**Title:**

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**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 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 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., 2012, 2015; O’Connor et al., 2024b; 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., 2024a) 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.

Here, we aim to better describe directionality of the individual relationships within the pathogen-vector-host system to determine whether white-tailed deer act as “dilution hosts” or “amplification hosts” (Figure 1). The directed acyclic graph (DAG) in Figure 1B highlights the difficulty when implicating white-tailed deer as drivers of disease risk; pathogen prevalence is a collider for white-tailed deer and *I. scapularis* while white-tailed deer are also causally related to *I. scapularis* density. This research takes advantage of the host preference of each of the *A. phagocytophilum* genotypes to deconstruct the DAG in Figure 1B. Using this method, there are a total of six components of the DAG to be assessed (Figure 1C), which allow for a more accurate description of the role of white-tailed deer play in the pathogen-vector-host system. To achieve this, we use longitudinal data from field-collected adult and nymphal *I. scapularis* samples which are genotyped to reveal the presence of Ap-ha or Ap-v1 *A. phagocytophilum.* We compare these results to a metric for forest connectivity used to infer white-tailed deer density. The results presented here describe the tickborne disease ecological and epidemiological cycles in the northeastern United States and may shed new light on the dilution and amplification effect discussion.

**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. The density of target developmental stage *I. scapularis* was calculated at each site visit as the number of target ticks divided by the total meters sampled.

*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). Summary values included counts of *I. scapularis* collected, tested, distance sampled, and total positive for Ap-ha and Ap-V1. An entomologic risk index (ERI) was calculated using these data as described previously (Mather et al., 1996). Briefly, ERI is calculated as the density of ticks at a specific location multiplied by the prevalence of a pathogen within those ticks. 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., 2024a) .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., 2024a) .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. Forest patches and corresponding patch-level SCR indices were matched to the nearest 834 unique tick sampling sites in NYS using the ‘sf’ package in R (Pebesma, 2018). 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 of all variables within the pathogen-vector-host system of white-tailed deer, *I. scapularis* and the Ap-ha and Ap-v1 genotypes of *A. phagocytophilum* (Figure 1C). Regression models were built assessing the relationship between white-tailed deer functional connectivity and *I. scapularis* density, *I. scapularis* density and Ap-ha/Ap-v1 *A. phagocytophilum* prevalence, white-tailed deer functional connectivity and Ap-ha/Ap-v1 *A. phagocytophilum* prevalence, and white-tailed deer functional connectivity and Ap-ha/Ap-v1 *A. phagocytophilum* ERI. For each relationship, separate regression models were built for adult and nymphal *I. scapularis*, resulting in 14 total final models. Models assessing Ap-ha and Ap-v1 prevalence used counts of infected ticks as dependent variables and were built as zero-inflated Poisson (ZIP) regression models where the log-transform of the total number of ticks tested was used as an offset. Models assessing Ap-ha and Ap-v1 ERI were built using a Tweedie distribution generalized linear mixed effects model (GLMM). Tweedie and ZIP models were built using the `glmmTMB` package in R (Brooks et al., 2017). Models assessing the relationship between white-tailed deer functional connectivity and *I. scapularis* density were built as a GLMMs using the `lme4` package in R (Bates et al., 2015). All models where white-tailed deer functional connectivity was used as an independent variable were built using either patch and/or landscape-level SCR, where the best model was selected as that with the lowest AIC. All models used either site-level or nested site and WMU-level random effects.

**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.

*White-tailed deer functional connectivity*

The patch and landscape-level SCR index was calculated for 66,295 forest patches and 92 WMUs in NYS, respectively. Of the 66,295 forest patches with patch-level SCR index values, 487 were matched to tick sampling sites with at least one tick genotyped for *A. phagocytophilum* variants. Of the 92 WMUs in NYS, four did not include any sampling sites within them. Maps and histograms of both patch-level SCR index values assigned to sampling sites and WMUs are shown in Figure 4. Patch-level SCR index values for 66,295 forest patches were lower on average ( = 0.336, = 0.203) than values associated with the 487 sampling sites ( = 0.446, = 0.218), reflecting study site selection preferences. Conversely, landscape-level SCR index values for WMUs appear positively skewed, where 67 of the 88 WMUs have values less than 0.1 ( = 0.094, = 0.170). The most connected WMUs correspond to those containing NYS’s largest forests and mountain ranges: the Adirondack Park, Catskill Park, and Allegheny National Forest. These values reflect the diverse ecological regions and various ecotones in NYS ranging from the most populous city in the United States (New York City) and the largest park in the contiguous United States (the Adirondack Park).

*Regression models*

Best fitting models comparing white-tailed deer functional connectivity to counts of Ap-ha included only landscape-level SCR index as an independent variable for adult and nymphal *I. scapularis*, while Ap-v1 models included both patch and landscape-level SCR (Table 2). Generally, models indicate opposite relationships between functional connectivity and each genotype; Ap-ha models indicate a positive relationship with functional connectivity for nymphal ( = 2.04, p = 0.006) and adult *I. scapularis* ( = 1.98, p = 0.051), while Ap-v1 models indicate a negative relationship with functional connectivity for nymphal ( = -1.69, p = 0.005) and adult *I. scapularis* ( = -1.19, p = 0.006). Coefficients in the models where Ap-ha is the dependent variable reflect a 1.23 and 1.22-fold greater rate of infection prevalence for every increase in 0.10 of landscape-level SCR index values, while coefficients in the models predicting Ap-v1 represent a 1.18 and 1.12-fold increase in counts of Ap-v1 when the patch-level SCR index decreases by 0.10.

Of the four models built comparing *I. scapularis* density to counts of Ap-ha and Ap-v1, two were statistically significant. The statistically significant models indicated a positive relationship between *I. scapularis* density and counts of Ap-ha infected *I. scapularis* in adults ( = 0.661, p = 0.008) and Ap-v1 infected *I. scapularis* in nymphs ( = 1.25, p = 0.002). The best fitting models comparing the density of *I. scapularis* to counts of Ap-ha and Ap-v1 *I. scapularis* are shown in Table 3.

The best fitting models comparing the SCR index and density of *I. scapularis* contained both patch and landscape-level SCR index as independent variables. However, *t-*statistic values for the landscape-level values were near zero. Patch-level coefficients for both nymphal ( = -0.027, t = -2.53) and adult *I. scapularis* ( = -0.060, t = -4.01) were negative. Final models comparing the SCR index for *I. scapularis* density are shown in Table 4.

Of the four models built to compare white-tailed deer functional connectivity to *A. phagocytophilum* ERI, only the model assessing Ap-v1 ERI within nymphal *I. scapularis* was statistically significant ( = -2.27, p = 0.002). Though the other models were not statistically significant, their coefficients followed the trend that Ap-ha ERI was positively related to white-tailed deer functional connectivity and Ap-v1 was negatively related to white-tailed deer functional connectivity. All models are shown in Table 5.

**Discussion:**

*Anaplasma phagocytophilum geography and epidemiology*

Changes in the prevalence and geography of *A. phagocytophilum* genotypes Ap-ha and Ap-v1 have been described previously and can be characterized by both the spatial expansion and increase in prevalence of the Ap-ha variant (O’Connor et al., 2021; Prusinski et al., 2023). Specifically, Ap-ha expanded northward and westward toward central NYS from 2011 to 2020, while Ap-v1, remained largely unchanged and confined to western and northern NYS along the Canadian border (Prusinski et al., 2023). These changes in Ap-ha prevalence brought about regionally-specific increases in the incidence of anaplasmosis in humans over the last 10 to 15 years, resulting in statistically significant incidence hotspots that have increased in size from 2011 to 2017 (Russell et al., 2021).

The genetic variant data presented here provide update the current understand of the genetic landscape of *A. phagocytophilum* in NYS, where it appears the prevalence of the pathogen Ap-ha variant peaks in 2021 in both adults (8.19%) and nymphs (4.04%) and slightly decreases in the years immediately following (Figure 2). Notably, 2022 and 2023 Ap-ha prevalence in adults (7.14% and 5.28%, respectively) and nymphs (1.62% and 1.57%, respectively) are within the top six prevalences recorded from 2007 to 2024, indicating that rates of Ap-ha are still elevated from previous years. The slowing growth of Ap-ha prevalence should lead to a decrease in anaplasmosis incidence, however, reported anaplasmosis incidence has increased steadily since 2010 (Figure 6). Given the northward and westward expansion of the Ap-ha variant described in earlier studies, it is plausible that Ap-ha is expanding into new areas that have been targeted less frequently for tick sampling and pathogen testing, which may result in a peak in the prevalence shown in in Figure 2. Further, areas included in the hypothesized expansion of Ap-ha include the Adirondack and Catskill mountains, two regions with decreased deer and tick density (O’Connor et al., 2024a). Decreased tick density in these regions may serve as natural barriers to the expansion of tickborne pathogens, possibly reflecting the slowed growth of Ap-ha prevalence.

*White-tailed deer functional connectivity and I. scapularis density*

The relationship between white-tailed deer functional connectivity and white-tailed deer density is paradoxical; previous calculations of landscape-level SCR within WMUs in NYS indicate the most connected forests have the lowest deer densities (O’Connor et al., 2024a). Generally, this discrepancy lies in the adaptive and scale dependent nature of deer resource selection. Areas with small resource patches with maximal edge habitat will require less movement to meet the resource needs of deer, while forests with large resource patches may require greater movement (Dechen Quinn et al., 2013). Resource patch size is also known to influence the home-range of white-tailed deer, as deer in suburban environments have lower annual home ranges than those in contiguous forests (Porter et al., 2004; Tierson et al., 1985). Other potentially influential variables include climate patterns, elevation, changes to deer behavior in response to urbanization, and the adaptive nature of deer to multiple types of environments (Dechen Quinn et al., 2013; Harveson et al., 2007; Hinton et al., 2022; Peterson et al., 2005; Williams et al., 2012).

Given white-tailed deer serve as the primary host related to the reproduction of *I. scapularis*, the inverse relationship between connectivity and deer density should also extend to *I. scapularis* density. Models presented in Table 4 confirm this hypothesis; the relationship between patch-level SCR and *I. scapularis* density is negative for both nymphs and adults, such that an increase in 0.10 of patch-level SCR decreases *I. scapularis* density by 16.52% in adults and 8.92% in nymphs. These results agree with previous research that highlights the relationship between forest fragmentation, forest edge, and tick populations (Allan et al., 2003; Brownstein et al., 2005; Li et al., 2012). However, other recent research has found that the influence of forest fragmentation on *I. scapularis* populations may not hold at all spatial scales or in all environmental contexts (Keesing et al., 2023; VanAcker et al., 2019). Allan et al. (2003) and Brownstein et al (2005), founds negative relationship between forest patch size and density of nymphal *I. scapularis* within a single county in NYS, and 12 towns in Connecticut respectively. Conversely, VanAcker et al. (2019) found that increasing white-tailed deer connectivity increased tick density in New York City, while Keesing et al. (2023) found that nymphal tick abundance was not related to the amount of forest fragmentation across six residential neighborhoods in a NYS county. The varying relationship between forest connectivity and tick density with spatial scale is reflected in the complexities of white-tailed deer movement and resource use. Though white-tailed deer reproduction may be aided by forest fragmentation over large scales, for example, NYS, it appears that this relationship can change within sub-state contexts (O’Connor et al., 2024a).

*Pathogen prevalence and the pathogen-vector-host system*

The scale-dependent complexities of white-tailed deer and *I. scapularis* density as they pertain to forest fragmentation are amplified when considering the entire pathogen-vector-host system. The model of the pathogen-vector-host system provides a useful framework for understanding the ecology and epidemiologic cycles of tickborne disease, however, understanding the role of an individual agent, variable, or state within a wider dynamic system is often context dependent and requires considering multiple confounding or intervening variables to understand its role. Examining pathogen prevalence in the pathogen-vector-host system highlights the difficulty of understanding how any one feature of the tick epidemiologic cycle relates to the infection prevalence of a particular pathogen, and therefore disease risk. When considering functional connectivity as an exogenous variable to the causal diagram in Figure 1, we can expect that as forest connectivity increases, white-tailed deer density, and therefore *I. scapularis* density, will decrease. Meanwhile, considerations for pathogens Ap-ha and *B. burgdorferi* are less clear. Lowered white-tailed deer density may increase the number of bloodmeals ticks take on pathogen-competent hosts, while at the same time may lower *I. scapularis* density due to lower availability of reproductive stage hosts. Here, including the non-pathogenic Ap-V1 variant of *A. phagocytophilum* in this analysis allows to control for variables within the different pathogen-vector-host systems. Unlike Ap-ha and *B. burgdorferi*, Ap-V1 uses white-tailed deer as a natural reservoir, thus, tick density and pathogen prevalence should both increase with increasing white-tailed deer density. The statistical results generally agree with this prediction; when considering only statistically significant independent variables, the SCR index was positively related to Ap-ha prevalence and negatively related to Ap-V1 prevalence (Table 3). When considering all variables, it appears the relationship between white-tailed deer functional connectivity and pathogen prevalence may be scale-dependent for each genetic variant of *A. phagocytophilum*. Figure 5 demonstrates directionally opposite slopes of the relationships between landscape-level SCR index values and prevalences of each *A. phagocytophilum* genotypes. Notably, the comparisons using the patch-level SCR index do not show a difference in slopes between the genotypes, though this figure does not immediately depict which slopes are statistically significant, nor does it utilize a ZIP model depicted in the statistical analysis. As the relationship between white-tailed deer connectivity and white-tailed deer density is scale-dependent, it follows that the relationship between white-tailed deer density and pathogen prevalence should also be scale dependent. In future analysis, more data may allow the scale-dependent relationship between pathogen prevalence and white-tailed deer connectivity to be defined more concretely.

*Deforestation, reforestation and the dilution and amplification effects*

Though white-tailed deer are a keystone species in the pathogen-vector-host system of *I. scapularis* and its associated pathogens, it is also important to consider how the availability of other hosts, particularly those that serve as pathogen reservoirs, may impact pathogen prevalence and tick density. The availability of additional hosts, i.e. biodiversity, is often assessed using forest fragmentation as a proxy, and debate continues about if increasing biodiversity acts through the dilution or amplification effects (Diuk-Wasser et al., 2021). The results here suggest white-tailed deer act as amplification hosts for the pathogenic Ap-ha *A. phagocytophilum* (and presumably *B. burgdorferi*). ~~The mechanism of this relationship can be summarized as when forest connectivity increases, deer density decreases, resulting in an increase in pathogen prevalence and a decrease in tick density~~

For Ap-ha / *B. burgdorferi*

(as connectivity increases and deer density decreases, Ap-ha prevalence increases, and tick density decreases).

For Ap-v1

(as connectivity increases and deer density decreases, Ap-v1 prevalence and tick density both decrease).

at the landscape level in both adult and nymphal *I. scapularis* (Table 3). Conversely, the SCR index was statistically significantly negatively related to Ap-V1 prevalence in both adult and nymphal scapularis at the patch-level, but positively related to Ap-V1 at the landscape level.

and *I. scapularis* density likely causes greater transfer of pathogens from tick vectors to mammalian hosts. and pathogen prevalence will increase. the consideration of white-tailed deer as a detriment to pathogen proliferation and a benefit to tick density and fecundity (Figure 1). The result of the conflict between these two relationships makes assessing the role of white-tailed deer in disease risk difficult. Notably, as

should also play a role in the geography of *A. phagocytophilum* variants and other *Ixodes*-borne pathogens. Adding functional connectivity as an exogenous variable to the causal diagram in Figure 1 would predict that increases in functional connectivity of deer would result in downstream decreases in pathogen prevalence of *B. burgdorferi* and Ap-ha, and an increase in Ap-V1.

Much discussion in the tickborne disease literature involves examining how single species of mammalian hosts, particularly white-tailed deer and white-footed mice, affect tickborne disease risk. White-tailed deer serve as a keystone species within the system as primarily increasing the reproductive ability of *I. scapularis*, while at the same time are unlikely to infect feeding *I. scapularis* with a pathogen.

**Conclusion:**

**Author contributions:**

**Tables and Figures:**



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.

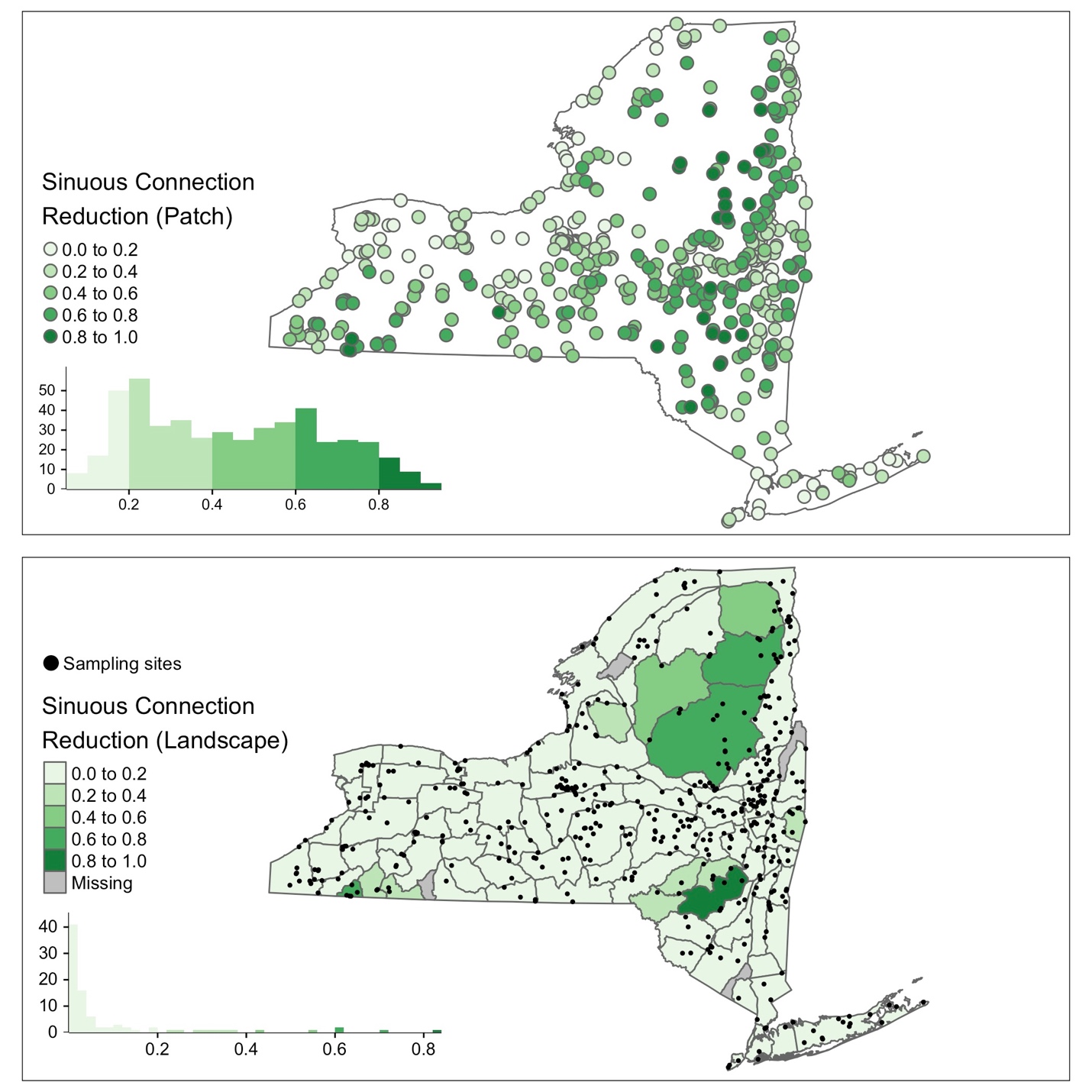


Figure 4: Patch-level Sinuous Connection Reduction (SCR) values for sampling sites with at least one *I. scapularis* tested for *A. phagocytophilum* (Upper) and landscape-level SCR values for Wildlife Management Units with at least one sampling site (Lower). Histogram of patch-level SCR is presented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

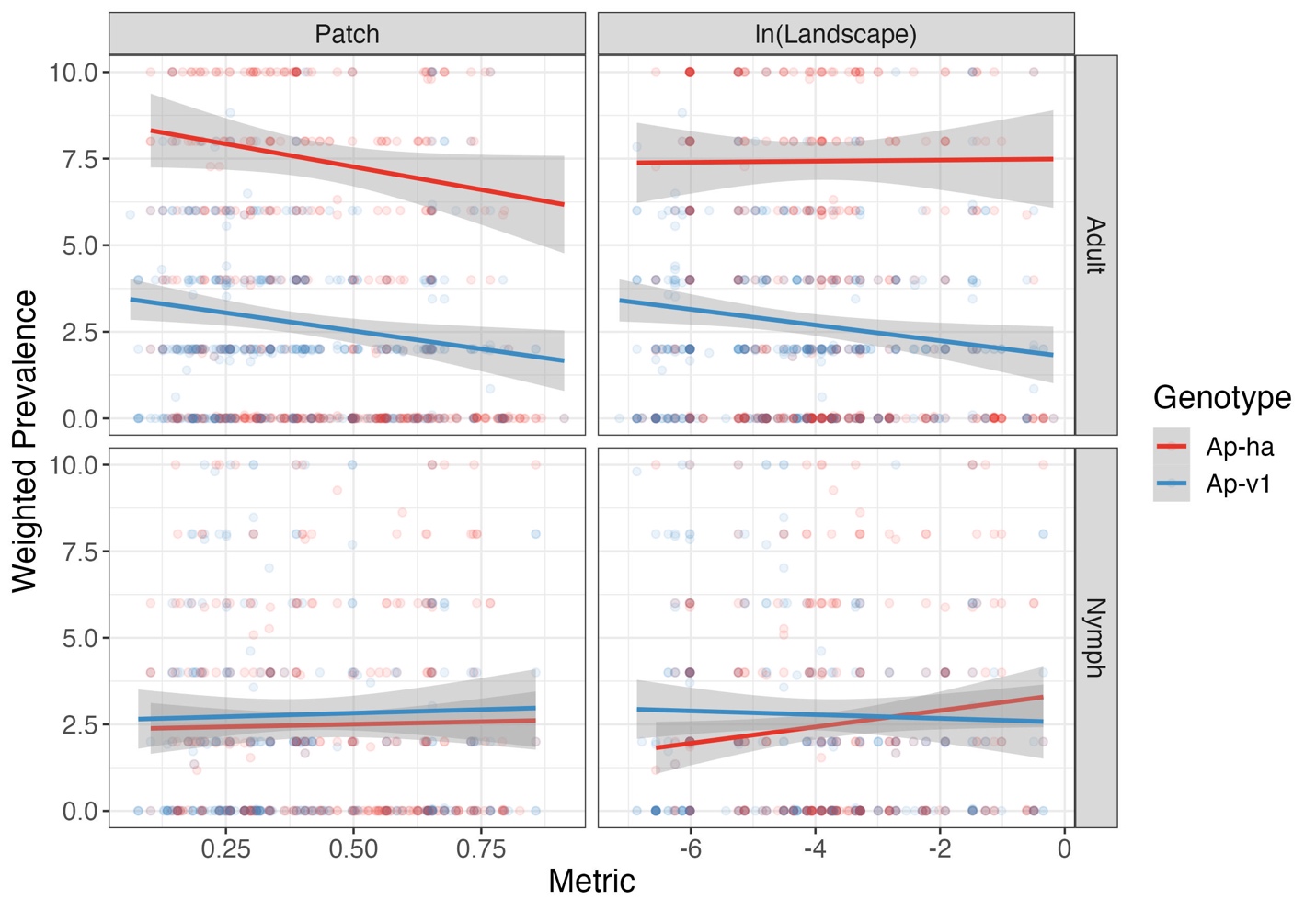


Figure 5: Linear relationships between landscape and patch-level sinuous connection reduction (SCR) index and the weighted prevalence of Ap-ha and Ap-V1 *A. phagocytophilum* in field-collected *I. scapularis*. Y-axis is scaled to only include weighted prevalence values up to ten, and prevalence values of zero are excluded. Linear models are created separately for type of SCR index, developmental stage of *I. scapularis* and *A. phagocytophilum* genotype.

A line graph with numbers

Description automatically generated

Figure 6: Incidence of anaplasmosis in New York State (excluding New York City) per 100,000 from 2010 to 2022. Data gathered from New York State Department of Health Communicable Disease Annual Reports (2010 – 2022).

|  |  |  |  |
| --- | --- | --- | --- |
|  |  |  |  |
|  | | 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.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Lifestage | Genotype | Parameters | AIC | |
| Adult |  |  |  |  | |  |
|  | ha |  |  |  | |  |
|  |  | SCR (patch) + SCR (landscape) |  | 4,784.99 | |  |
|  |  | SCR (landscape) |  | 4,782.00\* | |  |
|  |  | SCR (patch) |  | 4,896.74 | |  |
|  | v1 |  |  |  | |  |
|  |  | SCR (patch) + SCR (landscape) |  | 2,831.91\* | |  |
|  |  | SCR (landscape) |  | 2,837.63 | |  |
|  |  | SCR (patch) |  | 2,837.77 | |  |
| Nymph |  |  |  |  | |  |
|  | ha |  |  |  | |  |
|  |  | SCR (patch) + SCR (landscape) |  | 2,025.72 | |  |
|  |  | SCR (landscape) |  | 2,005.67\* | |  |
|  |  | SCR (patch) |  | 2,023.72 | |  |
|  | v1 |  |  |  | |  |
|  |  | SCR (patch) + SCR (landscape) |  | 2,034.27\* | |  |
|  |  | SCR (landscape) |  | 2,040.23 | |  |
|  |  | SCR (patch) |  | 2,034.77 | |  |

Table 2: Model fit of Zero Inflated Poisson Mixed-Effects Models comparing patch and landscape-level forest connectivity to the count of Ap-ha and Ap-V1 *A. phagocytophilum*-infected *I. scapularis*. Best fitting models are denoted by an asterisk.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| Lifestage | Genotype | Variable | β | IRR | p |
| Adult |  |  |  |  |  |
|  | ha |  |  |  |  |
|  |  | SCR (landscape) | 1.98 | 7.24 | 0.051 |
|  | v1 |  |  |  |  |
|  |  | SCR (patch) | -1.19 | 0.30 | 0.006\* |
|  |  | SCR (landscape) | 0.31 | 1.36 | 0.654 |
| Nymph |  |  |  |  |  |
|  | ha |  |  |  |  |
|  |  | SCR (landscape) | 2.04 | 7.69 | 0.006\* |
|  | v1 |  |  |  |  |
|  |  | SCR (patch) | -1.69 | 0.18 | 0.005\* |
|  |  | SCR (landscape) | 1.69 | 5.39 | 0.062 |

Table 3: Best fitting Zero Inflated Poisson Mixed-Effects Models comparing patch and landscape-level forest connectivity to the count of Ap-ha and Ap-V1 *A. phagocytophilum*-infected *I. scapularis*. Statistically significant variables are denoted by an asterisk.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Lifestage | Parameter | β | eβ | t |
| Adult |  |  |  |  |
|  | SCR (patch) | -1.80 | 0.16 | -5.057 |
|  |  |  |  |  |
| Nymph |  |  |  |  |
|  | SCR (patch) | -0.93 | 0.39 | -2.830 |

Table 4: Best fitting generalized linear mixed-models comparing patch and landscape-level forest connectivity to the density of field-collected nymphal and adult *I. scapularis*. Dependent variable is log transformed and the exponentiated estimate is shown.

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