The direct and indirect effects of white-tailed deer on black-legged ticks

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Abstract

As a consequence of climate change, habitat degradation, and increased human-wildlife interaction, vector-borne zoonotic diseases have been emerging at unprecedented rates. In the Northern hemisphere, the most prevalent vector-borne disease is Lyme disease, which is transmitted by a tick vector. In Canada Lyme disease has emerged in recent decades and is projected to expand geographically. Currently, the areas of greatest concern within Canada are Ontario, Quebec, and Nova Scotia. In Eastern North America the Lyme disease pathogen is transmitted by black-legged ticks that depend on specific habitat characteristics, environment, and set of vertebrate hosts to complete their life cycle and establish. White-tailed deer are considered an essential host for reproduction of ticks although they are incompetent Lyme disease reservoirs. As an essential host, the direct effect of deer abundance on tick abundance has been well studied. Furthermore, white-tailed deer are keystone herbivores, and in high densities, their browsing has detrimental ecosystem impacts across multiple trophic levels. However, the indirect impact of deer browsing on tick abundance is not well known. Understanding both the direct and indirect effects of deer on tick abundance is essential for informing future management strategies aimed at reducing human disease risk.

In this thesis, I first provide context on the emergence of Lyme disease in North America, with a focus on Quebec. I review the current knowledge on tick ecology, the historical and projected emergence and spread of the disease, and the role of white-tailed deer. Next, I investigate the direct and indirect impacts of deer on tick abundance at a UNESCO biosphere reserve located in Quebec. I measured deer abundance using motion-sensor camera traps, tick abundance by collection, and vegetation using deer exclosures at 15 sampling sites to determine the impact of deer browsing on vegetation, the effect of deer abundance on tick abundance, and

the effect of vegetation on tick abundance. I found that within deer exclosures there was an increased number of plants, an increased mean plant height, and in one sector of the reserve, an increased number of plant species. Further, I found that tick abundance was not affected directly by deer abundance, but the number of ticks decreased with the number of plants, and more ticks were present inside the exclosures vs outside. I then discuss the implications of the observed patterns and propose future studies that would explore these further. To conclude, I outline how this study and proposed future studies can inform deer-targeted management strategies for reducing human disease risk, especially in nature parks where the potential for human-tick contact is heightened.

Résumé

En conséquence du changement climatique, de la dégradation de l'habitat et de l'augmentation des interactions entre les humains et la faune, les maladies zoonotiques à transmission vectorielle émergent à un rythme sans précédent. Dans l'hémisphère nord, la maladie à transmission vectorielle la plus répandue est la maladie de Lyme, transmise par une tique. Au Canada, la maladie de Lyme est apparue au cours des dernières décennies et devrait s'étendre géographiquement. Actuellement, les régions les plus préoccupantes au Canada sont l'Ontario, le Québec et la Nouvelle-Écosse. Dans l'est de l'Amérique du Nord, le pathogène de la maladie de Lyme est transmis par des tiques à pattes noires qui dépendent des caractéristiques de l'habitat, de l'environnement et des hôtes vertébrés pour compléter leur cycle de vie et s'établir. Le cerf de Virginie est considéré comme un hôte essentiel pour la reproduction des tiques, bien qu'il soit un réservoir incompétent de la maladie de Lyme. En tant qu'hôte essentiel, l'effet direct de l'abondance des cerfs sur l'abondance des tiques a été bien étudié. En outre, le cerf de Virginie est un herbivore clé de voûte et, en cas de fortes densités, son broutage a des effets néfastes sur l'écosystème à plusieurs niveaux trophiques. Cependant, l'impact indirect du broutage des cerfs sur l'abondance des tiques n'a pas été bien étudié. Il est essentiel de comprendre les effets directs et indirects des cerfs sur l'abondance des tiques afin d'éclairer les futures stratégies de gestion visant à réduire les risques de maladies humaines.

Tout d'abord, je présente le contexte de l'émergence de la maladie de Lyme en Amérique du Nord, en mettant l'accent sur le Québec. Je passe en revue l'écologie des tiques, l'émergence et la propagation historiques et prévues de la maladie, ainsi que le rôle du cerf de Virginie. Ensuite, j'étudie les impacts directs et indirects des cerfs sur l'abondance des tiques dans une réserve de biosphère de l'UNESCO située au Québec. J'ai mesuré l'abondance des cerfs à l'aide de pièges photographiques à détecteur de mouvement, l'abondance des tiques par collecte, et la végétation à l'aide d'exclos de cerfs sur 15 sites d'échantillonnage afin de déterminer l'impact du broutage des cerfs sur la végétation, l'effet de l'abondance des cerfs sur l'abondance des tiques, et l'effet de la végétation sur l'abondance des tiques. J'ai constaté qu'à l'intérieur des exclos de cerfs, il y avait un plus grand nombre de plantes, une hauteur moyenne des plantes plus élevée et, dans un secteur de la réserve, un plus grand nombre d'espèces de plantes. De plus, j'ai constaté que l'abondance des tiques n'était pas directement affectée par l'abondance des cerfs, mais que le nombre de plantes avait un impact négatif sur le nombre de tiques. En outre, il y avait plus de tiques à l'intérieur des exclos qu'à l'extérieur. Je discute ensuite des implications des effets observés et propose des études futures qui permettraient de les explorer davantage. Pour conclure, j'explique comment cette étude et les études futures proposées peuvent éclairer les stratégies de gestion ciblant les cerfs pour réduire le risque de maladie humaine, en particulier dans les parcs naturels où le potentiel de contact entre les humains et les tiques est plus élevé.

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Contribution of authors

Thesis format

This thesis consists of two chapters. The first chapter is a literature review, and the second chapter is a manuscript which will be submitted for publication.

Chapter 1 - The emergence of Lyme disease in Quebec and Eastern North America: A literature review

Kari Hollett researched the literature and wrote the first chapter, Dr. Virginie Millien reviewed it.

Chapter 2 - The effect of white-tailed deer on the distribution and abundance of black-legged ticks

Kari Hollett designed and conducted the field study, completed the data analysis, and wrote the manuscript. Dr. Virginie Millien supervised and provided funding for the study, designed the field study, contributed to data analysis, and reviewed the manuscript.

General introduction

Global change and the rise of zoonotic diseases

The current rate of global change has been leading the earth's system towards dangerous thresholds that will have devastating consequences if crossed (Steffen et al. 2018; Lenton et al. 2019; GSDR 2019). Since 1981, global temperatures have been rising an average of 0.18 degrees Celsius each decade, with the ten warmed years occurring between 2010 –2022 (Lindsey and Dahlman 2023; NOAA 2023). Climate change impacts are known to have a cascading effect on the environment, economy, and human population (Hitz and Smith 2004; Arnell et al. 2016; Tol 2018; Lenton et al. 2019; Huckelba and Van Lange 2020; Weiskopf et al. 2020; Furtak and Wolińska 2023). One of the impacts we are witnessing is shifts in plant and animal species ranges, with previously unsuitable environments becoming habitable (Melles et al. 2011; Saikkonen et al. 2012; Williams and Blois 2018; Holland et al. 2020; Lenoir et al. 2020). As this occurs, new species in new areas can lead to significant changes to ecosystems, as interspecific competition increases and non-native species establish (Mainka and Howard 2010; Saikkonen et al. 2012; Valladares et al. 2014; Weiskopf et al. 2020; Usinowicz and Levine 2021).

Alongside the changing climate, global expansion and urbanization has intensified with the growing human population (Gerten et al. 2019). The consequences of this expansion include habitat degradation, which reduces biodiversity and resilience of ecosystems to future change (Dallimer et al. 2009; Mcdonald et al. 2015; Zhu et al. 2020). Beyond the environmental impacts, increased urbanization means the human desire to seek out a connection to nature through outdoor activities is increasing (Mcdonald et al. 2015; Winter et al. 2020). While there are numerous unprecedented impacts of global change, one major concern that has been accentuated by the warming climate, the destruction of habitat, and the increased exposure of humans to wildlife, is an increased rate of emergence of zoonotic diseases (Taylor et al. 2001; Jones et al. 2008; Swei et al. 2020; Napolitano Ferreira et al. 2021).

Zoonotic diseases are infectious diseases that are transmitted from non-human animal species to humans. The COVID-19 pandemic illustrated the devastating effect just one of these emergences can have on global health (Casale 2020; Shuja et al. 2020; Napolitano Ferreira et al. 2021). Globally, just over 60% of all emerging infectious diseases (EID) from 1940-2004 were zoonotic (Jones et al. 2008). Of these emerging zoonotic diseases, approximately 72% are transmitted from wildlife to humans, while the remainder have a domestic animal or unknown origin (Jones et al. 2008). Approximately 23% of all EID are vector-borne (Jones et al. 2008). Vector-borne zoonotic diseases are passed from vertebrates to humans via an animal vector. Various vector species from the Acari and Diptera families, including ticks, mites, and mosquitos, are responsible for almost 90% of all emerging vector-borne diseases (Swei et al. 2020). Since 2005, at least 53 additional vector-borne zoonotic diseases have emerged as numbers continue to rise (Swei et al. 2020).

Some of the most common vector-borne diseases globally include West Nile virus, dengue, yellow fever, chikungunya, and zika virus that are spread by various mosquito species, as well as Lyme disease, encephalitis, babesiosis, Crimean-Congo hemorrhagic fever, and rickettsioses that are spread by various tick species (Caminade et al. 2019; WHO 2020). In much of the Northern hemisphere, Lyme disease is the most common vector-borne disease (Kurtenbach et al. 2006; Rizzoli et al. 2011; Stone et al. 2017; Vandekerckhove et al. 2021). In Canada, West Nile is the most common vector borne-disease transmitted by a mosquito vector, and Lyme disease is the most common vector-borne disease transmitted by a tick vector (Public Health Agency of Canada 2016).

Lyme disease – A growing concern

Globally, Lyme disease is an increasing public health concern (Eisen & Eisen 2018). In eastern North America, the Lyme disease pathogen (*Borrelia burgdorferi* sensu stricto) is transmitted by the black-legged tick vector (*Ixodes scapularis*) which requires multiple vertebrate hosts to complete its life cycle (Ostfeld 2011; Barbour 2015). At each life stage, ticks will exhibit a host seeking behaviour called questing to obtain a blood meal. The bacterium is transmitted horizontally from infected hosts to ticks, and from ticks to the next host. Ticks rely on vegetation for questing at different heights as well as suitable habitat for themselves and for prospective hosts (Eisen and Eisen 2023). With only 144 cases reported in 2009, the number of human Lyme disease cases has grown exponentially in recent decades in Canada, with preliminary data from 2022 reporting 2,168 cases (Public Health Agency of Canada 2015; Public Health Agency of Canada 2023). Changes to climate and landscape contribute greatly to this spread as new suitable habitats become available for ticks and their vertebrate hosts (Simon et al 2014; Sonenshine 2018; Bouchard et al. 2019). The significant increase in Lyme disease cases is concerning as the disease is hard to diagnose, treat, and can lead to extensive health burdens if left untreated (Wormser et al. 2006; Aucott et al. 2022). Both public awareness and an understanding of the ecology of the tick-vector are essential for mitigating Lyme disease risk (Bouchard et al. 2019). As strategies for reducing Lyme and other tick-borne diseases are developed, a better knowledge is needed of how the tick vector and its host species' interact with their environment, how this results in disease spread, and which management targets will be effective for mitigation.

White-tailed deer

In Eastern North-America, white-tailed deer (*Odocoileus virginianus*) are an essential reproductive host for black legged ticks, contributing to the spread and maintenance of tick populations (Ostfeld 2011; Kilpatrick et al. 2014; Huang et al. 2019; Tsao et al. 2021). Despite being an essential host, deer do not contribute to the transmission of Lyme disease as they are considered incompetent reservoirs, as their serum kills *B. burgdorferi*, preventing them from transmitting it to a disease vector (Telford et al. 1988; Ostfeld 2011; Barbour 2017; Huang et al. 2019; Pearson et al. 2023). Many deer management strategies have been developed with the intention of mitigating Lyme disease with varying degrees of success and no clear solution (Eisen and Dolan 2016). Furthermore, the white-tailed deer is a keystone herbivore that can impact their environment across multiple trophic levels (Waller and Alverson 1997; Côté et al. 2004). When in high densities, the impact of deer is damaging for plant communities, insects, birds, and other mammals (Ostfeld et al. 1996; Waller and Alverson 1997; Côté et al. 2004; Martin et al. 2010; Kalisz et al. 2014; Averill et al. 2018; Rushing et al. 2020; VanGorder et al. 2021). Deer alterations to habitat and vertebrate communities creates potential for cascading indirect impacts on tick populations, small mammal hosts, and in turn disease risk, but exploration of these relationships has only begun in very recent years and needs further study (Gandy et al. 2021; Matsuyama et al. 2023). A better understanding of the direct and indirect impacts of deer abundance on tick abundance is of increasing importance, as climate change will reduce snow depth and increase survivability of deer, leading to increases in population size and range (Dawe and Boutin 2016; Weiskopf et al. 2019).

Thesis Objectives

Studies that incorporate both the direct and indirect impacts of deer on tick-borne disease risk are needed. As black-legged tick abundance and the prevalence of Lyme disease increases and spreads in Canada, it is necessary to understand the complex ecological mechanisms that accompany this emergence. Understanding the intricate role of deer in the current system and under future conditions will improve knowledge that will in turn contribute to tick-borne disease management strategies. While I focus on the relationship of white-tailed deer and Lyme disease in Southern Quebec as it is both a high-risk Lyme disease area and home to an overabundant deer population, the implications will be informative for various emerging tick-borne diseases for which deer act as a key vector host.

In the first chapter of this thesis, I provide context on Lyme disease in Eastern North America with a focus on Quebec. I review the ecology of the tick vector in this region, the historical context of the emergence and spread of the disease, the future projections of this spread, and the role deer play in the process.

In the second chapter of this thesis, I evaluate the direct and indirect impacts of white-tailed deer abundance on black-legged tick abundance at a UNESCO Biosphere reserve. Host to a dense deer population and located in a high Lyme disease risk region of Quebec, the reserve acts as a study case for exploring the complex relationship between deer and ticks. I measured deer abundance, vegetation, and tick abundance at 15 sampling sites across the reserve to explore the relationships between deer and ticks, deer and vegetation, and ticks and vegetation. I tested the hypothesis that deer abundance has a direct positive impact on tick abundance, but that this is hindered by an indirect negative impact of deer abundance on tick abundance, due to deer browsing negatively impacting the vegetation.

To conclude, the results of this study were synthesized in the context of the current literature. I reviewed studies analyzing the drivers of tick abundance in the context of deer exclosures and vegetation changes to propose future directions that would further our understanding of the relationships observed in this study.

Chapter 1 – The emergence of Lyme disease in Quebec and Eastern North America: A literature review

Lyme disease

Lyme disease is a bacterial infection transmitted by tick vectors of the Ixodidae family (Gray 1998; Steere et al. 2016; Stone et al. 2017), including the black-legged tick *(Ixodes scapularis*) in Eastern North America (Schwartz 2017; Public Health Agency of Canada 2023). The Lyme disease pathogen is a spirochete bacterium (*Borrelia burgdorferi* sensu lato) (Brisson et al. 2012). Generally, the Lyme disease pathogen is transmitted from hosts to ticks during a blood meal, and then can be transmitted from ticks to hosts during the next blood meal. A human can become infected by the bacterium if bitten by an infected tick. Symptoms of Lyme disease can include fever, muscle aches, and fatigue, or more severely, complications within the nervous system, arthritis, and heart infections (Asch et al. 1994; Barbour 2015; Geebelen et al. 2022).

Black-legged ticks

Black-legged ticks are hematophagous ectoparasites with a 1-2.5 year life cycle that requires three hosts to transition from one life stage to the next (Ostfeld 2011; Barbour 2015; Wolf et al. 2020). Geographic location, climate, and local temperature determine the phenology and exact timing of peak activity for each instar (Ostfeld 2011; Barbour 2015; Levi et al. 2015; Ogden et al. 2018; Ogden et al. 2021). In mid to late summer, the tick eggs hatch on the forest floor where they seek out their first host to feed for several days until engorged (Ostfeld 2011; Barbour 2015). They then drop off the host to molt into a nymph (Ostfeld 2011; Barbour 2015). The nymphs will then overwinter in the leaf litter, only to quest for a second host in late spring to early summer of the following year (Ostfeld 2011; Barbour 2015). At this time, they again take a several-day long blood meal before dropping off to molt into an adult tick (Ostfeld 2011; Barbour 2015). The adult tick seeks a host the same year, in mid to end of the fall (Ostfeld 2011; Barbour 2015). If the adult is female, it will overwinter while engorged to deposit its eggs in the following spring (Ostfeld 2011; Barbour 2015). During these blood meals, if the host from which the tick fed was infected with a bacterium, the tick can become infected and transmit it to the next host. While black-legged ticks are commonly known to transmit the Lyme disease pathogen (*Borrelia burgdorferi* sensu stricto), they have also been found to transmit bacteria responsible for diseases including anaplasmosis, babesiosis, tick-borne relapsing fever, Powasson virus, and ehrlichiosis (Eisen and Eisen 2018; Wolf et al. 2020)

The type of host species targeted by a tick often varies with life stage. Tick larvae and nymphs typically feed on a variety of small mammal species, including eastern chipmunks (*Tamias striatus*), shrews (*Blarina brevicauda* and *Sorex cinereus*), white-footed mice (*Peromyscus leucopus*), and deer mice (*Peromyscus maniculatus*) (Ostfeld 2011; Sonenshine 2018; Sosa et al. 2021; Tsao et al. 2021). For adult ticks, the white-tailed deer (*Odocoileus virginianus*) is considered an essential host, especially for tick reproduction (Ostfeld 2011; Kilpatrick et al. 2014; Huang et al. 2019; Tsao et al. 2021). The majority of adult female ticks feed on deer and male ticks attach to deer in search of a female, reproduction occurs on the deer host or in the vegetation, and females will use their last blood meal to overwinter and deposit eggs the following year (Ostfeld 2011; Roome et al. 2017; Wolf et al. 2020). Other hosts species of the black-legged tick include various small, mid-size, and large mammals, and greater than 100 bird species, most of which are ground dwelling (Halsey et al. 2018; Dumas et al. 2022).

In terms of disease risk, the type of hosts fed on during the ticks' blood meals affects the number of infected ticks, and therefore the disease risk. Not all hosts are considered equally competent reservoirs for *B. burgdorferi*. The white-footed mouse is considered a highly competent reservoir infecting 85-92% of feeding ticks, while the white-tailed deer is considered an incompetent reservoir infecting <5% of feeding ticks (Telford et al. 1988; LoGiudice et al. 2003; Brisson et al. 2007; Brunner et al. 2008; Ostfeld 2011; Barbour 2017; Huang et al. 2019). Due to host competence varying between host species, the effect of increasing host density and diversity on pathogen prevalence within a tick population has been a topic of debate. This debate focuses on two proposed theories, amplification, or dilution. The dilution theory predicts an increase in host diversity would lead to fewer infected ticks as more incompetent reservoir hosts become available (Norman et al. 1999; Levi et al. 2016). The amplification theory contradicts this, predicting an increase in the number of infected ticks as host density and diversity increases, as an increase in available hosts increases tick abundance, which corresponds to the number of infected ticks (Norman et al. 1999; Levi et al. 2016).

Beyond host availability, ticks rely on suitable environmental conditions for survival and establishing a population (Slatculescu et al. 2020; Nielebeck et al. 2023). When not attached to a host, ticks only travel up to a few meters as necessary for questing (Ostfeld 2011). Microhabitat and microclimate have been found to interact alongside small-mammal host abundance to influence fine-scale tick abundance (Ostfeld 2011; Ginsberg et al. 2017; Brennan et al. 2023). Preferring more humid environments to prevent desiccation (Berger et al. 2014; Sonenshine 2018), local characteristics such as ground slope (drainage), vegetation, and leaf litter which impact humidity can in turn impact tick survival (Burtis et al. 2019; Brennan et al. 2023). Multiple ecological factors that influence microclimate and abundance of vertebrate hosts have been found to significantly impact tick abundance, including temperature, density and type of understory, shrub abundance, dominant tree type, and high canopy cover (Clow et al. 2017; Talbot et al. 2019; Larson et al. 2022).

Emergence in North America

In the early 1970's in Lyme, Connecticut, a clustered epidemic of arthritis that peaked in summer and early fall led to the first description of Lyme disease (Steere et al. 1977; Steere et al. 2004). Similar symptoms found in patients in Europe suggested the disease was the result of a tick-borne pathogen (Steere et al. 2004). The tick-borne pathogen causing the epidemic in Lyme, Connecticut was identified in 1981 after the discovery of *B. burgdorferi* in the black-legged tick and subsequent testing in patients with the disease (Steere et al. 2004). Since the first emerging cases, the disease has spread throughout much of North America. In the United States, over 95% of human Lyme disease cases occur in the Northeast, upper Midwest, and mid-Atlantic regions (Spach et al. 1993; Steere et al. 2016; Schwartz 2017). In Canada as of 2021, over 95% of all human cases of Lyme disease occurred in the provinces of Ontario, Nova Scotia, and Quebec (Public Health Agency of Canada 2023). While the black-legged tick species is responsible for the spread of Lyme in the Eastern and central parts of Canada and the United States, the western black-legged tick (*Ixodes pacificus*) is the tick vector of concern along the western states and provinces (Schwartz 2017; Public Health Agency of Canada 2023).

In the United States, from 2008 – 2015, over 275,000 cases of Lyme disease were reported, a slight increase from the 248,000 cases reported from 1992-2006 (Schwartz 2017; Murphee Bacon et al. 2008). While the number of cases reported each year remained relatively stable throughout this time period with some states showing a slight decrease in the number of cases, low incidence states neighbouring high incidence states showed an increase in number of cases over time (Schwartz 2017). Additionally, the number of cases reported in the United States each year is vastly underestimated (Nelson et al. 2015; Cook and Puri 2020; Kugeler and Eisen 2020; Kugeler et al. 2021). Analyzing insurance data from 2005 – 2010 led to the conclusion that the actual number of new Lyme disease cases annually was ~ 329,000 (Nelson et al. 2015). Further, insurance data from 2010 – 2018 estimated ~ 476,000 new cases per year (Kugeler et al. 2021). This was supported by modeling based on testing of *Borrelia* samples in humans and dogs that estimated there were ~473,000 new cases of human Lyme disease in 2018 and that the total prevalence of cases in the United States is ~2.4 million (Cook and Puri 2020).

In Canada, cases of Lyme disease were voluntarily reported beginning in the 1980's and less than 40 cases were reported before 1995 (Ogden et al. 2009; Tutt-Guérette et al. 2021). In the early 2000s cases were rising and in 2009 clinicians were first required to report cases of Lyme disease to a national database; 144 cases were reported that year (Ogden et al. 2009; Public Health Agency of Canada 2023). Since then, the number has increased with the reported cases from 2009-2022 totalling over 17,000 (Public Health Agency of Canada 2015). The degree of under reporting of human Lyme disease cases occurring in Canada has been debated. Using Nova Scotia as a study case and serology testing results, Lloyd and Hawkins (2018) estimated the number of cases reported is less than 10% of the actual number of infections. However, Ogden et al. (2019) reported that the number of cases in Canada is not as severely underestimated as in the United States, and that the number of cases reported is likely one third of the actual number of cases, as observed in areas where Lyme disease has recently emerged. In both countries, the number of reported cases is highest during the summer, as tick questing activity coincides with the increased amount of time people spend outdoors (Schwartz 2017; Public Health Agency of Canada 2023).

A geographic range expansion of black-legged ticks has been occurring in recent decades, as tick populations become established in new areas (Khatchikian et al. 2015; Hahn et al. 2016; Clow et al. 2017; Sonenshine 2018; Tran et al. 2021; Public Health Agency of Canada 2023; Eisen and Eisen 2023). One of the main drivers of black-legged tick range expansion is climate change, as previously unsuitable habitats become suitable (Clow et al. 2017; McPherson et al. 2017; Sonenshine 2018; Hammond-Collins et al. 2022; Public Health Agency of Canada 2023). Under the warming climate, black-legged tick range has been shifting northward, a trend which is predicted to continue under future conditions (Ogden et al. 2006; McPherson et al. 2017; Burrows et al. 2021; Ripoche et al. 2022; Robinson et al. 2022; Tardy et al. 2023). Habitat suitability modelling also showed that the eastern regions are the most suitable for black-legged ticks and likely for range expansion to occur in this direction as well (Hahn et al. 2016; Slatculescu et al. 2020).

Multiple mechanisms are responsible for the physical spread of ticks including white-tailed deer movement and bird species seasonal migration (Madhav et al. 2004; Ogden et al. 2008; Leo et al. 2017; McPherson et al. 2017; Tardy et al. 2023). Birds alone are estimated to disperse between 50-175 million ticks across Canada during their northern migration each spring (Ogden et al. 2008). Once ticks have been deposited in a new area, they can establish or contribute to a growing population locally. As black-legged ticks are a generalist tick species, they do not rely on specific hosts to establish, but their populations are limited by the local habitat and climate conditions (Sonenshine 2018; Hammond-Collins et al. 2022). Temperature is a driver of increasing local tick abundance as the rate of tick reproduction increases under warmer conditions (Eisen et al. 2016; Winter et al. 2021). The subsequent increase in *B. burgdorferi* in a tick population is limited by the distribution of competent reservoirs hosts such as the white-footed mouse, which are in turn also limited by climate and landscape (Simon et al. 2014; Millien et al. 2023).

Emergence in Quebec

As the black – legged tick expanded its range north and east in Canada, Quebec has become the province with the third highest number of Lyme disease cases, trailing only Ontario and Nova Scotia (Public Health Agency of Canada 2023). Lyme disease has been reportable in Quebec since 2003, but the first human case where the disease was acquired in Quebec was reported in 2006 (Gouvernement du Québec 2023). Since then, the number of cases reported in Quebec has been increasing significantly; 32 cases were reported in 2011 and 586 cases were reported in 2022 (Gouvernement du Québec 2023). The proportion of cases that were caused by an infection acquired while in Quebec has increased from 50% in 2013 to ~90% in 2022 (Gouvernement du Québec 2023), reflecting the establishment of local tick populations. There are eight regions in Quebec with established black-legged tick populations (Gouvernement du Québec 2023). Currently, high Lyme disease risk areas in Quebec are concentrated in the Southern regions (INSPQ 2023a). The region of Estrie is the most affected by Lyme disease in Quebec, although the risk is concentrated towards the western territories (INSPQ 2022). Following Estrie, the region of Montérégie is the second most affected region in Quebec, and in contrast to Estrie, disease risk is dispersed throughout the area (INSPQ 2022).

The prevalence of *B. burgdorferi* among black – legged tick populations has been rising in conjuncture with the number of ticks reported. A study conducted by Gasmi et al. (2016)

showed that from 2008 – 2014, the number of ticks submitted for testing by healthcare professionals in Quebec rose from 174 to 962, and that the *B. burgdorferi* infection prevalence in ticks rose from 5.9% to 18.1%. Of the total ticks collected in the study from Gasmi et al. (2016), there were 1572 adult ticks and 70 nymphs collected in the Montérégie region, compared to the 605 adult ticks and 7 nymphs observed across all other regions of Quebec. Of the ticks submitted for testing in 2022, 44% came from the combined Estrie, Outaouais, and Montérégie regions (INSPQ 2023b). Increasing *B. burgdorferi* prevalence in the Montérégie supports the hypothesis that transmission cycles will become more proficient over time after becoming established (Ogden et al. 2013; Gasmi et al. 2016).

Over the past decade, human Lyme disease cases have been spreading northward within Quebec at rates varying from 18 – 32 km/year (Ogden et al. 2010). In 2022, black-legged ticks were reported in all regions of Quebec except for the regions furthest north (Nord du Quebec, Nunavik, Terres - Cries, and Baie – James) (INSPQ 2023b). Under future climate warming scenarios, the black-legged tick geographic range is predicted to increase by 31% in the northern regions of Quebec (Tardy et al. 2023). Under the worst climate scenario, the prevalence of infected black-legged ticks is predicted to spread northward in Quebec at a rate of 61km/year (Tardy et al. 2023). It is predicted that by 2027 range expansion of black-legged ticks will lead to 90% of Quebec's human population being at risk of tick exposure (Ripoche et al. 2022).

White-tailed deer

While the white-tailed deer are not a competent reservoir host for *B. burgdorferi*, they are considered a key host for black-legged tick reproduction (Rand et al. 2003; Ostfeld 2011; Roome et al. 2017; Huang et al. 2019; Wolf et al. 2020; Tsao et al. 2021). As such, deer are of special concern when studying the establishment and maintenance of black-legged tick populations. In Eastern North America, white-tailed deer have become overabundant in recent decades due to a reduction in hunting pressure from humans and natural predators, changing climate allowing for greater winter survival, reduced snow depth in the winter, and human habitat modifications (Côté et al. 2004; McShea 2012; Schuttler et al. 2017; St Laurent et al. 2021). In Eastern North America, their range overlaps with the regions considered highest risk for Lyme disease in the United States and Canada (Heffelfinger 2011; CDC 2023; Public Health Agency of Canada 2022).

The range of the white-tailed deer is widespread, its distribution spanning from the northern regions of South America to southern Canada (Heffelfinger 2011). In Quebec, white-tailed deer are the most abundant in regions south of the St. Lawrence River and on Anticosti Island (Lebel 2020). In the mainland regions of Quebec the number of deer harvested by hunters annually was approximately 1,000 during the 1970s (Lebel 2020). Currently the number of deer harvested annually is approximately 45,000 (Lebel 2020). However, in regions of Southern Quebec, deer have exceeded the environmental carrying capacity that the land can sustain, which is estimated at 5 deer/km^2 (Hout and Lebel 2012; Beauvais et al. 2016; Lebel 2020). The range of white-tailed deer is expected to continue expanding northward under future environmental and climatic conditions (Heffelfinger 2011). It is predicted that by 2100, deer will no longer be limited by winter conditions in the current northern edge of their range (Kennedy-Slaney et al. 2018).

Aside from their role as a tick host, the overabundance of white-tailed deer in Eastern North America has major impacts on ecological communities. White-tailed deer are keystone herbivores that impact ecosystems across various trophic levels (Waller and Alverson 1997; Rooney 2001). As herbivorous browsers deer have a direct impact on plant survival, growth, and reproduction. This browsing behaviour is selective and can greatly impact interspecific competition of plant species (Côté et al. 2004; Patton et al. 2021). When in high densities, over browsing by deer can alter ecosystem nutrient cycling, alter forest succession, and have adverse impacts on herbaceous plant species diversity (Waller and Alverson 1997; Côté et al. 2004; Martin et al. 2010; McShea 2012; Beguin et al. 2022; Villemaire-Côté et al. 2022). Further, the selective browsing behaviour of deer can facilitate the invasion of non-native plant species by preferentially browsing on native plants (Kalisz et al. 2014; Averill et al. 2018; Gorchov et al. 2021; Morrison et al. 2022). Birds, insects, and other mammals are also impacted by deer overabundance, both directly by competing for resources, and indirectly through cascading ecosystem impacts (Ostfeld et al. 1996; Waller and Alverson 1997; McShea 2000; Côté et al. 2004; Martin et al. 2010; Rushing et al. 2020; VanGorder et al. 2021).

While many studies have attempted to explore the relationship between deer and tick abundance, the exact nature of this relationship and mechanism driving it is still not clear (Kilpatrick et al. 2017). One aspect of this relationship that is well studied and generally accepted is that when deer abundance is low, tick abundance is also low (Gilbert et al. 2012; Levi et al. 2012; Kilpatrick et al. 2017; Martin et al. 2023). Further, there is evidence that there is a threshold of deer abundance, above which deer abundance is not a good predictor of tick abundance, but there is little consensus on the exact threshold value (Van Buskirk and Ostfeld 1995; Ostfeld et al. 2006; Jordan et al. 2007; Levi et al. 2012; Eisen and Dolan 2016; Levi et al. 2016; Telford 2017; Martin et al. 2023). It has also been found that fine-scale changes in deer spatial usage can lead to a fine-scale reduction in tick abundance (Mols et al. 2022). Previously, a reduction in deer density has also been shown to reduce the number of infected ticks in some cases (Wilson et al. 1990; Kilpatrick et al. 2014), and has showed no effect in others (Ostfeld et al. 2006). More recently it has been found that reducing deer density does not reduce *B. burgdorferi* prevalence, and in some cases it leads to an increase in prevalence (Martin et al. 2023). For high deer abundance to reduce disease risk however, any resulting reduction of infected ticks due to incompetent host dilution must be greater than the amplification impact deer have on tick abundance as a host if there are competent hosts present (Huang et al. 2019; Gandy et al. 2022).

Although the direct impact of deer abundance on ticks and disease risk has been extensively studied, only recently have the indirect impacts begun to be explored. One study in Scotland by Gandy et al. (2021) explored the effect of red deer (*Cervus elaphus*) on the number of infected *Ixodes ricinus* ticks through the impacts on vegetation and therefore small mammals. Another study in Japan by Matsuyama et al. (2023) explored the indirect impacts of sika deer (*Cervus nippon*) on ticks infected with *Rickettsia*, the bacterium known to cause spotted fever. The former study found that in plots with high deer density, vegetation and small mammal abundance was reduced, and that the tick density and density of infected nymphs was much greater in high deer density plots versus deer exclosures (Gandy et al. 2021). The latter found that deer herbivory did not affect tick density, but that the prevalence of infection in nymphs was greater in deer exclosed sites and sites where deer had reduced vegetation, compared to deer enclosed sites (Matsuyama et al. 2023). Further testing of the novel hypothesis that deer browsing has a negative indirect impact on tick abundance that goes beyond the direct positive impact of deer as a host warrants further exploration.

Due to the potential effects of deer abundance on ticks and tick-borne disease prevalence, deer are often a target of management strategies aimed to reduced disease risk for human populations. Deer reduction through culling is often considered, yet the threshold of deer density needed to reduce the number of infected host-seeking ticks is not known (Eisen and Dolan 2016). Deer exclusion through fencing is another tool that has been explored and showed a reduction in number of infected ticks over time (Gilbert et al. 2012; Eisen and Dolan 2016). Reducing deer abundance through either management methods is however complex, due to the ambiguous relationship of deer and tick abundance. Alternatively, acaricides have been used on deer and initially, a reduction in ticks was observed when first implemented, but evidence has since suggested they do not reduce tick or infected tick abundance (Eisen and Dolan 2016; Stafford and Williams 2017). Other proposed methods of deer-targeted management include an oral developmental inhibitor preventing tick reproduction, and a vaccine against black-legged ticks, both of which have challenges in implementation (Stafford and Williams 2017; Gandy et al. 2021). A deeper understanding of the complex relationship between deer and tick abundance (Matsuyama et al. 2023), as well as an integration of multiple methods (Jordan et al. 2007; Eisen and Dolan 2016), is necessary for successful deer targeted disease risk mitigation.

Linking Statement

In the first chapter of this thesis, I reviewed the emergence of Lyme disease in North America, with a focus on eastern North America and Quebec. I explored the ecological context of this emergence and the subsequent rise in human disease risk. There was a large focus on the role of white-tailed deer as drivers of tick abundance and *B. burgdorferi* prevalence. Synthesizing the current knowledge is essential for identifying knowledge gaps and informing management strategies aimed at reducing human disease risk.

The overabundance of deer in southern Quebec in areas of high human Lyme disease risk warrants further exploration of the relationship between deer and ticks. The literature highlighted that this relationship is not fully understood (Kilpatrick et al. 2017), and the indirect impacts of deer have not been sufficiently studied (Gandy et al. 2021; Matsuyama et al. 2023). The number of human Lyme disease cases in Quebec has risen significantly in recent decades (Gouvernement du Québec 2023), and as under future climate conditions, human disease risk will expand across the province (Ripoche et al. 2022), knowledge of what drives disease risk in this area will inform strategies to reduce it.

Building off the current knowledge, I present in my second chapter a field experiment at a nature park that is both home to a dense white-tailed deer population and located in a region of high Lyme disease risk. I analyzed both the direct and indirect effects of deer on tick abundance at this park as a study case. I observed the effects of deer on the local vegetation and habitat quality for ticks, the effect of deer browsing on tick abundance, and the effect of deer abundance on tick abundance.

Chapter 2 - The effect of white-tailed deer on the distribution and abundance of black-legged ticks

Introduction

Increased human-wildlife interactions, together with climate change and habitat degradation, are contributing to zoonoses emerging at unprecedented rates (Taylor et al. 2001; Jones et al. 2008; Conover and Vail 2014; Allen et al. 2017; Swei et al. 2020). Of all emerging vector-borne diseases, 40% are transmitted by an Ixodidae tick vector (Swei et al. 2020). Some of the most prevalent tick-borne diseases globally include encephalitis, babesiosis, Crimean-Congo hemorrhagic fever, rickettsioses, and Lyme disease (Caminade et al. 2019;WHO 2020). In Canada Lyme disease is the most common vector-borne disease transmitted by a tick vector (Public Health Agency of Canada 2016).

In eastern North America, the Lyme disease pathogen (*Borrelia burgdorferi*) is transmitted by a tick vector known as the black-legged tick (*Ixodes scapularis*), which relies on multiple mammal hosts – from small mammals to white-tailed deer (*Odocoileus virginianus*) – to complete its life cycle (Ostfeld 2011; Barbour 2015). The black-legged tick has three life stages: larvae, nymph, and adult. To seek a host at each life stage, ticks will perform an active behaviour called questing to seek out a host to obtain a blood meal. The life cycle of a black-legged tick generally lasts between 1-2.5 years and the phenology of the tick life cycle and the peak activity period of each instar can vary with geographic location, climate, and local temperatures (Ostfeld 2011; Barbour 2015; Levi et al. 2015; Ogden et al. 2018; Ogden et al. 2021). While feeding from a *B. burgdorferi* infected host, the tick can become infected with the spirochaete as well. These bacteria will remain in the tick's digestive system until the next blood meal, during which the tick can transmit *B. burgdorferi* and infect their next host (Ostfeld 2011; Barbour 2015).

A host organism that can become infected with *B. burgdorferi* and infect a new generation of tick vectors is considered a reservoir. Not all hosts are equally competent reservoirs, some host species are more likely to become infected and transmit the disease to feeding ticks than others. Many small mammal species are considered competent reservoirs (LoGiudice et al. 2003; Brisson et al. 2007; Brunner et al. 2008). Other hosts, such as white-tailed deer are considered incompetent reservoirs, infecting <5% of feeding ticks (LoGiudice et al. 2003; Brunner et al. 2008). Despite this, deer are considered essential in the transmission of Lyme disease as a reproductive host (Ostfeld 2011; Barbour 2017; Kilpatrick et al. 2017; Huang et al. 2019; Tsao et al. 2021). Tick copulation most often occurs on deer while female ticks feed in order to overwinter and deposit eggs the following year (Ostfeld 2011; Roome et al. 2017; Wolf et al. 2020).

Factors such as microhabitat, microclimate, and small mammal host abundance have been found to interact and impact tick abundance (Ostfeld 2011; Ginsberg et al. 2017; Brennan et al. 2023; Millien et al. 2023). Preferring more humid environments to prevent desiccation (Berger et al. 2014), the ideal environment for a black-legged tick is a deciduous forest with leaf litter and understory vegetation when free-living. A variety of landscape and weather characteristics, including understory vegetation can indirectly impact tick survivability by impacting the microclimate and host species communities (Burtis et al. 2019). This brings into question the potential indirect impact a host species may have on tick abundance if they have a significant effect on the environmental conditions ideal for the tick population.

Having become over-abundant in eastern North America in recent decades due to climate change, anthropogenic habitat alterations, and a reduction in natural predators and hunting pressure (Côté et al. 2004; McShea 2012; Schuttler et al. 2017), white-tailed deer have the potential to impact ticks beyond their role as a host. Deer overabundance can have detrimental effects on plant mortality, growth, and reproduction; their selective browsing behaviour also influences the outcome of interspecific competition and can modify many ecosystem processes (Waller and Alverson 1997; Rooney 2001; Côté et al. 2004; Auberson-Lavoie and Vellend 2020; Bernardo et al. 2020). Alterations to forest succession and nutrient cycling, reductions in herbaceous plant and tree species diversity, as well as the facilitation of invasive plant species have all been observed under the impact of high deer densities (Waller and Alverson 1997; Côté et al. 2004; Martin et al. 2010; McShea 2012; Kalisz et al. 2014; Averill et al. 2018; Gorchov et al. 2021; Reed et al. 2022). Further, through direct competition for browsing, and indirect impacts on habitat, deer can negatively impact communities of birds, insects, and other mammals (Ostfeld et al. 1996; Waller and Alverson 1997; McShea 2000; Côté et al. 2004; Martin et al. 2010).

The presence of deer as hosts regulates the emergence and maintenance of a tick population, but the impact of deer abundance on tick abundance is not clearly established (Kilpatrick et al. 2017). Evidence has shown that there is a threshold of deer abundance above which deer abundance has little effect on tick abundance (Van Buskirk and Ostfeld 1995; Ostfeld et al. 2006; Jordan et al. 2007; Levi et al. 2012; Eisen and Dolan 2016; Levi et al. 2016). Only recently have studies begun exploring both the direct and the indirect impacts of deer on tick density and disease prevalence; one in Japan explored the relationship of sika deer (*Cervus nippon*) and *Rickettsia* infection in tick populations (Matsuyama et al. 2023), and another in

Scotland explored the potential ecological cascade of red deer (*Cervus elaphus*) on Lyme disease risk (Gandy et al. 2021). The two studies reported differing results, and more empirical evidence is needed to fully understand this complex relationship. Determining the indirect effects of deer on tick populations may inform future deer-target management strategies aimed at reducing human disease risk. Assessing this relationship is especially important in areas where the human population is at heightened risk of encountering a tick, such as outdoor recreational parks and nature reserves.

Here, I explore the combined direct and indirect effect of white-tailed deer habitat use, distribution, and abundance on black-legged populations at a fine spatial scale at the Gault Nature Reserve (hereafter GNR). The region of Montérégie, Quebec, where the reserve is located, is not only a high-risk Lyme disease area, but also home to a dense white-tailed deer population (Lebel 2020; Tutt-Guérette et al. 2021; INSPQ 2023a). Within the GNR, juvenile deer are at risk of predation from coyotes (*Canis latrans*), but there are no large predators present or human hunting activity allowed in the reserve. The surrounding area of the GNR is comprised mainly of farmland and urban areas. As such, the reserve acts as a forest refugium for the deer population. The reserve is also located near Montreal, where surrounding areas have been experiencing an increasing number of recreationists under growing urbanization (Gouvernement du Québec 2018), and a network of hiking trails at the reserve hosts thousands of recreational visitors each year.

As an essential host for reproducing adult ticks, I predicted that tick abundance is increasing with deer abundance. Conversely, because deer browsing can alter the tick and their small mammal hosts habitat, an overabundance of deer locally may reduce tick abundance. I aimed to determine the fine-scale effect of deer abundance on tick abundance, the effect of deer browsing on vegetation, and the indirect effect this browsing may have on tick abundance. I tested the hypothesis that deer abundance positively affects tick abundance, but that this impact is reduced where deer browsing pressure is high, reducing habitat quality for questing ticks and small mammal hosts. I predicted that tick abundance would be positively impacted by the direct effect of deer, and negatively impacted by the indirect effects of deer, and I determined which would have a greater impact.

Materials and Methods

Study site

The Gault Nature Reserve (hereafter GNR) (45.5525° N, 73.1554° W) is a UNESCO biosphere reserve located at Mont-St Hilaire, approximately 40 km outside of Montreal, Quebec that protects over 1,000 hectares of temperate deciduous forest. Used for research by McGill University since 1958, it was given official UNESCO status in 1978 (Maycock 1961; Béliveau et al. 2017; McGill University 2021a). The GNR is a unique study site, as in 1970 it was separated into three distinct management zones with varying levels of human usage (McGill University 2021a). The three sectors within the reserve are the public, the preservation (or private), and the service sector. The smallest sector is the service sector, used mainly for buildings and small roads (McGill University 2021b). The other two sectors are approximately the same size and cover the majority of the GNR's area (Figure 1). The public sector is open to recreational visitors who have access to a network of hiking trails throughout one side of the mountain (McGill University 2021b). The private sector is used for conservation of ecosystems and biological diversity and has minimal human disturbance, with access restricted to only park staff and researchers (McGill University 2021b) .

Field sampling

Field surveys took place from May 2022 to October 2022 at sites across both the public and private sectors of the reserve. A total of 15 sites were sampled with eight in the public and seven in the private sector (Figure 1). At each site, a deer exclosure was present, previously installed in 2019. Each exclosure was a 4 m^2 fenced-in circle that prevented deer browsing, and a corresponding control peg was located between 5 – 10 m away. At each site, we collected data through camera traps to characterize deer abundance, vegetation surveys to estimate habitat quality and deer browsing pressure, and field collections of black-legged ticks.

Vegetation surveys

The vegetation at each site was sampled three times, once in June, once in August, and once in October. The exclosure at each site was separated into four quadrants of 1m^2 using rope and pegs. The first peg marked 0^o and was placed at a metal bar at the opening of the exclosure, and each new quadrant was 90^o from the previous peg (Figure 2). At the control, peg and ropes were used to create four quadrants of the same area, with the first peg due north (Figure 2). For each plant, we identified the species using botanical identification keys and species identifying mobile applications (Peterson and McKenny 1968; Newcomb et al. 1977; Farrar and Canadian Forest Service. 1995; Lamoureux et al. 2002; iNaturalist). The plant height, the largest leaf length from the tip to the base of the leaf, and the flowering state were also recorded. For each plant, the distance from the center point of the quadrant and the angle from the designated 0^o peg was also measured.

Tick sampling

To estimate the black-legged tick abundance at our study sites, ticks were sampled using an active method of tick surveillance that involves using a cloth dragger to collect questing ticks (Wilson et al. 2019). Considering the general life cycle of the tick, we surveyed four times throughout the study period to capture all life stages. Sampling took place in June, July, August, and October.

At each site, ticks were collected inside the exclosure, and outside of it along three parallel transects of 30 m each. The first transect was located with the vegetation control peg in its centre, with 15 m measured in each direction from the peg using a rope set up parallel to the exclosure (Figure 3). The other two transects were parallel to the first with one in between the exclosure and the control peg, and one on the opposite side of the exclosure (Figure 3). Tick dragging was done using a rectangular 1m x 1.4m sheet of white flannel attached to a rope handle with a pocket for a heat pack and a small CO^2 cartridge attached at the top of the dragger (TicksBuster). The heating pack and CO^2 cartridge act as attractants for questing ticks that orient themselves towards infrared radiation and carbon dioxide (Ostfeld 2011), in addition to questing ticks attaching to the fabric in anticipation of a mammal host. The tick dragging apparatus was run along the entire area of the exclosure once for sampling internally, and in a zig-zag pattern along the external transects. Both sides of the fabric sheet were checked for ticks after dragging inside the exclosure, and every 5 meters along the transects. Collected ticks were placed in tubes containing 95% ethanol and later identified by species and life stages using taxonomic keys (Lindquist et al. 2016; Dubie et al. 2017).

White-tailed deer distribution and abundance

At each exclosure site, a camera trap (Spypoint Force-10) was set up on a tree approximately 75 cm above the ground. Upon movement detection, the cameras were set to take 3 burst photographs with no delay. The camera traps were active from May 1st, 2022, to October 13th, 2022. The cone of detection for each camera was measured by walking back and forth perpendicular to the front of the camera, slowly moving closer. The radius and length of the cone were then measured from where the walker was first detected. The detection cone represents the area captured by each camera at each individual site as it may vary due to terrain.

We used the package "camtrapR" (Niedballa et al. 2016) in R version 4.0.3 (R Core Team 2023) to create a data table recording the date, time, site, camera number, and the file name for each image. For each photo of white-tailed deer, the number and segment (male, female, juvenile) were recorded. Males were identified by the presence of antlers, females by lack of antlers, and juveniles by their size and coat pattern. Individuals that could not be assigned to one of these three segments were categorized as 'unknown'.

Statistical analyses

Data processing

All analyses were conducted in R version 4.0.3 (R Core Team 2023). The R package "ggplot2" (Wickham 2016) was used for figures, and the "sjPlot" (Lüdecke 2023) package was used for data visualization. and the "DHARMa" (Hartig 2022) package was used for statistical model diagnostics. The data from the field surveys was divided into three distinct periods, period one captured May – early July, period two early July – early August, and period three captured early August – early October (Table 1). One vegetation survey was completed in each sampling period and sampling effort remained the same throughout the season. The mean plant height was calculated for each site x sampling period combination. Two tick surveys were completed in the first sampling period, and one in each subsequent period. For the first sampling period, the number of ticks was averaged for each site. To account for differing sampling effort between inside and outside the exclosure, the number of ticks (or average for period one), was divided by the area sampled. Outside of the exclosure the area sampled was $90m^2$, and inside the exclosure it was 4 m^2. The area outside of the exclosure was calculated by multiplying the total length of the transects at each site by the width of the tick dragging sheet. To account for potential biases in deer count, observations of the same segment within 10 minutes of one another were removed. All segments were then combined into a deer count. To account for sampling effort in each period, the number of deer captured was divided by the number of active camera days ending when the SD cards were changed for the start of the next period. Due to malfunctioning cameras, two sites on the private sector did not have usable photographs and were excluded from the data. Additionally, a third site in the private sector had a malfunctioning camera in the third sampling period only, and was excluded from that sample.

Data analyses

I first investigated the effects of the GNR sector, the deer exclosure, and the sampling period on the vegetation. I ran three distinct generalized linear mixed-effects models (GLMM), each with one vegetation characteristics as a response variable (number of individual plants, number of plant species, and average plant height). In all three models, the sector (public vs private), exclosure (in vs out) and sampling period (a factor with three levels) were included as fixed effects, and the site was included as a random effect (Table 2; Appendix A). Model one had number of plants as the response variable and was run with a negative binomial distribution and a log link using the "glmer.nb" function in the R package "lme4" (Bates et al. 2015) . Model two had number plant species as the response variable and was a GLMM that uses template model builder (TMB) with the "glmmTMB" package in R (Brooks et al. 2017) with a Conway-Maxwell-Poisson (compois) distribution and a log link. The compois distribution in the "glmmTMB" package was used as the number of plant species was under dispersed ($Var = 2.29 < Mean = 3.28$). Finally, model three had the mean plant height as a response variable and was a GLMM with the "lme4" package in R (Bates et al. 2015) with a gamma distribution and log link, and site was included as a random effect (Table 2).

I then investigated the direct and indirect effects of deer on tick abundance. Across all sampling periods, more than two thirds of all the individual site samples resulted in zero ticks, and only 10 observations had more than one tick. As such, for both analyses, the data was combined across all sampling periods. For the first analysis, it was completed in two steps to account for zero-inflation. First, I ran model four^{a} as a presence/absence generalized linear model (GLM) with a binomial distribution and logit link using the "stats" base package in R (R Core Team 2020); sector and exclosure or control were the independent variables, and presence or absence of black-legged ticks was the response variable (Table 3; Appendix A). Next, I ran model four^{b} as a GLM on the presence data, with a gamma distribution and log link using the "stats" base package in R (R Core Team 2020); sector and exclosure or control were the independent variables, the number of ticks per sampling effort was the response variable (Table 3; Appendix A). In a second analysis, I investigated the effects of the number of plants, the mean plant height, and the number of deer per sampling effort, on the number of ticks using a subset of the data from outside of the exclosures. To do so, model five a GLM, with scaled deer per sampling effort, scaled mean plant height, and number of plants as independent variables, and number of ticks as the response variable (Appendix A), In this model, the number of plant species was not included as an independent variable, as it was highly correlated with the number of plants. I used a negative binomial distribution and a log link using the “glm.nb” function from the “MASS” package in R (Venables and Ripley 2002) (Table 3).

Results

White-tailed deer

Across all sampling periods and both reserve sectors there were 2522 instances of deer captured by the cameras. The mean number of active camera days across all sites was 160.36 (SD = 15.49, range = 108.92 – 165.86). The mean number of active camera days varied between sampling periods but was similar between sectors within each sampling period (Table 4). The number of deer per sampling days varied over the season (Table4; Figure 4D), and a t-test showed no significant difference in the number of deer per sampling days in either sector ($p>0.05$).

Vegetation

Across all sampling periods, a total of 3989 plants were surveyed. Of these plants, 28 species were found, including any unidentifiable plants listed as either “unknown” or “unknown wildflower” (Appendix B). The two most abundant plant species observed across all sampling periods were American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*). In the private sector the most abundant plant species found at the controls was blue cohosh (*Caulophyllum thalictroides*) and inside the exclosures the most abundant plant species was sugar maple. In the public sector the most abundant plant species inside the exclosures and at the controls was the American beech.

The mean number of plants was significantly greater inside the exclosures in the public sector ($p<0.001$; Table 5; Figure 4A; Appendix C), and the private sector ($p<0.001$; Table 5; Figure 4A; Appendix C). The mean number of plants was significantly greater in the private sector compared to the public ($p<0.05$; Table 5; Figure 4A; Appendix C). Sampling period did not result in significant variation in the number of plants observed ($p > 0.05$; Table 5; Figure 4A; Appendix C). The mean number of plant species was significantly greater in the private sector compared to the public ($p < 0.05$; Table 6; Figure 4B; Appendix D). In the public sector, the number of plant species was significantly greater inside the exclosures ($p < 0.05$; Table 6; Figure 4B; Appendix D), but no significant effect of exclosure on the number of plant species was found in the private sector ($p > 0.05$; Table 6; Figure 4B; Appendix D). Further, there were significantly fewer plant species observed in the third sampling period ($p < 0.01$; Table 6; Figure 4B; Appendix D). Mean plant height was significantly lower in the public sector compared to the private ($p < 0.001$; Table 7; Figure 4C; Appendix E). Mean plant height was significantly higher inside the exclosures in the public sector ($p < 0.001$; Table 7; Figure 4C; Appendix E), and in the private sector ($p < 0.05$; Table 7; Figure 4C; Appendix E). Sampling period did not have a significant effect on mean plant height ($p > 0.05$; Table 7; Figure 4C; Appendix E).

Black-legged ticks

Overall, across all sites and sampling periods, a total of 141 black-legged ticks were collected, *Ixodes scapularis* was the only species of tick found. Ticks of all three life stages (larvae, nymph, adult) were present at the reserve (Table 8). Only larvae and nymphs were found in the first two sampling periods, and only nymphs and adults were found in the third sampling period. The number of ticks per sampling effort varied across the sampling period (Table 9; Figure 4E).

The probability of tick presence was not significantly higher in either sector ($p > 0.05$; Appendix F) nor between the deer exclosures and controls in the private ($p > 0.05$; Appendix F) or public ($p > 0.05$; Appendix F) sectors. However, when ticks were present, significantly more ticks were observed in the public compared to the private sector ($p < 0.001$; Appendix G). Furthermore, the number of ticks per sampling effort was significantly higher inside the exclosures in both the public sector ($p < 0.001$; Appendix G) and the private sector ($p < 0.001$; Appendix G). When excluding data from inside the deer exclosures, the number of plants had a significant negative effect on the number of ticks ($p < 0.05$; Appendix H). Neither deer per sampling effort ($p > 0.05$; Appendix H), mean plant height ($p > 0.05$; Appendix H), nor any interactions between fixed effects (Appendix H), were found to significantly affect the number of ticks observed outside of the deer exclosures.

Discussion

I tested the direct and indirect effects of deer abundance on tick abundance within the GNR, where thousands of recreational visitors are present each year. I observed that deer were more abundant in the public sector of the GNR and were reducing the number of plants and plant height in both sectors of the reserve and reducing the number of plant species in the public sector. I also found that the number of plants, number of plant species, and mean plant height is reduced in the public sector compared to the private sector of the GNR. When analyzing tick abundance, there was not a greater probability of observing a tick in either sector or between the exclosure and control, but when ticks were present, they were more abundant in the exclosures in both sectors and overall, in the public sector compared to the private. Finally, the number of ticks observed outside the exclosures was greater when fewer plants were present, but tick abundance was not affected by deer abundance or mean plant height. The results do not support my hypothesis and instead suggest there is no direct effect of deer abundance on tick abundance but, there may be a positive indirect effect of deer on tick abundance.

Deer browsing

There is high browsing pressure from white-tailed deer at the GNR, but the effect of this browsing differs across the two sectors. The greater plant height and number of plants observed inside the exclosures in both sectors is consistent with other deer exclosure studies analyzing height and percent plant cover (Kelly 2019; Morrison and Woldemariam 2022). The number of plants, height and number of plant species showing a reduction in the public sector compared to the private suggests there is greater browsing pressure in the public sector. However, while a significantly greater number of plant species was observed in the exclosures compared to the control in the public sector, this was not observed in the private sector. When analyzing the species composition of the two sectors further, I found that four of the species unique to the public sector are avoided by deer or resistant to deer browsing (Appendix B; Horsley et al. 2003; Rawinski 2008; Soderstrom 2009). In the private sector I found that nine plant species unique to this sector are avoided by deer or resistant to deer browsing (Appendix B; Horsley et al. 2003; Rawinski 2008; Soderstrom 2009). When plants that are browsing resistant or avoided by deer are dominant in an area it can indicate that there has previously been high browsing pressure; a return of species that deer preferentially browse has also been observed after deer management strategies were implemented to reduce browsing (Horsley et al. 2003; Rawinski 2008; Abella et al. 2020; Parker et al. 2020; VanderMolen and Webster 2021; Knauer et al. 2023). While further study is needed, the initial results suggest that the private sector has experienced greater over browsing in the past, leading to an abundance of deer resistant species. The lower plant height and number of plants in the public sector with fewer deer resistant species suggests there is an ongoing high browsing pressure.

Drivers of tick abundance and distribution

When ticks were present, they were more abundant in the public sector. Looking only at ticks outside of the exclosure, the higher abundance of ticks in the public sector is supported by the result of a fewer number of plants leading to increased tick abundance, as the public sector had fewer plants compared to the private. However, significantly more ticks were found inside the exclosures compared to outside in both sectors despite having a greater number of plants inside versus outside. The ambiguity in the results could be explained by the complex relationship of ticks and tick hosts with their environment. For instance, the effect of deer exclosures on tick abundance in the past has been scale dependent.

Large-scale deer exclosures have resulted in a reduction in tick abundance inside compared to outside (Daniels et al. 1993). A study analyzing the effect of deer exclosure size on tick abundance by Perkins et al. (2006), found that as exclosure size is reduced, the effect shifts from negative to positive and exclosures < 2.5 ha in size can lead to increased number of ticks observed on small mammal hosts inside the smaller exclosures. This observation is supported by mathematical models and other field studies exploring the same relationship that also observed an increase in ticks inside small exclosures (Ginsberg and Zhioua 1999; Pugliese and Rosa 2008; Titcomb et al. 2018).

Opposing results of smaller sized exclosures have also been observed (Del Fabbro 2015; Hofmeester et al. 2017; Gandy et al. 2021; Matsuyama et al. 2023). In Scotland Gandy et al. (2021) found that the effects of red deer (*Cervus elaphus*) at a very high density (>35.5 deer/km^2) led to fewer sheep ticks (*Ixodes ricinus*) inside small exclosures. When small exclosures were implemented by Del Fabbro (2015) in Italy (in meadowlands rather than forested areas), they found a reduction in sheep ticks inside exclosures compared to outside where mainly roe deer (*Capreolus capreolus*) were present. Another small exclosure study found that sika deer exclusion did not have an effect on tick abundance, but did have a positive effect on the number of nymphs infected with the *Rickettsia* pathogen (Matsuyama et al. 2023). Variations in results from previous studies can also be attributed to the range of deer and tick species as host importance, tick behaviour, and environmental factors vary.

Although the size of deer exclosure used in this study is much smaller than many other studies, some similar mechanisms may be occurring. While deer browsing negatively impacts small mammals abundance through reduction of vegetation (McShea 2000; Smit et al. 2001; Côté et al. 2004; Gandy et al. 2021), the scale of our exclosures make it unlikely that there are more small mammals abundant inside versus outside as observed by Perkins et al. (2006). However, the increased number of ticks inside versus outside could be a result of small mammals venturing in and out of the exclosure and leaving ticks inside unable to find another host nearby (Buck and Perkins 2018). The reduced opportunity for hosts inside our small exclosures due to lack of deer and space for small mammal habitat may have led to an increased number of questing ticks when surveying with tick drags. This relationship however has mainly been suggested when there is an abundance of adult ticks inside exclosures due to a lack of deer hosts (Ginsberg and Zhioua 1999; Buck and Perkins 2018), which was not the case in this study. Additionally, the more favourable habitat inside the exclosures may lead to deposited ticks thriving more inside compared to outside.

While the effect of exclosure on tick abundance may be due to the availability of questing ticks inside compared to outside, the effect of sector, number of plants, and lack of direct effect of deer abundance is potentially independent. The significantly greater number of ticks observed in the public sector compared to the private suggests there is a driver in the public sector increasing tick abundance. The fewer number of plants observed in the public sector considered alongside the negative effect that number of plants had on tick abundance at the controls suggests that the lower plant abundance in the public sector may be driving the increased tick abundance. This, however, contradicts many studies which have observed that vegetation is a predictor of tick abundance and survival (Burtis et al. 2019; Ginsberg et al. 2020; Mathisson et al. 2021; Brennan et al. 2023). One possible explanation is that deer may be spending more time browsing in the public sector as indicated by the vegetation results. This is contradicted, however, by the lack of direct effect of deer abundance on tick abundance at the controls. At high densities, deer abundance has not been found to increase tick abundance, although the threshold of deer density beyond which there is no effect has not been determined (Van Buskirk and Ostfeld 1995; Ostfeld et al. 2006; Jordan et al. 2007; Levi et al. 2012; Eisen and Dolan 2016; Levi et al. 2016), except in extreme cases where deer are significantly displaced (Mols et al. 2022). The lack of direct effect of deer abundance on tick abundance indicates that the density of deer at the GNR may exceed the threshold for this area. While no fine-scale effects of deer abundance were observed, further study is needed to determine if deer abundance or movement behaviour between sectors is driving tick abundance.

Limitations

While this study was conducted across both sectors of the GNR, the initial set up of the deer exclosures in 2019 was designed specifically for studying deer browsing. As such, the size of the exclosure is much smaller than typical deer exclosures used in tick surveys, even when they are classified as small (Perkins et al. 2006; Ginsberg et al. 2017; Hofmeester et al. 2017). The sites are also concentrated towards the centre of the reserve in both sectors (Figure 1). The placement of the exclosures while representing the public and private sectors, does not capture all the various ecotypes at the reserve (Appendix D) or the service sector which could indicate further potential drivers of tick abundance variation. Also, the pooled data used to analyze the direct effect of deer abundance and vegetation on tick abundance at the control had a small sample size (n=13). Results from small sample sizes should be cautiously interpreted as they can lead to false negatives (Lemoine et al. 2016; Parker et al. 2016).

Both the vegetation and tick surveys may also have been limited by the duration of the study. At the time of the field survey the deer exclosures had been installed for approximately three years. Longer-term studies using deer exclosures found that after periods of time up to 20 years, the relationship of deer browsing and vegetation composition is still not clear (McGarvey et al. 2013; Chollet et al. 2021; Knauer et al. 2023). The tick sampling in this study, while taking place multiple times in a season to capture all life stages, only captured one year. Multi-year studies have found variation in tick abundance, life stage composition, activity, and prevalence of disease pathogens (Rodgers et al. 2007; Burtis et al. 2016; Burrows et al. 2021; Christie et al.

2022). Sampling multiple times over the course of multiple years would have resulted in more robust conclusions about the pattern of tick abundance and distribution at the GNR (Christie et al. 2022).

Future directions

Understanding the drivers of tick abundance is critical for informing future management strategies aimed at reducing disease risk. A large part of reducing this risk stems from public awareness (Sharareh et al. 2017; Bouchard et al. 2019). This is especially important in areas where the chances of human – tick contact are increased such as outdoor nature parks. The results of this study highlight that tick abundance is greater in the public sector compared to the private at the GNR and outline some potential drivers, but this discrepancy should be explored further for proper disease mitigation strategies. Repeating this study in a more expansive way and over a longer period would provide more robust results and potentially identify more drivers at play (Christie et al. 2022). As microhabitat and microclimate have also been found to affect tick abundance (Ostfeld 2011; Ginsberg et al. 2017; Brennan et al. 2023), surveying multiple ecotypes would add another driver for consideration. Additionally, future study at the existing exclosure sites should incorporate small mammal trapping. Small mammal trapping can estimate the abundance and density of various species (Weldy et al. 2019; Torre et al. 2022) and estimate the tick load and infection rate on small mammal hosts (Bespyatova et al. 2019; Larson et al. 2021; Millien et al. 2023). If the tick load or small mammal abundance varies between the private and public exclosure sites where deer browsing varies, it could add to our understanding of the mechanisms observed in the results of this study. Also, submitting collected tick samples to be tested for the pathogen would determine if the pathogen prevalence in addition to tick abundance varies between the sectors.

Furthermore, this study identifies that recreational parks should analyze their tick populations to observe potential drivers of variation in abundance in a local context. As the public sector of the GNR where human visitors are allowed has a greater abundance of ticks, other reserves may have similar mechanisms driving localized variations in abundance. Identifying these areas and determining the drivers would inform management strategies and public awareness campaigns. Finally, while deer and black-legged ticks were used as a study case in this research, further exploration should be conducted on the direct and indirect effect of various deer species on various tick species responsible for other emerging infectious diseases. As the number of tick-borne diseases continues to rise globally (Swei et al. 2020), assessing the complex interactions of ticks and their environments has never been more important.

Tables

Table 1. Sampling period starting and ending periods. Dates vary due to sampling taking place over the course of multiple days.

Sampling period	*Start*	*End*
One	May 1 2022	July 14 – July 15 2022
Two	July 14 – July 15 2022	August 17 – August 18 2022
Three	August 17 – August 18 2022	October 10 – October 14 2022

Table 2. Variables, distribution, and R package used for each vegetation analysis model.

Vegetation model	*Response variable*	*Fixed factors*	*Random factors*	*Distribution*	*Link*	*R package*
One	Number of plants	Sector Exclosure or Control Sampling period	Site	Negative binomial	log	"lme4"
Two	Number of plant species	Sector Exclosure or Control Sampling period	Site	Conway-Maxwell-Poisson	log	"glmmTMB"
Three	Mean plant height	Sector Exclosure or Control Sampling period	Site	Gamma	log	"lme4"

Table 3. Variables, distribution, and R package used for each hypothesis testing model.

Hypothesis testing model	*Response variable*	*Fixed factors*	*Distribution*	*Link*	*R package*
Four[a]	Presence or absence of ticks	Sector Exclosure or Control	Binomial	logit	“stats”
Four[b]*	Ticks per sampling effort	Sector Exclosure or Control	Gamma	log	“stats”
Five*	Number of ticks	Deer per sampling effort (scaled) Mean plant height (scaled) Number of plants	Negative binomial	log	“MASS”

***For model Four[b], only data when ticks were present was used as part of a two-step model.**
****For model Five, only data from outside of the exclosures was used.**

Table 4. Mean number of deer, sampling days, and deer per sampling days within the private and public sectors across the three sampling periods.

Sampling period	*Sector*	*Mean number of deer*	*Standard deviation*	*Range*	*Mean number of sampling days*	*Mean number of deer per sampling days*
One *(May – July)*	Private	109.6	81.52	53-252	74.31	1.47
	Public	123.25	77.35	55 – 290	74.78	1.65
Two *(July – Aug)*	Private	25.40	15.21	11 – 46	34.60	0.73
	Public	38.88	24.06	14 – 87	33.21	1.17
Three *(Aug – Oct)*	Private	20.75	12.45	11 – 39	55.95	0.37
	Public	62.17	41.20	19 – 149	56.87	1.10

Table 5. Mean number of plants recorded for each treatment within the private and public sectors across the three sampling periods. Eight sites were sampled in the public sector and seven in the private.

Sampling period	*Sector*	*Treatment*	*Mean number of plants*	*Standard deviation*	*Range*
One *(May – July)*	Private	Exclosure	84.57	69.92	21 – 187
		Control	20.71	6.21	10 – 29
	Public	Exclosure	84.13	76.00	6 – 213
		Control	9.38	7.31	2 – 20
Two *(July – Aug)*	Private	Exclosure	71	63.43	16 – 183
		Control	11	8.46	2 – 24
	Public	Exclosure	87.38	79.04	4 – 181
		Control	5.25	5.20	0 – 12
Three *(Aug – Oct)*	Private	Exclosure	66.14	75.38	0 – 187
		Control	5.86	4.63	0 – 14
	Public	Exclosure	82	84.11	1 – 200
		Control	3.63	2.92	1 – 9

Table 6. Mean number of plant species recorded for each treatment within the private and public sectors across the three sampling periods. Eight sites were sampled in the public sector and seven in the private.

Sampling period	*Sector*	*Treatment*	*Mean number of plant species*	*Standard deviation*	*Range*
One *(May – July)*	Private	Exclosure	4.43	0.98	3 – 6
		Control	4.86	1.21	4 – 7
	Public	Exclosure	3.50	0.93	2 – 5
		Control	3.31	1.25	1 – 5
Two *(July – Aug)*	Private	Exclosure	3.71	1.60	2 – 7
		Control	3.23	1.38	2 – 5
	Public	Exclosure	4	1.31	2 – 6
		Control	2.63	1.92	0 – 5
Three *(Aug – Oct)*	Private	Exclosure	3	1.83	0 – 6
		Control	2.29	1.38	0 – 4
	Public	Exclosure	3	1.31	1 – 4
		Control	1.88	0.83	1 – 3

Table 7. Mean plant height recorded for each treatment within the private and public sectors across the three sampling periods. Eight sites were sampled in the public sector and seven in the private.

Sampling period	*Sector*	*Treatment*	*Mean plant height (cm)*	*Standard deviation (cm)*	*Range (cm)*
One *(May – July)*	Private	Exclosure	16.38	10.06	1.5 – 90
		Control	14.83	9.81	2.5 – 75
	Public	Exclosure	13.16	10.19	2.5 – 170
		Control	9.33	9.98	1.3 – 78
Two *(July – Aug)*	Private	Exclosure	17.24	11.05	1– 82
		Control	14.00	7.38	0.5 – 50
	Public	Exclosure	13.42	7.92	2– 109
		Control	7.33	6.07	1.2 – 30
Three *(Aug – Oct)*	Private	Exclosure	16.45	9.56	0.5 – 101
		Control	14.15	8.76	4.5 – 51
	Public	Exclosure	14.47	7.64	1.2 – 82
		Control	7.26	4.45	12 – 15.5

Table 8. The number of ticks surveyed across all sampling periods separated by life stage, sector, and treatment.

Life stage	*Public*		*Private*	
	Exclosure	**Control**	**Exclosure**	**Control**
Adult	0	1	0	3
Nymph	1	11	2	5
Larvae	14	99	2	3
Total	**15**	**111**	**4**	**11**

Table 9. The abundance of ticks within each sector and exclosure or control treatment for each sampling period.

Sampling period	*Sector*	*Treatment*	*Abundance of ticks (number of ticks per meters sampled)*
One *(May – July)*	Private	Exclosure	0.0179
		Control	0.0048
	Public	Exclosure	0.0313
		Control	0.0069
Two *(July – Aug)*	Private	Exclosure	0.0357
		Control	0
	Public	Exclosure	0.3438
		Control	0.1375
Three *(Aug – Oct)*	Private	Exclosure	0.0714
		Control	0.0079
	Public	Exclosure	0.0625
		Control	0.0028

Figures

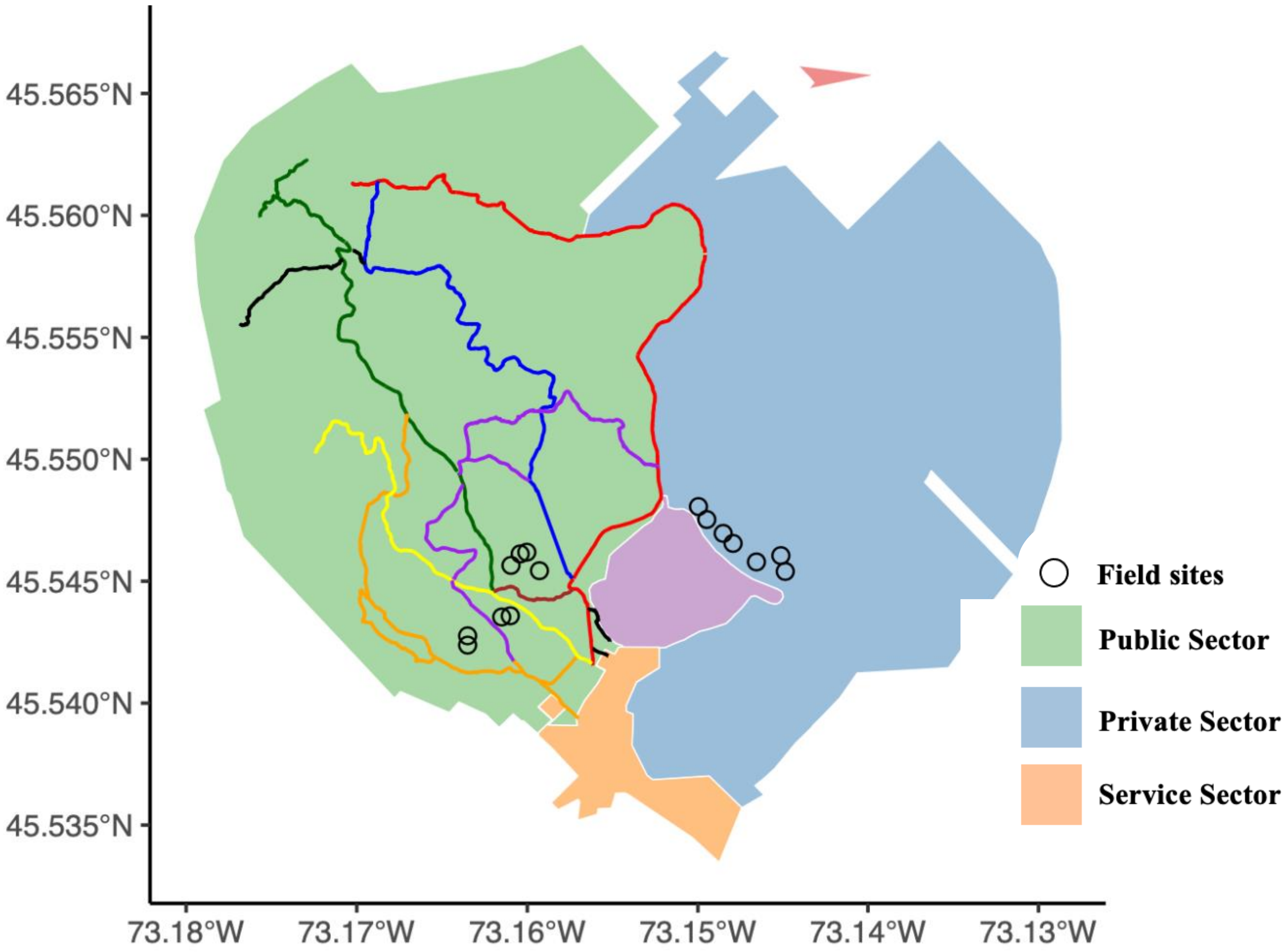

Figure 1. A map of the Gault Nature Reserve depicting the different sectors, the recreational hiking trails, and field sites.

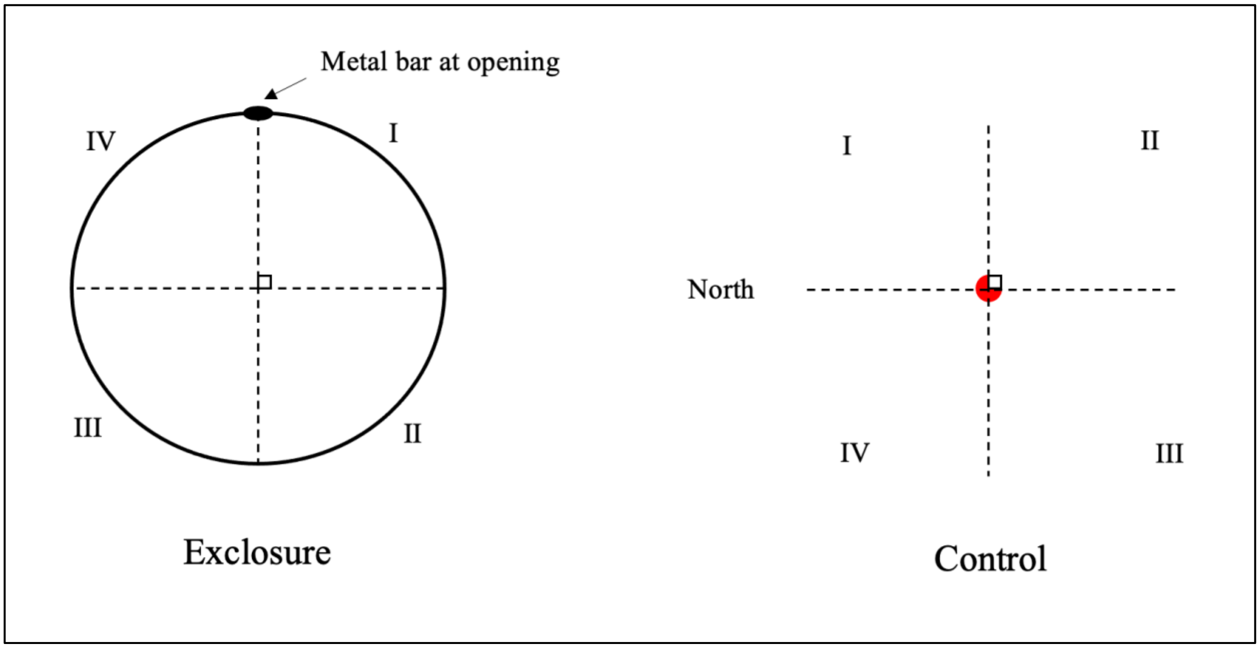

Figure 2. A diagram of the vegetation sampling set up. The metal bar at the opening and North for the control represent 0 degrees. The quadrats I-IV are placed successively at 90 degrees.

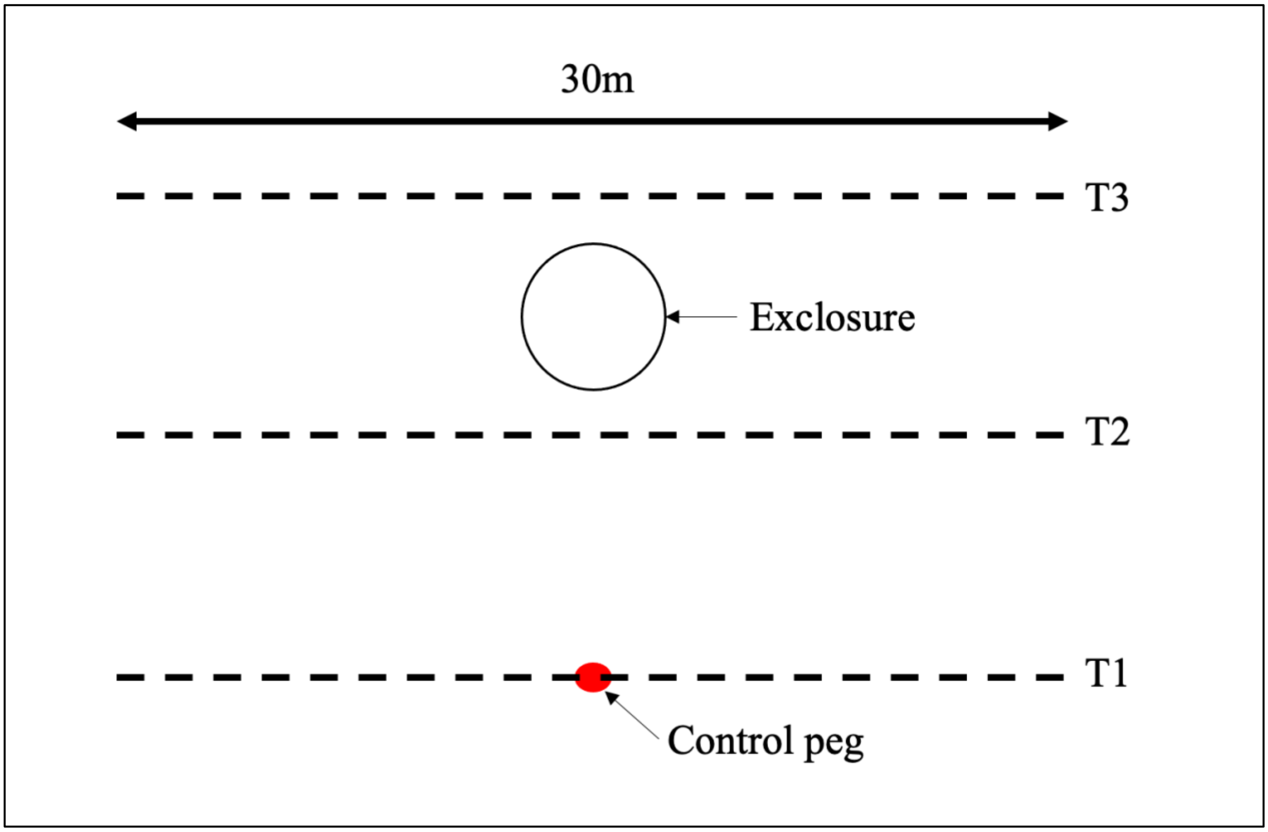

Figure 3. A diagram of the placement of transects used for tick dragging at each field site relative to the exclosure and control.

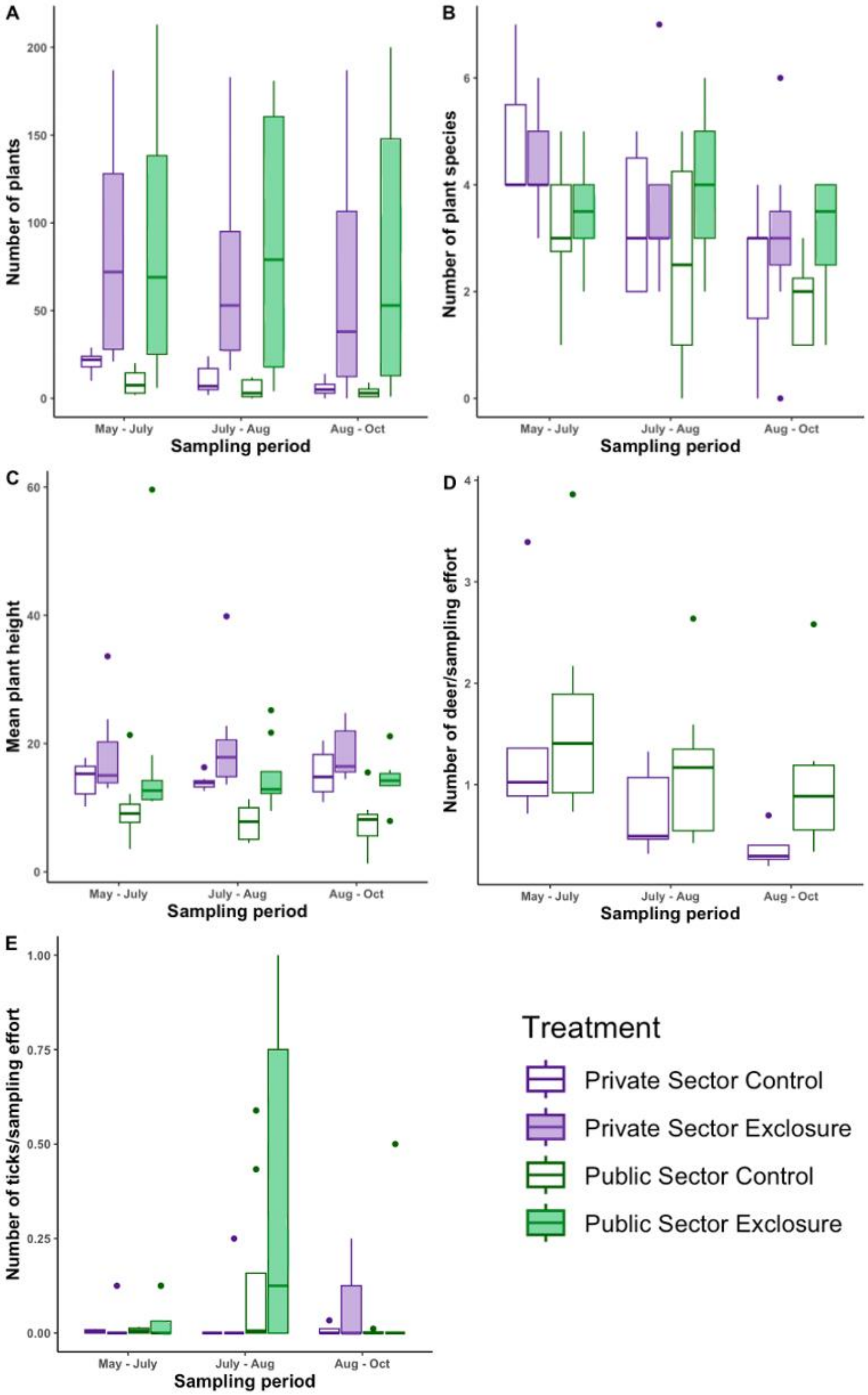
A
Number of plants
0
50
100
150
200
May - July
July - Aug
Aug - Oct
Sampling period
B
Number of plant species
0
2
4
6
May - July
July - Aug
Aug - Oct
Sampling period
C
Mean plant height
0
20
40
60
May - July
July - Aug
Aug - Oct
Sampling period
D
Number of deer/sampling effort
1
2
3
4
May - July
July - Aug
Aug - Oct
Sampling period
E
Number of ticks/sampling effort
0.00
0.25
0.50
0.75
1.00
May - July
July - Aug
Aug - Oct
Sampling period
Treatment
Private Sector Control
Private Sector Exclosure
Public Sector Control
Public Sector Exclosure

Figure 4. Variation of the number of plants (A), the number of plant species (B), the mean plant height (C), the number of deer per sampling effort (D), and the number of ticks per sampling effort (E) between sectors, treatment, and sampling period.

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Comprehensive scholarly discussion of all the findings

Throughout the comprehensive literature review and subsequent field study of this thesis, I determined that further understanding of ticks and tick-borne diseases has never been more important. As tick abundance and tick-borne disease prevalence increase in Canada with changing environmental conditions, research alike to this thesis will contribute to mitigating human risk. Here, I expand on the themes and findings of this thesis in various contexts to solidify the importance of this research in mitigating risk and highlight future directions that should be explored or considered further.

Deer and Recreation

This thesis identified that tick abundance could potentially be impacted both directly and indirectly by deer abundance. Predicting the effects of deer on tick abundance, and consequently human disease risk is ever important, but for a full comprehension of the system, the factors influencing deer abundance and distribution should also be understood. In nature parks such as the GNR which was used as a study case in the second chapter of this thesis, humans are not only at higher risk of encountering a tick, but they may be impacting disease risk through their impact on deer movement behaviour. The presence of recreationalists in parks in addition to recreational infrastructure such as trails can modify ecosystem processes, lead to habitat degradation, and alter the distribution and behaviour of wildlife (Ballantyne and Pickering 2015; Malherbe et al. 2021). The impacts of human recreationalists on wildlife can be short or long term and are dependent on the species, the isolation and geographic location of the park, the season, and the type of recreation (Miller et al. 2001; Knight and Gutzwiller 2013; Coppes et al. 2017; Patten and Burger 2018; Miller et al. 2020). The effect of humans on wildlife varies greatly resulting in displacement, attraction, or habituation under different conditions.

Recreationalists elicit strong fine-scale behavioural responses in deer which vary across season and interact with other driving factors such as predators and competitors (Visscher et al. 2023). A study conducted by Coppes et al. (2017) in the Southern black forest of Germany found that red dear avoided recreational trails and surrounding area during the daytime, but were attracted to these areas at night when the park was closed; additionally deer altered their spatial usage during the winter versus summer months when different areas of the park were used for different recreational activities. Another study by Green et al. (2023) in Utah found that mule deer (*Odocoileus hemionus*) did not alter their diel activity pattern in response to an increased number of recreational visitors on weekends compared to week days. However, some large herbivores increase their time spent near human infrastructure, or reduce their vigilance behaviour, as predators typically avoid these areas with high human disturbance (Berger 2007; Muhly et al. 2011; Rogala et al. 2011; Shannon et al. 2014).

Variation in responses to recreation by deer and other large herbivores makes predicting the response of deer in nature parks difficult. As the GNR is split into areas of high and low human usage and has a lack of large predators and hunting, predicting deer behaviour and spatiotemporal usage is even more complex. A field study conducted in the Netherlands by Mols et al. (2022b) analyzing spatial usage of red deer and fallow deer (*Dama dama*) had a similar unique set up to the GNR. The set up included three distinct areas, one with neither human recreation or hunting, one with recreation but no hunting, and one with both recreation and hunting. They found that deer spatial usage was highest in the zone with no recreation or hunting, but deer avoided recreational trails in the other zones. Further, another analysis of the same system by Mols et al. (2022a) which also measured tick abundance, found that the fine-scale spatial avoidance by deer also reduced the fine scale tick abundance when there was high human recreation. Expanding on the research done in this thesis at the GNR by incorporating a design to observe the effects of human recreationalists on deer behaviour between sectors and near recreational trails would contribute to knowledge informing disease mitigation strategies, especially those targeted at deer.

A comprehensive understanding of both the drivers of deer behaviour and the cascading impacts of deer on tick abundance in a local context can contribute to more robust management planning surrounding deer. Deer management planning, especially if deer culling is proposed, can often be controversial. For example, an urban park located in the city of Longueuil, in the Montérégie region of Quebec, has proposed culling of deer as there are greater than 100 individuals in a 2km^2 area (CBC News 2023). The proposal was met with resistance leading to a multi-year dispute and a Quebec superior court case (CBC News 2023). As such, deer management strategies aimed at mitigating disease risk or reducing the ecological impacts of deer should be thoroughly examined and informed through local research to present the most thorough proposal to the public.

Amplification or dilution

One of the potential indirect effects of deer on tick abundance and disease prevalence discussed in this thesis is the impact of deer on other mammal hosts. As reservoir competence varies between host species, the diversity of hosts available to ticks can impact *B. burgdorferi* prevalence. Two theories known as dilution and amplification have been proposed and examined to understand the relationship of increased host biodiversity and pathogen prevalence in a tick population. An amplification effect means an increase in hosts would increase the tick population, maintaining the disease, and a dilution effect means more incompetent reservoir hosts available leads to fewer ticks becoming infected and disease prevalence decreasing (Norman et al. 1999; Levi et al. 2016).

Due to the contrasting nature of the two theories, debates have followed on whether reducing deer abundance will lead to a decrease or increase in Lyme disease incidence (Ratti et al. 2021). A study conducted in Scotland by Gandy et al. (2022) observed that the positive effect of roe and red deer as a host on questing *Ixodes ricinus* nymphs was balanced with the negative effect of their reservoir incompetence on infection incidence. However, if increased diversity of host species leads to competition or predation that reduces the population of competent reservoirs such as small mammals, dilution may still occur (Levi et al. 2016). Model simulations under varying conditions have found that dilution may occur when populations of competent reservoirs are low, but amplification may occur when populations of competent reservoirs are high (Ratti et al. 2021).

The indirect effect of deer on more competent small mammal hosts by altering the habitat quality through browsing may be important to determining which mechanism is occurring in a local context. Areas with high deer density such as southern Quebec where overabundance and browsing has detrimental ecosystem impacts may experience dilution if competent reservoirs are negatively affected. This may contrast areas where deer density and subsequent impacts on competent reservoirs are lower. Building off the work in this thesis, incorporating the effects of deer on small mammal host abundance and testing for pathogen presence among ticks would develop a deep understanding of the indirect effects of deer on disease prevalence beyond tick abundance.

Biases in Lyme disease research

Throughout this thesis I identified that the understanding of the effects of deer on tick abundance is not complete. A debate has remained in the literature in recent decades, and the results of the field study at the GNR were inconclusive. As such, stepping back and reviewing the big picture, in addition to further exploring the impacts of deer may be necessary. There is a taxonomic bias in tick ecology research towards deer and small mammals, whereas research surrounding birds, meso-mammals, and reptiles is lacking (Zikeli and Zohdy 2020). Bird species contribute to long-range dispersal of ticks, spreading tens of millions of individuals across Canada each year (Ogden et al. 2008). Additionally, the western fence lizard (*Sceloporus occidentalis*) is borreliacidal and may be the cause of low prevalence of *B. burgdorferi* among western black legged ticks in North America (Dizon et al. 2023). As tick-borne diseases including Lyme become more prominent with changing climate, it is important not to neglect other drivers that may be increasing disease prevalence or drivers that are useful in reducing it.

Future directions

Examining the literature surrounding tick ecology, the outcome of studies is often complex and dependent on local factors. Due to this, planning and predicting the outcome of management strategies would benefit from understanding of the system within a local context. The findings of this thesis demonstrate the need for analysis of disease risk from multiple angles, taking into consideration past studies and unique variables at the study level. The division of the GNR into distinct areas of high and low human usage was one unique variable in this thesis, and a significant difference in the abundance of ticks between sectors was observed. While further exploration is needed to determine what is causing this difference, identifying it as a local factor the GNR should consider in management planning is the first step to mitigating disease risk.

General conclusion

In this thesis I first outlined the emergence of Lyme disease in North America, with a specific focus on Quebec. Black-legged ticks and their hosts are experiencing a geographic range shift northward, driven in part by climate change (Sonenshine 2018; Hammond-Collins et al. 2022; Ripoche et al. 2022; Robinson et al. 2022; Eisen and Eisen 2023). This expansion led to the emergence of Lyme disease in Quebec where the number of human Lyme disease cases has increased significantly over the past decade (Gouvernement du Québec 2023 Jul 4). It is predicted that 90% of Quebec residents will be at risk of tick exposure in the next five years (Ripoche et al. 2022; Tardy et al. 2023).

In Quebec, white-tailed deer are overabundant in regions that overlap with high human Lyme disease risk (Lebel 2020; INSPQ 2023b Jun 8). White-tailed deer are key reproductive hosts for black-legged ticks (Ostfeld 2011; Roome et al. 2017; Wolf et al. 2020) as well as keystone herbivores that impact ecosystems across all trophic levels (Waller and Alverson 1997; Rooney 2001; Côté et al. 2004; Gorchov et al. 2021; Beguin et al. 2022; Morrison et al. 2022; Villemaire-Côté et al. 2022). Through my review I determined that the direct effect of deer abundance on tick abundance is well-studied but not fully understood (Kilpatrick et al. 2017), and the indirect effect of deer on tick abundance through cascading ecosystem impacts is understudied (Gandy et al. 2021; Matsuyama et al. 2023).

I then presented a field study testing the direct and indirect impacts of white-tailed deer on black-legged ticks at a nature park in a high-human Lyme disease risk area of Quebec. I found that there were significantly more ticks in the public sector of the reserve where visitor access is allowed. I also found that deer did not have a direct effect on tick abundance, but the number of plants had a significant negative impact on the number of ticks. The density of deer at the Gault

Nature Reserve may surpass a threshold where after no effect on tick abundance will be found, as has been observed previously (Van Buskirk and Ostfeld 1995; Eisen and Dolan 2016; Telford 2017; Martin et al. 2023). However, the negative effect of vegetation on the number of ticks, considered alongside the higher tick abundance and browsing pressure in the public sector, indicates movement behaviour of deer within the reserve may still be impacting tick abundance. Further, significantly more ticks were observed inside deer exclosures versus outside, although the majority of the ticks inside were not questing adults, as has been the case in studies that showed similar results with small exclosures (Ginsberg and Zhioua 1999; Buck and Perkins 2018). Altogether, I have highlighted the spatial variation in tick abundance at the Gault Nature Reserve and the potential for a higher human disease risk in the public access sector, but further study is needed to understand the mechanisms driving this variation.

The risk of contracting Lyme disease is not solely driven by the likelihood of encountering an infected tick, but also an understanding of risky behaviour and preventative measures that can be taken (Sharareh et al. 2017; Bouchard et al. 2019). Social-behavioural risk of contracting Lyme disease can inflate ecological risk. In southern Quebec, not only is the ecological risk of Lyme disease high, but behavioural disease risk is high as the region is popular for outdoor activities and tourism (Tutt-Guérette et al. 2021). In recent years, the number of recreationalists using parks in the Sothern regions of Quebec near large cities have been increasing (Gouvernement du Québec 2018). The abundance of nature parks in this region offers a way for people to connect with nature under growing urbanization but heightens the risk of encountering an infected tick. It is essential that the numerous recreational visitors and outdoors workers are aware of the risks and precautions they can take (Forest-Bérard et al. 2021). Despite Quebec hosting some of the highest risk areas for Lyme disease in Canada, a survey on public knowledge before and after a social awareness campaign found Quebec had the lowest initial knowledge and the smallest increase post-campaign (Aenishaenslin et al. 2016). The future of Lyme disease mitigation in Quebec depends on incorporating further studies of the complex ecological risks including the dynamics of deer, ticks, and environmental interactions into disease management planning and public awareness campaigns.

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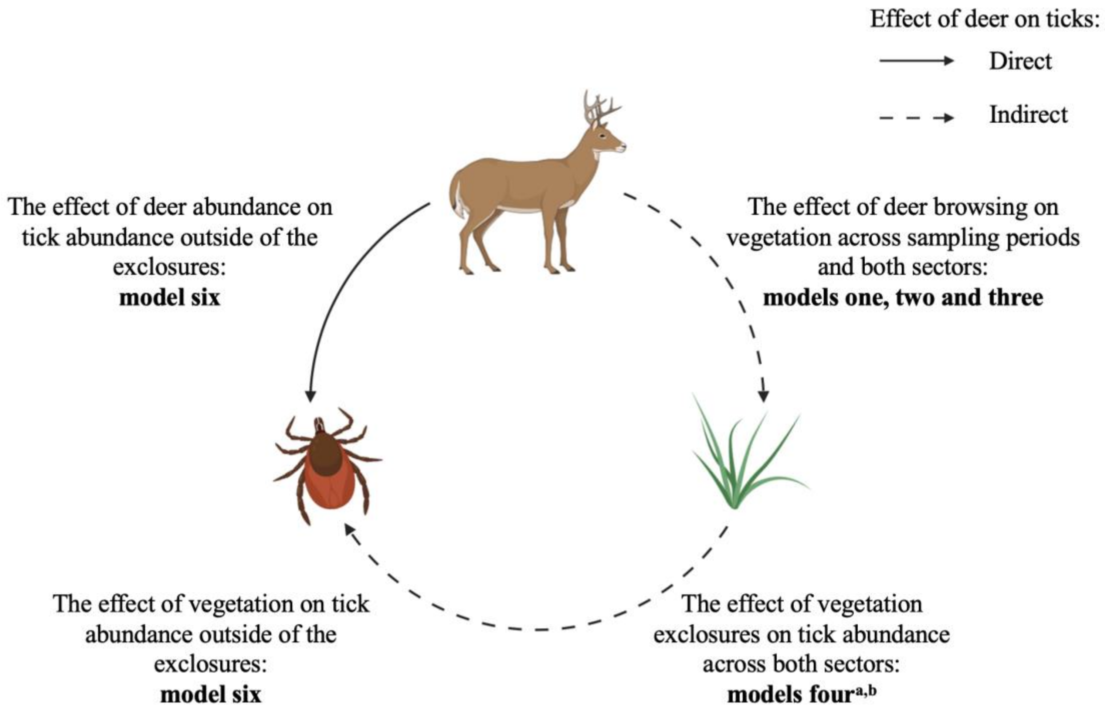
Supplementary materials

Appendix A. A figure representing the models used in this study in the context of their analyzing the direct or indirect effect of deer on ticks.



Appendix B. List of plant species observed in each sector at the GNR. Plants that are resistant to deer browsing or avoided by deer and unique to either the public or private sector of the GNR are in bold font.

Public sector	*Private Sector*
Beech	Beech
Beech drops	Beech drops
Birch	Birch
Black cherry	Bloodroot
Bloodroot	**Blue cohosh**
Grapeseed fern	**Bluestem goldenrod**
Grass	Canada mayflower
Maple (non-sugar or silver)	**Early meadow rue**
Oak	**False – Solomon's seal**
Sessile bellwort	**Hellebore**
Silver maple	**Jack-in-the-pulpit**
Sugar maple	Maple (non- sugar or silver)
Trillium	**Scouring rush**
Trout lily	Silver maple
Unknown	Sugar maple
Unknown Wildflower	Trillium
Whorled loosestrife	Unknown
Wild Sarsaparilla	Unknown wildflower
	Xmas fern

Appendix C. Results of a generalized linear mixed effect model with a negative binomial regression and log link describing the effect of sector, sampling period, and exclosure on the number of plants. Site was included as a random effect.

	Number of plants		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	11.45	6.00 – 21.86	**<0.001**
Sector [Public]	0.40	0.17 – 0.92	**0.032**
Period [One]	1.42	0.94 – 2.15	0.097
Period [Three]	0.77	0.51 – 1.18	0.229
Sector [Private] × EorCExclosure	4.88	2.86 – 8.33	**<0.001**
Sector [Public] × EorCExclosure	12.44	7.36 – 21.03	**<0.001**
Random Effects			
σ^2	0.48		
τ_{00} Site	0.41		
ICC	0.46		
N Site	15		
Observations	90		
Marginal R^2 / Conditional R^2	0.589 / 0.778		

Appendix D. Results of a generalized linear mixed effect model using template model builder with a Conway-Maxwell-Poisson distribution and log link to test effect of sector, sampling period, and exclosure on the number of plant species. Site was included as a random effect.

	Number of plant species		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	3.55	2.83 – 4.46	**<0.001**
Sector [Public]	0.73	0.55 – 0.98	**0.034**
Period [One]	1.16	0.96 – 1.39	0.128
Period [Three]	0.75	0.60 – 0.92	**0.007**
Sector [Private] × EorCExclosure	1.07	0.85 – 1.34	0.566
Sector [Public] × EorCExclosure	1.37	1.08 – 1.74	**0.008**
Random Effects			
σ^2	0.46		
$\tau_{00\ \mathrm{Site}}$	0.02		
ICC	0.05		
N $_{\mathrm{Site}}$	15		
Observations	90		
Marginal R^2 / Conditional R^2	0.104 / 0.147		

Appendix E. Results of a generalized linear mixed effect model with a gamma distribution and log link to test the effects of sector, sampling period, and exclosure on the mean plant height. Site was included as a random effect.

	Mean plant height		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	14.09	11.06 – 17.94	**<0.001**
Sector [Public]	0.57	0.42 – 0.76	**<0.001**
Period [One]	1.10	0.91 – 1.34	0.325
Period [Three]	1.01	0.83 – 1.24	0.903
Sector [Private] × EorCExclosure	1.29	1.02 – 1.64	**0.035**
Sector [Public] × EorCExclosure	1.88	1.50 – 2.35	**<0.001**
Random Effects			
σ^2	0.17		
$\tau_{00\ \text{Site}}$	0.02		
ICC	0.09		
N $_{\text{Site}}$	15		
Observations	86		
Marginal R^2 / Conditional R^2	0.336 / 0.397		

Appendix F. Results of a generalized linear model with a binomial distribution and logit link to test the effect of sector and exclosure on the presence or absence of ticks compiled across all sampling periods.

	Ticks' presence/absence			
Predictors	*Log-Odds*	*std. Error*	*CI*	*p*
(Intercept)	1.79	1.08	0.02 – 4.73	0.097
Sector [Public]	16.77	2306.10	-210.09 – NA	0.994
Sector [Private] × EorCExclosure	-2.08	1.32	-5.30 – 0.28	0.116
Sector [Public] × EorCExclosure	-17.47	2306.10	NA – 355.54	0.994
Observations	30			
R^2 Tjur	0.241			

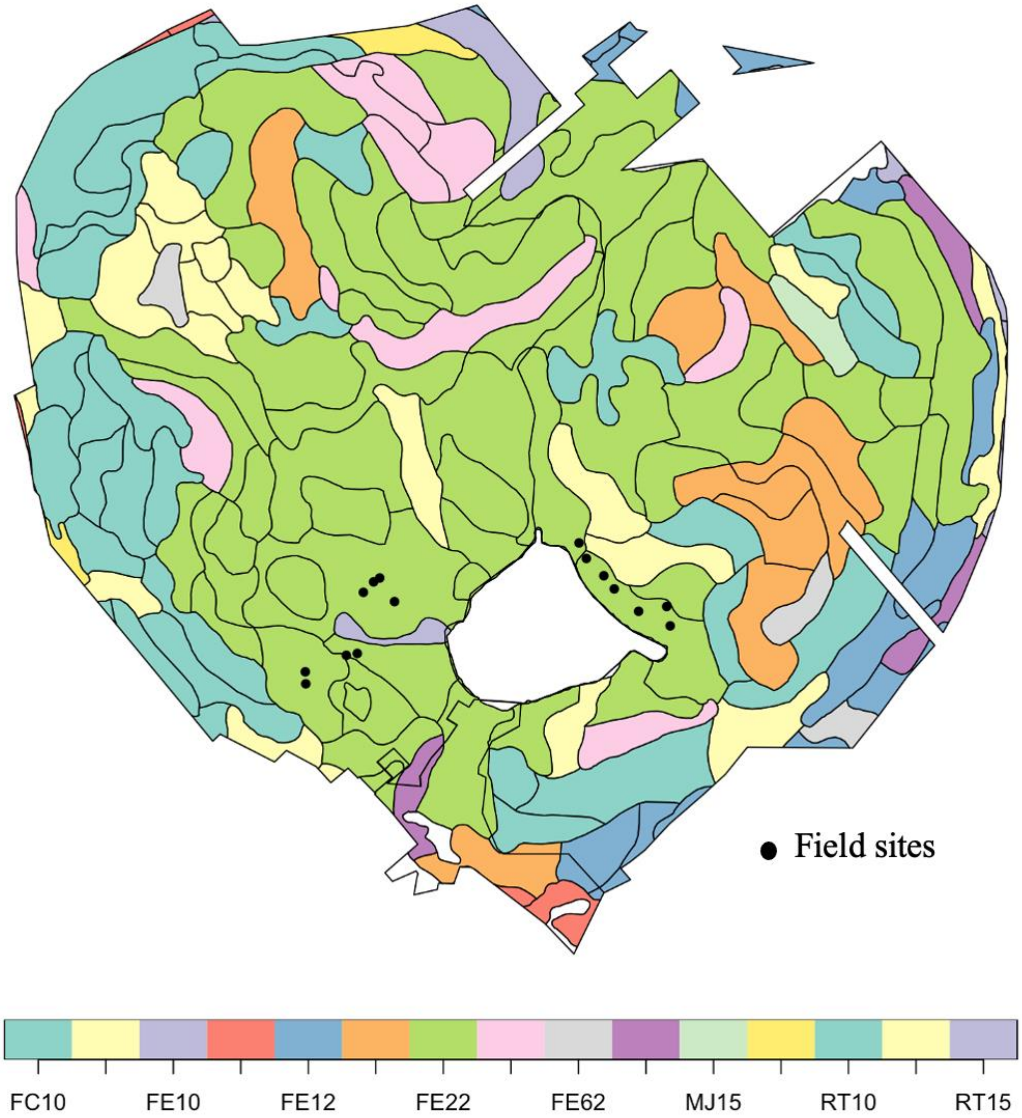
Appendix G. Results of a generalized linear model with a gamma distribution and log link to test the effect of sector and exclosure on the number of ticks per sampling effort. Using only presence data, complied across all sampling periods.

	Ticks per sampling effort		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.01	0.00 – 0.01	**<0.001**
Sector [Public]	10.87	5.94 – 19.58	**<0.001**
Sector [Private] × EorCExclosure	12.86	6.06 – 29.17	**<0.001**
Sector [Public] × EorCExclosure	3.55	1.97 – 6.49	**<0.001**
Observations	23		
R^2 Nagelkerke	0.895		

Appendix H. Results of a generalized linear model with a negative binomial distribution and log link testing the effects of the number of plants, the number of deer per sampling effort (scaled), and the mean plant height (scaled) on the number of ticks outside of exclosures complied across all sampling periods.

	Number of ticks		
Predictors	*Incidence Rate Ratios*	*CI*	*p*
(Intercept)	24.66	9.09 – 79.68	**<0.001**
Number of plants	0.94	0.88 – 0.99	**0.035**
Deer per sampling effort	1.92	0.25 – 17.53	0.508
Mean plant height	0.28	0.07 – 1.05	0.056
Number of plants × Deer per sampling effort	0.92	0.82 – 1.02	0.114
Number of plants × Mean plant height	0.98	0.92 – 1.04	0.487
Deer per sampling effort × Mean plant height	1.68	0.61 – 4.76	0.298
(Number of plants × Deer per sampling effort) × Mean plant height	0.99	0.95 – 1.04	0.742
Observations	13		
R^2 Nagelkerke	0.989		

Appendix I. A figure of the ecotypes present at the Gault Nature Reserve. All study sites were in ecotype FE22 which is described as a basswood maple grove with thin to thick mineral deposits, medium texture, and mesic drainage (Cartographie du cinquième inventaire écoforestier du Québec méridional)



Appendix J. Raw data used for the analysis of models in Chapter 2, Table 3.

Site	Excl. or Cont.	Sector	# Plants	Mean plant height	Ticks	Ticks/ Sampling effort	Deer	Deer/ Sampling effort
FT03	Control	Private	43	14.976744	1	0.00277778	98	0.60282759
FT05	Control	Private	67	15.164179	4	0.01111111	81	0.49138169
FT06	Control	Private	25	16.796	0	0	177	1.0742498
FT07	Control	Private	46	14.81087	1	0.00277778	87	0.79872973
FT08	Control	Private	17	12.035294	3	0.00833333	315	1.90966759
FT09	Control	Public	41	9.992683	3	0.00833333	133	0.81191733
FT10	Control	Public	5	9	34	0.09444444	143	0.87286908
FT11	Control	Public	16	8.71875	35	0.09722222	243	1.48257774
FT12	Control	Public	34	9.55	43	0.11944444	144	0.87917306
FT13	Control	Public	11	5.51	10	0.02777778	526	3.17232868
FT14	Control	Public	31	4.13871	56	0.15555556	234	1.41113328
FT15	Control	Public	3	11.166667	17	0.04722222	207	1.24804626
FT16	Control	Public	5	15.06	5	0.01388889	134	0.80803981

Appendix K. Raw data used for the analysis of models in Chapter 2, Table 2.

Site	Sample period	Excl. or Cont.	Sector	# Plants	# Plant species	Mean plant height	Ticks/ # of samples	Ticks/ Sampling effort	# Deer	Deer/ Sampling effort
FT01	One	Exclosure	Private	187	4	14.32513	0	0		
FT02	One	Exclosure	Private	72	6	13.47222	0	0		
FT03	One	Exclosure	Private	33	3	33.61212	0	0		
FT05	One	Exclosure	Private	21	4	23.79524	0	0		
FT06	One	Exclosure	Private	175	4	16.71486	0	0		
FT07	One	Exclosure	Private	81	5	15.03086	0	0		
FT08	One	Exclosure	Private	23	5	13.03913	0.5	0.125		
FT09	One	Exclosure	Public	106	3	12.48491	0	0		
FT10	One	Exclosure	Public	139	4	10.98921	0.5	0.125		
FT11	One	Exclosure	Public	138	3	12.86957	0	0		
FT12	One	Exclosure	Public	213	4	12.91268	0	0		
FT13	One	Exclosure	Public	6	3	11.13333	0.5	0.125		
FT14	One	Exclosure	Public	8	2	59.5875	0	0		
FT15	One	Exclosure	Public	31	4	11.35484	0	0		
FT16	One	Exclosure	Public	32	5	18.20625	0	0		
FT01	One	Control	Private	22	4	15.29091	0.5	0.00555556	NA	NA
FT02	One	Control	Private	20	6	10.61	1	0.01111111	NA	NA
FT03	One	Control	Private	23	4	16.4	0.5	0.00555556	66	0.88793385
FT05	One	Control	Private	29	4	17.78966	0	0	53	0.7131173
FT06	One	Control	Private	16	5	16.5125	0	0	101	1.35906181
FT07	One	Control	Private	25	7	13.712	0	0	76	1.02280947
FT08	One	Control	Private	10	4	10.19	1	0.01111111	252	3.39155982
FT09	One	Control	Public	20	3	10	0.5	0.00555556	62	0.83885006
FT10	One	Control	Public	3	2	9	1	0.01111111	70	0.94638823
FT11	One	Control	Public	10	4	9.17	0	0	135	1.79974309
FT12	One	Control	Public	19	5	12.16316	1.5	0.01666667	90	1.20216278
FT13	One	Control	Public	5	3	3.56	0	0	290	3.86178342
FT14	One	Control	Public	13	4	3.869231	0	0	163	2.17011834
FT15	One	Control	Public	2	1	9	0.5	0.00555556	121	1.61015055
FT16	One	Control	Public	3	3	21.33333	1.5	0.01666667	55	0.73181076
FT01	Two	Exclosure	Private	183	3	13.60874	0	0		
FT02	Two	Exclosure	Private	53	7	15.93208	0	0		
FT03	Two	Exclosure	Private	20	2	39.84	0	0		
FT05	Two	Exclosure	Private	35	4	22.75143	0	0		

FT06	Two	Exclosure	Private	135	4	17.86889	0	0		
FT07	Two	Exclosure	Private	55	3	18.36364	1	0.25		
FT08	Two	Exclosure	Private	16	3	13.7625	0	0		
FT09	Two	Exclosure	Public	181	4	12.39006	0	0		
FT10	Two	Exclosure	Public	136	5	12.53897	0	0		
FT11	Two	Exclosure	Public	165	4	13.21818	1	0.25		
FT12	Two	Exclosure	Public	159	6	13.59497	4	1		
FT13	Two	Exclosure	Public	4	2	9.5	3	0.75		
FT14	Two	Exclosure	Public	12	3	21.7	3	0.75		
FT15	Two	Exclosure	Public	20	5	11.77	0	0		
FT16	Two	Exclosure	Public	22	3	25.19546	0	0		
FT01	Two	Control	Private	4	2	13.875	0	0	NA	NA
FT02	Two	Control	Private	7	3	12.62857	0	0	NA	NA
FT03	Two	Control	Private	20	5	13.34	0	0	16	0.463491
FT05	Two	Control	Private	24	4	14.4875	0	0	17	0.491807
FT06	Two	Control	Private	6	2	16.3	0	0	37	1.070517
FT07	Two	Control	Private	14	5	13.94286	0	0	11	0.317313
FT08	Two	Control	Private	2	2	13.15	0	0	46	1.325746
FT09	Two	Control	Public	12	4	11.35	1	0.011111	43	1.267403
FT10	Two	Control	Public	1	1	10	0	0	54	1.59282
FT11	Two	Control	Public	2	2	4.5	0	0	39	1.186093
FT12	Two	Control	Public	10	5	5.26	39	0.433333	14	0.423557
FT13	Two	Control	Public	4	3	7.825	6	0.066667	87	2.636757
FT14	Two	Control	Public	12	5	4.891667	53	0.588889	38	1.152115
FT15	Two	Control	Public	0	0	NA	0	0	18	0.545726
FT16	Two	Control	Public	1	1	10	0	0	18	0.54584
FT01	Three	Exclosure	Private	187	3	14.45775	0	0		
FT02	Three	Exclosure	Private	55	6	16.24727	0	0		
FT03	Three	Exclosure	Private	0	0	NA	0	0		
FT05	Three	Exclosure	Private	11	4	24.77273	0	0		
FT06	Three	Exclosure	Private	158	3	16.63608	1	0.25		
FT07	Three	Exclosure	Private	38	2	23.7079	0	0		
FT08	Three	Exclosure	Private	14	3	15.37143	1	0.25		
FT09	Three	Exclosure	Public	76	4	15.12763	0	0		
FT10	Three	Exclosure	Public	131	3	13.34504	0	0		
FT11	Three	Exclosure	Public	200	4	14.6605	2	0.5		
FT12	Three	Exclosure	Public	198	4	13.79546	0	0		
FT13	Three	Exclosure	Public	1	1	13.5	0	0		
FT14	Three	Exclosure	Public	4	1	7.925	0	0		

FT15	Three	Exclosure	Public	16	3	15.89375	0	0		
FT16	Three	Exclosure	Public	30	4	21.14	0	0		
FT01	Three	Control	Private	3	2	14.33333	0	0	NA	NA
FT02	Three	Control	Private	9	4	11.9	1	0.011111	NA	NA
FT03	Three	Control	Private	0	0	NA	0	0	16	0.28661048
FT05	Three	Control	Private	14	3	10.88571	3	0.033333	11	0.19648092
FT06	Three	Control	Private	3	3	19.3	0	0	39	0.6967484
FT07	Three	Control	Private	7	1	20.47143	1	0.011111	NA	NA
FT08	Three	Control	Private	5	3	15.28	0	0	17	0.30346255
FT09	Three	Control	Public	9	3	8.166667	0	0	28	0.50011887
FT10	Three	Control	Public	1	1	8	0	0	19	0.33922437
FT11	Three	Control	Public	4	3	9.7	1	0.011111	69	1.23166988
FT12	Three	Control	Public	5	2	8.2	1	0.011111	40	0.71475105
FT13	Three	Control	Public	2	2	*NA*	0	0	149	2.58060326
FT14	Three	Control	Public	6	2	3.216667	0	0	33	0.5714375
FT15	Three	Control	Public	1	1	15.5	0	0	68	1.17748115
FT16	Three	Control	Public	1	1	1.3	0	0	61	1.05661482