A map of the states with different colored dots

Description automatically generated with medium confidence

Figure 3: Average site-level weighted prevalence of Ap-ha and Ap-v1 *A. phagocytophilum* in nymphal and adult *I. scapularis* populations from 2007 to 2024. If 50 or greater ticks were tested, true prevalence was used in the average calculation. If fewer than 50 ticks were tested, the prevalence was weighted by dividing the total positive ticks by 50 and multiplying this number by the true prevalence.

A map of new york state with different colored dots

Description automatically generated

Figure 4: Patch-level Sinuous Connection Reduction (SCR) values for sampling sites with at least one *I. scapularis* tested for *A. phagocytophilum* (Upper) and landscape-level SCR values for Wildlife Management Units with at least one sampling site (Lower). Histogram of patch-level SCR is presented in legend of upper panel. Sampling sites from upper panel are shown as black dots in lower panel.

|  |  |  |  |
| --- | --- | --- | --- |
|  |  |  |  |
|  | | Adults | Nymphs |
| Site visits | | 1,839 | 1,573 |
|  |  |  |  |
| Specimens collected | | 100,565 | 48,636 |
|  |  |  |  |
| Total Tested | | 55,941 (55.63%) | 32,980 (67.81%) |
|  |  |  |  |
| *A. phagocytophilum* positive | | 4,564 (8.16%) | 1,562 (4.74%) |
|  |  |  |  |
|  | Ap-ha positive | 3,452 (6.17%) | 691 (2.10%) |
|  |  |  |  |
|  | Ap-v1 positive | 987 (1.76%) | 786 (2.38%) |
|  |  |  |  |
|  | Ap-ha/Ap-v1 coinfected | 26 (0.05%) | 0 (0.00%) |
|  |  |  |  |
|  | Undetermined | 151 (0.27%) | 85 (0.26%) |

Table 1: Field sampling, pathogen testing, and *A. phagocytophilum* genotyping results for host-seeking tick collections where *I. scapularis* was the target tick species. Sampling events took place between November 2007 and April 2024. *I. scapularis* determined to be coinfected with Ap-ha and Ap-v1 are counted in both the coinfected row and the individual genotype rows.

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