

The background of the cover features a stylized illustration. On the left, a dark green plant with long, narrow leaves and small, pointed seed pods extends upwards. In the center-right, a lighter green plant with broad, pointed leaves is shown. Two black ticks are depicted: one is on a leaf of the central plant, and the other is on a leaf of the plant to its right. In the background, a city skyline with various building silhouettes is visible against a light yellow background. The foreground is a solid light green color.

# **TICKS**

**– ECOLOGY,  
NEW HAZARDS  
AND RELEVANCE  
FOR PUBLIC HEALTH**

THÉRESE JANZÉN

SÖDERTÖRN DOCTORAL DISSERTATIONS



**TICKS**  
– ECOLOGY,  
NEW HAZARDS  
AND RELEVANCE  
FOR PUBLIC HEALTH

THÉRESE JANZÉN

Subject: Environmental Science  
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## Abstract

Ticks and tick-borne diseases are ranking second only to mosquitoes as vectors of pathogens responsible for diseases in both humans and domestic animals. In the countries around the Baltic Sea, two medically important tick species are increasing both in range and abundance, and the public health threat posed by tick-borne diseases in this area is steadily growing. The aim of this thesis was to study the eco-epidemiological dynamics and mechanisms of ticks and bacterial tick-borne pathogens along the natural-urban gradient.

Green spaces have become important intersections between humans, domestic animals, ticks, and tick-borne pathogens. Along the natural-urban gradient in Stockholm County, Sweden, we examined the impact of green space characteristics on tick abundance and pathogens prevalence. In this study all questing ticks were molecularly identified as *Ixodes ricinus*. Questing ticks were abundant in natural and semi-natural habitats, but also present in urbanized parks. Important drivers of tick abundance included significant negative effects of local vegetation height and positive effects of mixed coniferous forests in the surrounding landscape.

The prevalence of *Borrelia burgdorferi* sensu lato was 24% and that of *Anaplasma phagocytophilum* 7.5%. *B. miyamotoi* was found at a few sites with a prevalence of 0.9%. The dominant *B. burgdorferi* (s.l.) genospecies was *B. afzelii*. Tree stem density had a significant positive effect on *B. burgdorferi* (s.l.) prevalence. Broadleaved forests and total forest edge had significant positive effects on *A. phagocytophilum* prevalence, persisting even in highly urbanized areas. The tick-borne disease equine granulocytic anaplasmosis (EGA) significant increased from 2002 to 2015, with a yearly peak in late summer and early fall.

The public health risk for tick-borne diseases in an urban green space was estimated from hazard data on tick abundances and pathogen prevalence combined with exposure data using residential population densities and green space visitor numbers. The results indicated a medium to high risk of tick-borne diseases at most sites. Structured interviews with visitors showed that even if visitors showed a high tick awareness and attempted to avoid ticks, most protective measures were only practiced during specific recreational activities

The findings from this doctoral project show a notable risk of encountering ticks and tick-borne pathogens along the entire natural-urban gradient, even in highly urbanized areas traditionally perceived as having a low risk. The information on the eco-epidemiological drivers of EGA is important also for the medical health field since the agent causing EGA is identical to the agent causing human disease. Despite ticks and their pathogens green spaces still continue to play a vital role in public health, but the omnipresent risk of tick-borne diseases highlights the need for public health initiatives to mitigate this risk.

**Keywords:** Baltic Sea region, eco-epidemiology, habitat, *Ixodes persulcatus*, *Ixodes ricinus*, landscape, risk, urbanization



## Sammanfattning (Summary in Swedish)

Fästingar är näst efter myggor de viktigaste vektorerna för spridning av sjukdomar både till människor och husdjur. I länderna runt Östersjön finns två medicinskt viktiga fästingararter som ökar i utbredning och antal, vilket också utgör ett ökat hot mot folkhälsan. Syftet med avhandlingen var att studera eko-epidemiologisk dynamik och viktiga mekanismer för spridningen av fästingar och fästingburna bakterier i en urban gradient.

Grönområden i och runt städer utgör mötesplatser för människor, husdjur, fästingar och fästingburna patogener. I Stockholms län undersöktes effekterna av grönområdenas egenskaper på förekomst av fästingar och deras patogener utefter den urbana gradienten. Alla insamlade fästingar artbestämdes med molekylära metoder, och samtliga tillhörde arten *Ixodes ricinus*. Fästingar var vanliga i rurala områden och naturliga miljöer, men förekom även i urbana parker. Viktiga faktorer för förekomst av fästingar var den signifikant negativa effekten av vegetationshöjd vid insamlingsplatsen, och den signifikant positiva effekten av barrblandskog i det omgivande landskapet.

I studien av patogener var prevalensen av *Borrelia burgdorferi* sensu lato 24% och för *Anaplasma phagocytophilum* 7.5%. Fästingar infekterade med *B. miyamotoi* påträffades vid några få platser med en prevalens på 0.9%. Den dominerande arten inom gruppen av *B. burgdorferi* (s.l.) var *B. afzelii*. Trätdensitet runt insamlingsplatsen hade en signifikant positiv effekt på prevalensen av *B. burgdorferi* (s.l.). Utbredningen av lövskogar och skogskanter hade signifikant positiva effekter på prevalensen av *A. phagocytophilum*, och fästingar infekterade med *A. phagocytophilum* förekom även i urbana parker. Den fästingburna sjukdomen granulocytär anaplasmos hos häst, ökade signifikant från 2002 till 2015, med flest fall på sensommaren och tidig höst.

Folkhälsorisker för fästingburna sjukdomar i ett urbant grönområde uppskattades med hjälp av information om fästingförekomst, patogenprevalens, befolkningstäthet och besöksantal. Resultatet visade en måttlig till hög risk för fästingburna sjukdomar i hela det undersökta grönområdet. Vid intervjuer med besökare påvisades en hög medvetenhet om fästingar och fästingspridda sjukdomar, men att skyddsåtgärder endast tillämpades vid specifika fritidsaktiviteter såsom bärplockning.

Resultatet från avhandlingen visar på en betydande risk för spridning av fästingburna sjukdomar längs med hela den urbana gradienten, inklusive områden som traditionellt ansetts ha en låg risk. Resultaten som visar på eko-epidemiologiska mekanismer för spridning av granulocytär anaplasmos hos häst är relevanta också ur ett folkhälsoperspektiv eftersom bakterierna orsakar sjukdom även hos människor. Trots risker med fästingar och deras sjukdomar är grönområden ytterst viktiga för folkhälsan utifrån andra hälsoaspekter, men det behövs initiativ och medvetenhet för att motverka riskerna.



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## List of papers

This thesis is based on the following papers, which are referred to in the text by Roman numerals (I–IV):

**Paper I.** Janzén, T., Hammer, M., Petersson, M., & Dinnétz, P. (2023). Factors responsible for *Ixodes ricinus* presence and abundance across a natural-urban gradient. *Plos one*, 18(5), e0285841.

**Paper II.** Janzén, T., Larsson, J., Hammer, M., Petersson, M., Dinnétz, P. *Ixodes*-borne bacterial pathogens across a natural-urban gradient (Submitted to *Parasites & Vectors*).

**Paper III.** Janzén, T., Petersson, M., Hammer, M., Aspán, A., & Dinnétz, P. (2019). Equine granulocytic anaplasmosis in Southern Sweden: Associations with coniferous forest, water bodies and landscape heterogeneity. *Agriculture, Ecosystems & Environment*, 285, 106626.

**Paper IV.** Janzén, T., Hammer, Choudhury, F., M., Petersson, M., Dinnétz, P. Ticks–public health risks in urban green spaces (under review in *BMC Public Health*).

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## Contributions of the author to the different manuscripts

The author planned and designed the study (papers I–IV), collected the data (papers I–IV), performed the laboratory work and genetic analyses (papers III and IV), analyzed the data using GIS and statistics (papers I–IV), and wrote the manuscript as main author (papers I–IV).



## Abbreviations

BLAST	Basic Local Alignment Tool
BMD	<i>Borrelia miyamotoi</i> disease
CNS	Central nervous system
CONTAG	Contagion
CORINE	Coordination of Information on the Environment
EDTA	Ethylenediaminetetraacetic acid
EGA	Equine Granulocytic Anaplasmosis
GIS	Geographical information system
GLMM	Generalized linear mixed models
GLMMTMB	Generalized linear mixed models using Template Model Builder
HGA	Human Granulocytic Anaplasmosis
LB	Lyme Borreliosis
PCR	Polymerase Chain Reaction
PLAND	Percent of forest cover
RF	Relapsing fever
SCB	Statistiska centralbyrån (Statistics Sweden)
SHDI	Shannon's diversity index
SVA	Statens veterinärmedicinska anstalt (Swedish Veterinary Agency)
TBE	Tick-borne encephalitis
TE	Total forest edge
VIF	Variance inflation factor



# Introduction

Urbanization, including landscape changes and increases in urban populations, poses a risk to public health through the emergence and spread of infectious diseases (Connolly et al., 2021). The conversion from natural areas to urban landscapes alters ecological dynamics beyond the urban boundary (Deacon and Samways, 2021). This transformation modifies biotic interactions, landscape configurations, and ecosystem processes, consequently changing species compositions and interactions (Alberti et al., 2020). Species interaction networks play an important role in determining pathogen transmission and spread in ecological communities (Figueroa et al., 2020). Disturbances in ecological communities exemplified by urbanization, can result in altered and new interactions, facilitating the transmission of pathogens from wildlife to humans (Combs et al., 2022). Tick-borne diseases involve vectors that serve as a bridge for pathogen transmission, connecting wildlife pathogens with humans and domestic animals (Wilke et al., 2019). Ticks are increasingly identified as important vectors for a wide array of pathogens also in urban landscapes, with recent reports of abundant tick populations in green spaces used for recreational activities (Gregory et al., 2022; Hansford et al., 2022).

Ticks are obligate hematophagous ectoparasites, or blood-feeding arthropods that prey on multiple vertebrates including birds, reptiles and mammals, including humans (Fogaca et al., 2022). Globally, ticks are second only to mosquitoes as vectors of public health importance; they are capable of transmitting a range of pathogens, including bacteria, viruses, fungi, and protozoans (Brites-Neto et al., 2015). Tick-borne diseases cause a large health burden for humans and domestic animals and are driven by the increasing abundance and geographical expansion of medically important tick species (Gilbert et al., 2021). Urban landscapes, characterized by a diversity of wildlife hosts adapting to anthropogenic environments, can serve as conducive habitats for tick-borne diseases (Madhav et al., 2020). The cohabitation of humans, wildlife and ticks creates interfaces where pathogen transmission can occur (Van-Acker et al., 2022). Given that 55% of the global human population lives in urban areas today, with projections suggesting a rise to 70% by 2050 (United Nations, 2019), there is an urgent need to understand ticks and tick-borne pathogens within urban landscapes (Hansford et al., 2023).

The Nordic countries around the Baltic Sea are located in a region characterized by the overlapping geographical distributions of two medically important tick species, *Ixodes ricinus* and *I. persulcatus* (Laaksonen et al., 2017; Jaenson et al., 2019). As the geographical ranges of these *Ixodes* species expand, the overall public health threat posed by tick-borne diseases in this area is steadily increasing and will affect

more human populations (Jaenson & Wilhelmsson, 2019; Kjær et al., 2019; Uusitalo et al., 2022). Climate change has affected the distribution pattern of ticks and tick-borne pathogens (Gray et al., 2009; Ogden et al., 2021), but climate alone cannot account for the large variation in the local distribution of ticks and tick-borne pathogens, or the frequency of contact between infected ticks and humans and domestic animals (Medlock et al., 2013). Recently, the role of ecological factors in the emergence and transmission of tick-borne diseases has become increasingly apparent (Pfäffle et al., 2013). Therefore, an eco-epidemiological approach is needed to understand the tick–host–pathogen relationship and to determine the appropriate measures for the surveillance, prevention and control of tick-borne diseases (Diuk-Wasser et al., 2021; Nadal et al., 2021; Gray & Kahl, 2022).

## Ticks and urbanization

Tick-borne disease transmission occurs when ticks, pathogens and hosts all interact in a suitable environment (Reisen et al., 2010). Therefore, a habitat suitable for the presence and propagation of tick-borne pathogens must primarily meet the basic requirements of ticks and their hosts (Jaenson et al., 2012; Pfäffle et al., 2013). Urbanization affects the abundance and movement of wildlife which are tick blood-meal hosts and pathogen reservoirs (Estrada-Peña & de la Fuente, 2014). Wildlife dispersal patterns among green spaces along the natural-urban gradient may be facilitated through corridors or green wedges. Additionally, forests, parks and gardens serve as conducive habitats, providing shelter and nesting sites for wildlife animals (Wang et al., 2020). The tendency to preserve green spaces in and around cities is not only a positive aspect for humans but also for wildlife species (Borşan et al., 2020). For generalist *Ixodes* tick species, the majority of the wildlife species present in urban landscapes can serve as hosts for the blood meals (Mysterud et al., 2015).

Exophilic *Ixodes* ticks spend only a small fraction of their life attached to their hosts, instead most of their life is spent on the ground (Sonenshine & Mather, 1994; Parola & Rault, 2001). Exophilic ticks are sensitive to environmental conditions, and off-host survival is an important factor for tick population dynamics and tick species distributions in different habitats (Rizzoli et al., 2014). Humidity plays a crucial role in tick life cycles and affects questing activities (Leal et al., 2020). Ticks often hide in leaf litter, a microhabitat that helps the tick maintain hydration levels (Needham & Teel, 1991). Spatial variation in questing tick density is therefore related to site-specific determinants, including microhabitat conditions and the composition of the local host population (Hartemink et al., 2019; Hansford et al., 2023). Along the urbanization gradient, information on microhabitat conditions suitable for ticks has been outlined as a knowledge gap (Iijima et al., 2022; Van Gestel et al., 2022). Several important questions concerning the drivers of tick presence and abundance in urban green spaces have yet to be answered (Skinner et al., 2023).

## Green spaces along the urbanization gradient

The periphery of cities forms an urbanization gradient—a continuous scale depicting the gradual transition from natural and semi-natural areas to highly modified urban landscapes (Vignoli et al., 2013; Steinparzer et al., 2023). Natural landscapes are characterized by large green spaces such as forests, pastures and meadows (Herzon et al., 2021), and rural semi-natural areas feature low levels of built infrastructure, dominated by green spaces used for farming and forestry (Vizzari & Sigura, 2015). Peri-urban areas are characterized by intermediate to low levels of built environments and intermediate population densities at the outskirts of cities (Cattivelli et al., 2021). In peri-urban areas, green spaces are often forests and large open grasslands used for recreational activities (Žlender & Gemin, 2020). An urban area is a region with a high proportion of built environments usually within and surrounding a city center, with high human population density (Miles et al., 2019). Urban green infrastructures comprise parks, forest patches and green spaces used for recreational activities and are highly frequented by people (World Health Organization, 2016; Breuste et al., 2022).

Urban green spaces provide a myriad of benefits to urban residents (Green et al., 2016). In addition to their aesthetic appeal, urban green spaces contribute to biodiversity, climate change mitigation and human health and well-being (Demuzere et al., 2015). The health benefits of urban green spaces have long been recognized, and arise via several mechanisms including stress reduction, opportunity and motivation for physical activity, and opportunities for social contact (Wheeler et al., 2015). However, in contrast to their health benefits, there is increasing concern about growing health risks, since urban green spaces can provide suitable habitats for ticks infected with various tick-borne pathogens (Mathews-Martin et al., 2020). The risk varies not only with the abundance of infected ticks in different habitats, but also with human behavior and movement patterns in green spaces (Sormunen et al., 2020).

Urban green spaces used for recreational activities are frequently designated as nature reserves or similarly protected nowadays (Bell et al., 2007). National and cultural differences can largely influence the different activities performed in urban green spaces (Sayan et al., 2013). In many parts of Europe, access to green spaces is restricted to protected green infrastructures and publicly owned land (Aasetre et al., 2016). However, in Scandinavia, the tradition to access nature freely is made possible by the right of public access to both public and private land (Sandell & Fredman, 2010). For many citizens, engaging in outdoor recreation is an essential lifestyle and a quality-of-life factor that is associated with important mental and physical health benefits (Hansen et al., 2023). The dominating recreational activities have been linked with nature and include hiking, picking berries or mushrooms, hunting, fishing, and other outdoor activities (Hörnsten et al., 2000; Pröbstl et al., 2010). Outdoor recreational activities are increasingly practiced among all Europeans and new activities such as biking and recreational horse riding, keep being added to this list (Zasada et al., 2013; Hammer et al., 2017).

Since green spaces have the potential to benefit human populations with a wide range of public health goals, there are plans to increase urban and peri-urban green space on a national and international scale (Lindholm et al., 2016; World Health Organization, 2017). Several European cities have established green belts around the city or are planned with green wedges of forests and greenery that extends from the rural landscape toward the city center (Ignatieva et al., 2011). However, the presence of ticks and tick-borne pathogens in urban landscapes, not only is a potential public health challenge but could also undermine public health gains from urban green spaces (Hansford et al., 2023).

## Rationale for thesis

The incidence and public health burden of tick-borne diseases have increased in Europe during recent decades (Gray et al., 2009; Rochlin & Toledo, 2020; Springer et al., 2020; Jenkins et al., 2022). The most frequently reported tick-borne disease is Lyme borreliosis (LB), a systemic infection caused by *Borrelia burgdorferi* sensu lato (s.l.) spirochetes transmitted by ticks from the genus *Ixodes* (Wolcott et al., 2021). An emerging *Ixodes*-borne disease is *B. miyamotoi* disease (BMD), which is caused by spirochetes from the relapsing fever (RF) *Borrelia* group (Kubiak et al., 2021). Infections with *Anaplasma phagocytophilum* are the most common tick-borne diseases in Europe and include tick-borne fever, equine (EGA), canine, and human granulocytic anaplasmosis (HGA) (Matei et al., 2019). Tick-borne encephalitis (TBE) is an infection of the central nervous system (CNS) caused by the TBE-virus is also transmitted by *Ixodes* ticks in several European countries (Kunze et al., 2022). Furthermore, with the additional detection of emerging or reemerging pathogens that cause less well-known infections or the introduction of nonendemic tick species, tick-borne diseases are becoming a growing threat to public health (Grochowska et al., 2020). Urban landscapes are increasingly recognized as frontiers for tick-borne disease expansion within endemic regions, but the risk factors for acquiring tick-borne diseases in these areas are largely unknown (Gregory et al., 2022; Hansford et al., 2023)

Several studies on tick abundance and the prevalence of tick-borne pathogens in questing ticks have been performed (Lommano et al., 2012). However, comprehensive data on tick densities and pathogen prevalence in urban landscapes remain scarce, especially in northern European countries in the Baltic Sea region (Sormunen et al., 2020). Public health authorities in this region describe tick-borne diseases as one of the greatest risks to public health, emphasizing both severity and probability, and have called for preparedness and risk assessments (Folkhälsomyndigheten, 2021; Uusitalo et al., 2020). Bacterial tick-borne infections are notifiable only in a few European countries (Azagi et al., 2020; Vandekerckhove et al., 2021), with numerous cases unreported (Azagi et al., 2020; Petrulionienė et al., 2020). Surveillance of medically important tick species and pathogen prevalence, therefore, has become an important tool for monitoring and preventing bacterial tick-borne diseases (Fracasso et al., 2023).

Human exposure to ticks depends both on the density of infected ticks and on human movement patterns and protective behaviors (Zeimes et al., 2014; Diuk-Wasser et al., 2021). Urban green spaces are highly frequented by humans; thus, high tick densities could lead to an increased risk of human infection by tick-borne diseases (Mathews-Martin et al., 2020). The absence of human vaccines for many bacterial tick-borne pathogens has led to a focus on individual preventative measures

to reduce the risk of tick-borne diseases (Slunge & Boman, 2018). Although these methods can be highly effective at preventing tick attachment, the utilization of appropriate prevention measures among visitors to urban green spaces have has been infrequently studied (Bayles et al., 2013; Niesobecki et al., 2019). By improving our understanding of the underlying ecological processes that affect the spatial distribution of ticks and tick-borne pathogens and human behavior and movement patterns in urban green spaces, the conclusions drawn from this study will provide useful information on how to reduce the public health risks of tick-borne diseases.

## Aim of the thesis

The overall aim of this thesis was to study the eco-epidemiological dynamics and mechanisms of ticks and bacterial tick-borne pathogens along the natural-urban gradient. To investigate this, I focused on the following research questions:

- I. What is the impact of urbanization on tick abundance and pathogen prevalence?
- II. Which local and landscape level variables are associated with tick abundance and pathogen prevalence in natural and urban green spaces?
- III. How the hazard, exposure and risk of tick-borne infections are affected by habitat characteristics, human population densities and individual behaviors?



## Eco-epidemiology and public health

The study of the distribution and determinants of diseases and its application to control health issues is called epidemiology (Bonita et al., 2006). The disease triangle of epidemiology, which describes the interactions and interdependence of the host, agent, and environment, is a traditional model used to explain how infectious diseases are caused and transmitted (Frost, 1976; Scholthof, 2007; Coleman et al., 2018). The agents used are bacteria, viruses, parasites, or other factors that may cause diseases (Levitt et al., 2010). A host is an organism that harbors the disease (James et al., 2015). Moreover, hosts may be ill from the disease or may carry a pathogen asymptotically (Casadevall & Pirofski, 2000). The environment includes all conditions in the surroundings that, if favorable, allow for the disease to develop and be transmitted (Reisen, 2010). Pathogens reach and infect a susceptible host through transmission (Li, 2017). However, the traditional disease triangle's environmental category overlooks the elements that are essential in infectious disease transmission. Notably, it fails to address the importance of transmission mechanisms and how pathogens reach and infect hosts (Escudero-Pérez et al., 2023). In contrast, ecology, which describes the interrelationships of organisms with one another and with their environment (Priyadarsini et al., 2020; John & Kompithra, 2023), offers a more comprehensive approach. Therefore, to fully understand the environment of disease pathogens and to identify their sources, their ecology must be understood (Nikolaenko & Fiedler, 2020).

Eco-epidemiology is an emerging field where the means through which biological and environmental factors influence infectious diseases are explored (Diuk-Wasser et al., 2023; Jana et al., 2022; Heidecke et al., 2023). When the concept of eco-epidemiology was first presented, Susser and Susser (1996) underlined the limits of the black-box paradigm commonly used in epidemiological studies. This paradigm focuses on the circulation of pathogens primarily at the individual level and considers populations as a sum of individuals and consequently neglects many aspects including social and environmental factors (Susser & Susser, 1996). Eco-epidemiology is built on the consideration of a multilevel system and the fact that no level can be isolated from the other (Susser & Susser, 1996). Combining different scales, such as population and spatial scales, and a mechanistic approach that integrates both population dynamics and pathogen dynamics are essential in understanding disease dynamics (Tompkins et al., 2011). With the involvement of a vector such as a tick-borne disease, this multilevel approach is even more essential since the infection of a host depends on the presence, abundance, and vectorial capacity of the pathogen,

which are all dependent on multiple factors ranging from molecular characteristics to environmental factors (Giraudoux et al., 2008).

The eco-epidemiological framework was adopted for this thesis to study ticks and tick-borne pathogens along the natural-urban gradient. To study the dynamics and mechanisms of ticks and bacterial tick-borne pathogens, an Eco-Epi model was developed as a guiding structure (Figure 1). The model was constructed from a forum paper focusing on how land use changes have shaped the eco-epidemiology of *Ixodes scapularis* in the eastern United States (Diuk-Wasser et al., 2021). To explore how different landscape characteristics and habitat features influence tick–host–pathogen relationships, conceptual theories from the fields of landscape ecology, population ecology, and epidemiology were utilized. The assessment of the public health risk of tick-borne diseases includes a combination of factors related to the identification of the tick hazards and the characterization of human exposure. In addition, the degree to which individuals get in contact with infected ticks is dependent on individual human behavior, and protection against tick bites.

### Landscape characteristics

Landscape ecology is the study the of interaction between spatial patterns and ecological processes, that is, the ecological understanding of spatial heterogeneity across spatial scales (Turner et al, 2001). Urban landscapes are highly heterogenous, exhibiting different compositions and spatial configurations, where composition refers to the type of different land covers, and configuration refers to the spatial arrangement of land cover classes (Carrara et al., 2015). Landscape configuration and forest fragmentation may influence wildlife host movement and habitat usage, which in turn affects the distribution of ticks and pathogens across spatial scales and levels of urbanization (Turner et al., 1989; Wiegand et al., 2005; Heylen et al., 2019) (Figure 1). Fragmentation of habitats caused by urbanization also increases habitat edge length, which may represent altered biotic and abiotic conditions (Diuk-Wasser et al., 2021). Although habitat fragmentation decreases the habitat area, the resulting heterogeneity may increase the opportunities for certain species and their associated hosts (Tardy et al., 2022).

### Habitat and microhabitat features

The spatial distribution of resources in heterogeneous landscapes can have significant effects on the growth, reproduction, and dispersal of species (Turner et al., 2001). When the landscape is divided into smaller isolated patches, biodiversity may be affected, which may be an important aspect of understanding animal movement and foraging patterns (Turner et al., 2001). Generally, heterogeneous habitats support greater species diversity, and larger habitats allow for larger population sizes than do smaller habitats (Rybicki et al., 2020). Large habitats can also include more local environmental variability, diverse microhabitat conditions, topographic differences

and variation in the field layer (Ficetola, et al., 2020). The microhabitat represents the variability of conditions found within a specific habitat (Ziesche & Roth, 2008). Exophilic *Ixodes* ticks spend most of their time close to the ground or actively questing for hosts on vegetation near the ground (Daniel et al., 2015). This off-host resting, or questing phase represents 98–99% of the tick lifecycle, which is why the microhabitat determines tick population density and questing activities (Boehnke et al., 2017) (Figure 1). Along the urbanization gradient, a mixture of forested and developed land generates patchy habitats with varying abilities to support ticks and their hosts (Piedmonte et al., 2018).

### Maintenance and reservoir hosts

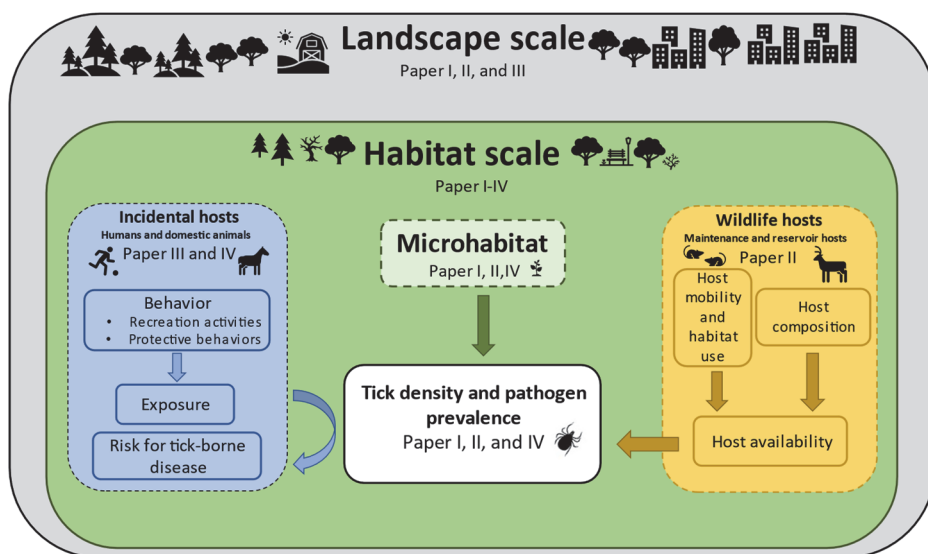
Urbanization is one of the leading causes of wildlife extinction (McKinney, 2006), which is explained by the inability of many native species to cope with the environmental alterations linked with urban development (Mackenstedt et al., 2015). However, the impact of urbanization on biodiversity depends on the ecological structure of the urban landscape, and peri-urban and urban green spaces can be very attractive for wildlife species (Bradley & Altizer, 2007). In addition, green wedges or green belts surrounding cities play integral roles in ecological networks and can be used for wildlife dispersal (Žlender & Thompson, 2017). The biodiversity of plants and animals within urban landscapes may even exceed the biodiversity in large natural and semi-natural areas due to the proximity of and variation in different habitat types (McDonnell & Hans, 2008). Moreover, the availability of alternative food resources for wildlife species, such as waste, pet food, or garden produce, is far greater than that in natural and semi-natural areas. This approach is particularly important since many wildlife species that thrive in urban environments can be important reservoir hosts for tick-borne pathogens (Rizzoli et al., 2014) (Figure 1).

Ticks are obligate parasites, and interactions with their wildlife hosts are central to tick population dynamics and pathogen prevalence (Tsao et al., 2021). The different life stages of generalist *Ixodes* ticks are found on a wide range of different vertebrates commonly found in urban landscapes (Borşan et al., 2020). Large and medium-sized mammals play a significant role as maintenance hosts for ticks, functioning as a food resource for ticks in both nymphal and adult stages and possibly bringing them closer to urban areas (Rizzoli et al., 2014). Small to medium-sized mammals are important maintenance hosts for larvae but are also reservoir hosts for tick-borne pathogens (Jahfari et al., 2017). Pathogen persistence in different habitats across the urbanization gradient depends on the degree of isolation of the habitat patches (Millins et al., 2018). The habitats where tick-transmitted pathogens circulate are very focal, and the term “foci of transmission” is commonly used to describe the spatial distribution of tick-borne pathogens (Randolph, 2002). These foci are defined not only by the habitat characteristics but also by the presence of reservoir hosts, which are necessary for the maintenance of the pathogens. Elucidating the role of maintenance and reservoir hosts across the urbanization gradient will contribute valuable insights into

the intricate relationships between urbanization patterns and the eco-epidemiology of tick-borne diseases (Figure 1).

### Public health risk of tick-borne diseases

Landscape changes and urbanization induce ecological change, consequently altering the epidemiology of diseases (Hassell et al., 2017). Changes in wildlife habitats lead to frequent human contact with tick vectors, thus posing a risk to public health (Eremeeva et al., 2015). While green spaces in urban areas are important for public health, they may also expose residents to tick-borne diseases (Heylen et al., 2019). Human exposure depends both on the density of infected ticks and on individual outdoor activities and movement patterns of humans (Diuk-Wasser et al., 2021) (Figure 1). Since the risk of infection by human tick-borne diseases largely depends on individual human behavior, this risk is difficult to measure and, therefore, the most poorly understood aspect of the transmission cycle (Hassett et al., 2020).



**Figure 1.** Components of the Eco-Epi-model impacting tick densities and pathogen prevalence along the natural-urban gradient encompassed various factors. Landscape characteristics play a pivotal role in influencing tick abundance and pathogen prevalence through their impact on habitat features and host populations within the environment. Furthermore, individual human behavior, including the type of outdoor activity performed and the use of protective measures, influences public health risks due to ticks.

A core principle of the theoretical concepts underpinning many public health risk reduction programs is the recognition that awareness of a health threat is important for the adoption of risk mitigation strategies (Glanz et al., 2015). However, knowledge and perceived risk, especially in urban green spaces, may lead to levels of protection that are not optimal from either an individual or a public health perspective (Slunge

& Boman, 2018; Niesobecki et al., 2019). The identification of individual behavior and movement patterns including the usage of protective measures becomes important for identifying visitor tick-borne risks (Figure 1). This information can be strategically targeted through optimized communication strategies for the prevention of tick bites among visitors to green spaces.



# The tick

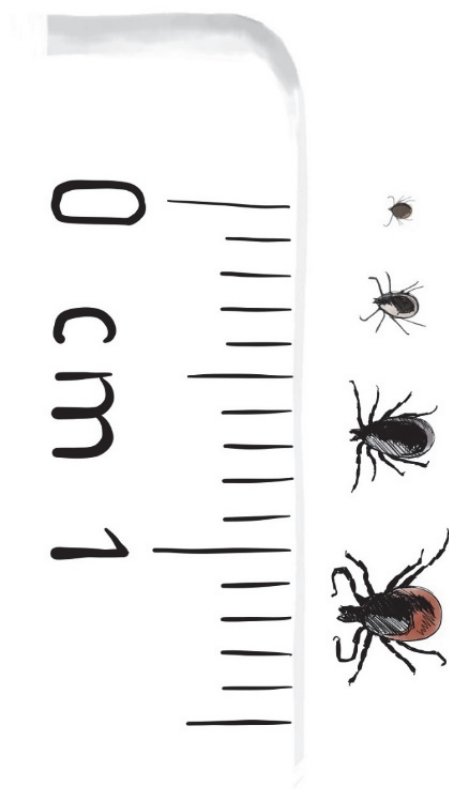
Ticks are currently among the most common public health and veterinary problems in the world, but ticks and tick-borne pathogens have been around long before humans walked the earth (Brites-Neto et al., 2015). Ancient ticks fossilized in amber show that ticks were found to have existed more than 99 million years ago and fed on dinosaurs and certain ancient birds (Peñalver et al., 2018). Ticks and their associated pathogens have survived dramatic climate shifts and they have also adapted to multiple vector–host interactions (Mysterud et al., 2021).

Together with spiders, scorpions and mites, ticks are arthropods that belong to the class Arachnids (Arachnida) (Steen et al., 2004; Léger et al., 2015). More than 900 tick species have been found throughout the world, and many of them are vectors of pathogens of importance for human and animal health (Ahmed et al., 2007; Gasmi et al., 2018). Ticks are further placed into the class Acari, which includes three families: Argasidae (soft ticks), Ixodidae (hard ticks) and Nuttalliellidae (monotypic) (Mans et al., 2012). Hard ticks are distinguished from soft ticks by the presence of a hard, chitinous covering on their dorsal surface called the scutum (Madder et al., 2014). Hard ticks have a prominent capitulum (head and feeding parts) located in front of the body, which is different from that of soft ticks where the capitulum is located beneath the body (Getahun et al., 2016). *Ixodes* ticks have no eyes, but they have sensory organs called the Haller’s organ on the tip of their front leg that can help them sense carbon dioxide, heat, odors, and movements (Allan et al., 2010). *Ixodes* ticks may transmit disease-causing agents, including bacteria, viruses, and parasites, through their saliva while feeding on their hosts (Capligina et al., 2016). Among the blood-sucking arthropods, ticks rank first in terms of the diversity of pathogens they can transmit and second in terms of the disease burden in humans and animals (Jia et al., 2020).

## *Ixodes* tick species

After mosquitoes, ticks are the second most common agent of vector-borne diseases in the world but rank first as the most common agent of vector-borne diseases in the Northern Hemisphere (Gilbert et al., 2021). The *Ixodes* tick species that transmit tick-borne pathogens the most important are *I. ricinus* and *I. persulcatus* in Europe and Asia and *I. pacificus* and *I. scapularis* in North America (Andersson, 1989). The distribution of *I. ricinus* extends from Ireland in the west to Russia and from the northern parts of Scandinavia to North Africa. The distribution of the taiga tick *I. persulcatus* ranges from Scandinavia to Japan (Uusitalo et al., 2022). *I. ricinus* is the predominate tick species in the southern parts of the Baltic Sea region, and the distribution of this tick is more scattered along the northern coasts. During the last 2 decades,

*I. persulcatus* has spread to new areas from eastern Finland all the way to eastern Sweden (Sormunen et al., 2016; Jaenson & Wilhelmsson, 2019). Although *I. persulcatus* may spread southward and *I. ricinus* northward, the exact geographical distributions of the two tick species are still unknown or changing (Sormunen et al., 2020).



**Figure 2.** Sizes of *Ixodes ricinus* ticks at all life stages. From top to bottom: larva, nymph, adult male and adult female. Illustration: Terése Arvidsson.

### Life of *Ixodes* ticks

The *Ixodes* tick has three active life stages, larva, nymph, and adult (Grigoryeva, 2022) (Figure 2). To proceed to their next life stage, ticks must feed on blood from a host (Süss et al., 2008). The female lays eggs that subsequently hatch into six-legged larvae (Kučera, 2015). Due to their susceptibility to desiccation, larvae mostly remain on the ground until a suitable host is encountered (Leal et al., 2020). When the questing tick finds a host, the tick grasps on and crawls up on the host using its forelegs (Földvári et al., 2016). With the sensory palps, the tick searches for an area where the skin is soft to insert its feeding organ—the hypostome—and starts to feed (Richter et al., 2013). Various substances, including enzymes, vasodilators, anti-inflammatory elements,

and anticoagulants, produced in the salivary glands of ticks, are injected into the host (Slovák et al., 2000). These substances have a local anesthetic effect, which may explain why tick bites on humans can go unnoticed (Parola et al., 2001). The feeding duration of *Ixodes* ticks ranges between 2 and 15 days depending on a variety of factors, including tick species, life stage, host species, and site of attachment (Petney et al., 2011). The larva commonly feed on small mammals such as rodents. After the blood meal is digested, the larva drops to the ground and tries to find a place with high humidity (Randolph et al., 1999). After digesting the bloodmeal, the larva metamorphoses into an eight-legged nymph. The nymph searches for a new host and, after a blood meal molts into sexual maturity as an adult tick (Bonnet et al., 2009).

The female tick has two tasks before she can complete her life cycle: mating with an adult male and ingesting a final bloodmeal before she can produce eggs (Charrier et al., 2018). Mating between adult ticks usually occurs on the last host where the male ticks try to find the female (Randolph, 1980). An adult male rarely feeds on a host and never engorges; his primary focus is to mate with a female (Ioffe-Uspensky & Uspensky, 2017). In mating, the male dispenses the sperm by inserting his mouthparts into the genitals of the female tick. A successfully mated female can produce several thousand eggs (Anderson et al., 2008). The mated engorged females drop from the host animal and lay all the eggs on the ground close to where they landed. After approximately one month, the eggs hatch into larvae, which, under suitable environmental conditions, can begin new quests for bloodmeals (Edman & Spielman, 2020).

## Tick ecology

Most of their time, ticks hide near the ground, where they are protected from sunlight and desiccation (Leal et al., 2020). During questing, ticks climb to the top of the vegetation, extend their front legs, and wait for a passing host (Leal et al., 2020). Larvae are at the most sensitive stage of ticks and generally quest for hosts on the ground or on low vegetation where the humidity is high (Oorebeek et al., 2009). The nymphs can also quest on the ground but usually climb vegetation a few decimeters above ground (Tack et al., 2012). Adult ticks can climb vegetation up to 1.5 meters above the ground in their quest for a host (Mejlon & Jaenson, 1997). Because *Ixodes* ticks require at least 80% relative humidity they have been considered forest dwellers (Boehnke et al., 2017). However, as tick-borne diseases expand into urban areas, key questions regarding what ecological and sociobehavioral conditions enable the establishment of the enzootic cycle and pathogen spillover to humans and our companion animals arise.



## Tick-borne pathogens

Ticks have been acknowledged as human parasites for thousands of years and were previously described by ancient Greek writers, including Homer and Aristotle (Sonenshine, 2013). Despite the extensive historical study of ticks, the confirmation that they transmitted infectious diseases occurred in the late 19<sup>th</sup> century and was confirmed through the work of Smith and Kilbourne (Nelson & Williams, 2007). The major impact of tick-borne diseases on the general public in the USA and Europe first became apparent with the detection of *Borrelia burgdorferi* (s.l.) as the causative agent of Lyme borreliosis in the 1980s (Burgdorfer et al., 1982). Since then, the number of recognized, medically important tick-borne diseases has increased dramatically (Lommano et al., 2012; Pfäffle et al., 2013).

### *Borrelia burgdorferi* sensu lato

The etiologic agent of Lyme disease is a spirally shaped type of bacteria called spirochetes. These bacteria are microaerophilic bacteria with a parasitic lifestyle, meaning that they cannot live outside the body of a tick or a host (Chaconas et al., 2020). The spirochetes owe their shape and spiraling motility to their periplasmic flagella. The genus *Borrelia* comprises many species, and the *B. burgdorferi* (s.l.) complex is a group that may cause human Lyme borreliosis (LB) (Margos et al., 2018). The *Borrelia* complex constitutes more than 20 different species that have been found in *Ixodes* ticks, six of which are known human pathogens (Steinbrink et al., 2022). However, new species are being constantly identified, so the current number is likely not the final number (Steinbrink et al., 2022).

The prevalence and distribution of *Borrelia* species in ticks are among the most essential components of risk assessment for LB and these species have been extensively studied in Europe (Burn et al., 2023). In a recent meta-analysis with results from over 100 publications, the mean *B. burgdorferi* (s.l.) prevalence was 14.2% for nymphs and 21.1% for adult ticks (Hansford et al., 2022). A higher proportion of adult ticks are usually infected with *B. burgdorferi* (s.l.) compared to nymphal ticks, which is probably related to the fact that adult females ingest one more bloodmeal than nymphs (Kubiak et al., 2019). The most common *Borrelia* species detected in *Ixodes* ticks in Europe is *B. afzelii*, followed by *B. garinii*, *B. burgdorferi* sensu stricto, *B. valaisiana*, *B. lusitaniae*, and several untypeable species (Mysterud et al., 2019; Burn et al., 2023). Studies have also shown that *Ixodes* ticks collected from different regions of Europe harbor small percentages of *B. spielmanii*, *B. bissetti*, and *B. bavariensis* (Kubiak et al., 2019). The genus *Borrelia* can be divided into two well-defined groups: the LB group and the relapsing fever (RF) group.

### *Borrelia miyamotoi*

One of the emerging *Ixodes*-borne diseases in Europe is *B. miyamotoi* disease (BMD), which is caused by spirochetes from the RF group *Borrelia* (Kubiak et al., 2021). Initially, isolated from questing *I. persulcatus* ticks in Japan in 1994, *B. miyamotoi* has since been identified in other tick species, including *I. scapularis*, *I. pacificus*, and *I. ricinus* (Franck et al., 2020). Prior to 2011, when the first documented symptomatic infection in humans occurred in Russia, *B. miyamotoi* was regarded as non-pathogenic species (Platonov et al., 2011). Subsequent cases of BMD have been reported in the USA, Europe, and Japan (Hoornstra et al., 2022). Symptoms of BMD are nonspecific and vary and including influenza-like symptoms characterized by fever, nausea, myalgia, fatigue, headache, or chills (Platonov et al., 2011; Krause et al., 2015). The prevalence of *B. miyamotoi* in ticks in Europe is typically low, approximately 1% (Wilhelsson et al., 2013, Hoornstra et al., 2022)

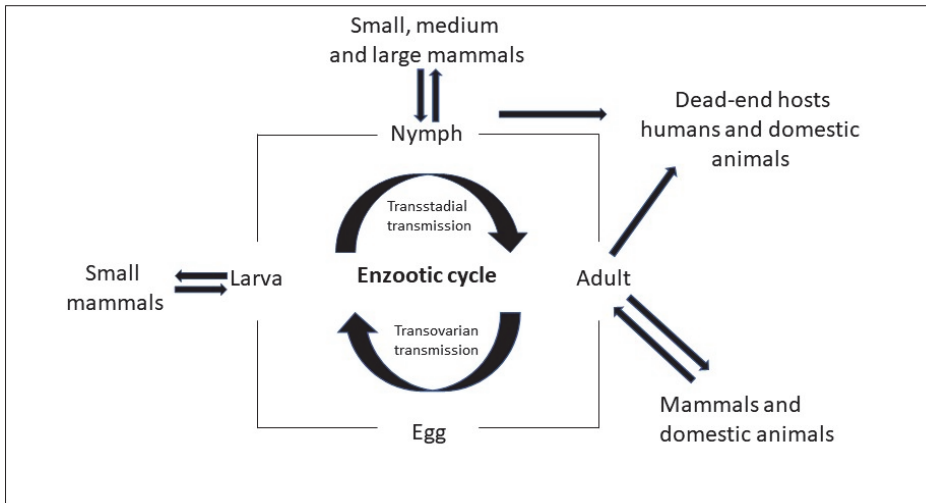
### *Anaplasma phagocytophilum*

*A. phagocytophilum* of the family *Anaplasmatatacae* in the order Rickettsiales, is an intracellular pathogen that causes disease in humans and domestic animals (Brown, 2012). The family *Anaplasmatatacae* includes five well-known genera namely *Ehrlichia*, *Anaplasma*, *Neorickettsia*, *Aegyptianella* and *Wolbachia* (Rikihisa, 2011). Even though it is less known, *A. phagocytophilum* is among the most important tick-borne bacteria both for veterinary and public health in Europe (de la Fuente et al., 2005). Infection in domestic animals was first described in 1940, is generally referred to as tick-borne fever (TBF) and is responsible for important economic losses to the cattle and sheep industries (Stuen, 2007). Equine granulocytic anaplasmosis (EGA) was first recognized as a disease of horses in California in 1969 and later found in other parts of the USA and Europe (Dumler et al., 2005). The disease was long thought to be limited to domestic animals and wild reservoir hosts, but the first case of human granulocytic anaplasmosis (HGA) was found in 1996 (Woldehiwet, 2010).

HGA is commonly transmitted via tick bites; however, HGA cases have also been reported from perinatal transmission (Dhand et al., 2007) and transmission via transfusion (Annen et al., 2012). The disease also affects butchers and hunters via infection through the handling of blood infected with *A. phagocytophilum* (Bakken et al., 2015). In China, there have also been reports of possible hospital-acquired infections, which could constitute the first human-to-human transmission (Zhang et al., 2008). The most common risk factor for HGA, however, includes outdoor recreational activities such as hiking or gardening in tick-infested areas (Stuen et al., 2013). *A. phagocytophilum* has been detected in *Ixodes* ticks in most European countries, and its prevalence ranges from 0.4 to 66.7% (Pilloux et al., 2019). In Sweden, studies have shown that the prevalence of *A. phagocytophilum* in ticks ranges from 1.3% to 15% (Severinsson et al., 2010).

### Transmission routes of bacterial tick-borne pathogens

The circulation of tick-borne pathogens is maintained in nature in enzootic cycles (Figure 3), which include ticks and different vertebrate hosts (Juwaied et al., 2019). A tick acquires bacterial pathogens primarily through feeding on an infected host, so-called horizontal transmission, which is defined as a vertebrate host species that is capable of passing pathogens to a feeding tick vector (Turell, 2020). Bacterial tick-borne pathogens persist in ticks and are maintained transstadially during the molting process (Cayol et al., 2017). Bacterial transmission from tick to tick occurs through direct passage between cofeeding ticks (Karbowiak et al., 2018). Cofeeding occurs when a cluster of ticks feed close together on the same host. In this way, pathogens can spread between ticks without systemically infecting the host. The *Borrelia* species that cause tick-borne relapsing fever (TBRF) may be passed from adult females to eggs via transovarian transmission; however, this transmission appears to be rare for other bacterial tick-borne pathogens (Diaz et al., 2015; Belli et al., 2017).



**Figure 3.** Illustration of the circulation of tick-borne pathogens that are maintained in nature in enzootic cycles. Horizontal transmission occurs when a tick acquires tick-borne pathogens while feeding on an infected host. Bacterial tick-borne pathogens are maintained transstadially as ticks process through different life stages. *Borrelia miyamotoi* can be transmitted from the female tick to the egg, through transovarian transmission. Humans and domestic animals are considered accidental hosts for ticks and dead-end hosts for tick-borne pathogens.

The tick gut is the initial site of colonization for *Borrelia* spp. and *A. phagocytophilum* (Liu et al., 2011; Kurokawa et al., 2020). Bacteria must overcome several barriers to persist in the tick, such as tick immune defense and the avoidance of endocytic digestion in tick gut epithelial cells (Kurokawa et al., 2020). Most bacterial pathogens remain in the lumen of the tick gut before migrating to the salivary glands during subsequent feeding (Kurokawa et al., 2020.) When an infected tick ingests a new

blood meal from a host, the bacterial pathogen migrates to the salivary glands and is disseminated into the host (Schwan et al., 2022).

### Epidemiological situation

Lyme borreliosis (LB) is the most common and well-known tick-borne disease in the Northern Hemisphere, and its incidence has increased significantly in the recent decades both in Europe and the USA (Grochowska et al., 2020). Approximately 476,000 cases are diagnosed and treated annually in the United States, and more than 200,000 cases are diagnosed and treated annually in western Europe (Marques et al., 2021). The cause of BMD, *B. miyamotoi* has been increasingly documented in several European countries. However, the current incidence of this diseases is likely to be underreported, as suggested by tick exposure and prevalence data, as well as through the absence of clinical presentation hallmarks, making assessing the impact of BMD infection challenging (Jahfari et al., 2014; Cutler et al., 2017). Human granulocytic anaplasmosis (HGA) cases, have only been occasionally reported throughout Europe (Azagi et al., 2020). On the other hand, in North America, HGA is a common tick-borne infection, that can be severe or even fatal. According to an epidemiological investigation of HGA conducted on humans in southern Sweden, the seroprevalence ranged between 22 and 24% and increased with age (Johansson et al., 2017).

Since bacterial tick-borne infections are not notifiable diseases in numerous European countries, the figures for both LB, BMD and HGA are highly uncertain. Humans are considered incidental hosts for ticks and dead-end hosts for both ticks and pathogens (Dennis & Piesman, 2005; Rajakaruna & Eremeeva, 2023). Therefore, when a human case of a tick-borne disease is identified, we can observe only the top of the pathogen circulation iceberg. Indeed, many factors must be considered when studying ticks and tick-borne pathogens including the distribution and density of the tick population, the prevalence of tick-borne pathogens, and human activities and prevention practices (Estrada-Peña et al., 2014).

## Prevention of tick bites and tick-borne bacterial pathogens

The most efficient way to reduce the risk of tick-borne pathogens is to avoid tick bites (Eisen, 2022). Currently, there is a new LB vaccine in a phase 3 trial that is planned to reach the market in a few years (Hook et al., 2022). In the absence of vaccines against bacterial tick-borne pathogens and to protect against other tick-borne diseases, public health authorities recommend individual prevention strategies, including the avoidance of tick habitats, the use of protective clothing and regular tick checks when spending time in tick endemic areas (Slunge & Boman, 2018). If a tick is found attached to the skin, it is advisable to remove the tick as soon as possible to reduce the risk of bacterial tick-borne transmission (Roupakias et al., 2011). It is frequently stated that if ticks are removed within 24-48 hours of their attachment, the risk of bacterial tick-borne infection is very low. A literature review has revealed that in animal models, transmission can occur in < 16 hours, and the minimum time for transmission has never been established (Cook, 2014). If an attached tick is removed from the skin, the area of the bite should be observed for expanding redness, which could suggest Erythema migrans (Stanek & Strle, 2018). However, since many tick bites go unnoticed and ticks can transfer several bacteria, viruses, and protozoa, it is useful to learn about the signs and symptoms of different tick-borne diseases. Controlling ticks by habitat management and pesticide use may be possible for smaller areas such as gardens but may be difficult in large natural and semi-natural areas (Clark & Hu, 2008).

Tick activity in northern Europe is seasonal, and ticks are active and questing for hosts when temperature and humidity conditions are suitable (Cayol et al., 2017). *Ixodes* ticks are usually active from spring to fall and are usually not active from December to February when the temperatures fall below 5°C (Uusitalo et al., 2022). However, recent evidence has shown that winter-active *Ixodes ricinus* nymphs and females feed on roe deer during winter, when the temperature is well below 5°C, which may have implications for the epidemiology of tick-borne pathogens in northern Europe (Kjellander et al., 2023). Tick bites can occur during all periods of tick activity, but there are usually peaks in the summer months. This may be explained by the influence of temperature on both tick activity and human behavior, such as an increase in outdoor activities and the use of light clothing (De Keukeleire et al., 2015). An understanding of tick ecology can first help in identifying spatial and temporal patterns of ticks and tick-borne pathogens but also contribute to delineating of the eco-epidemiology of tick-borne diseases.

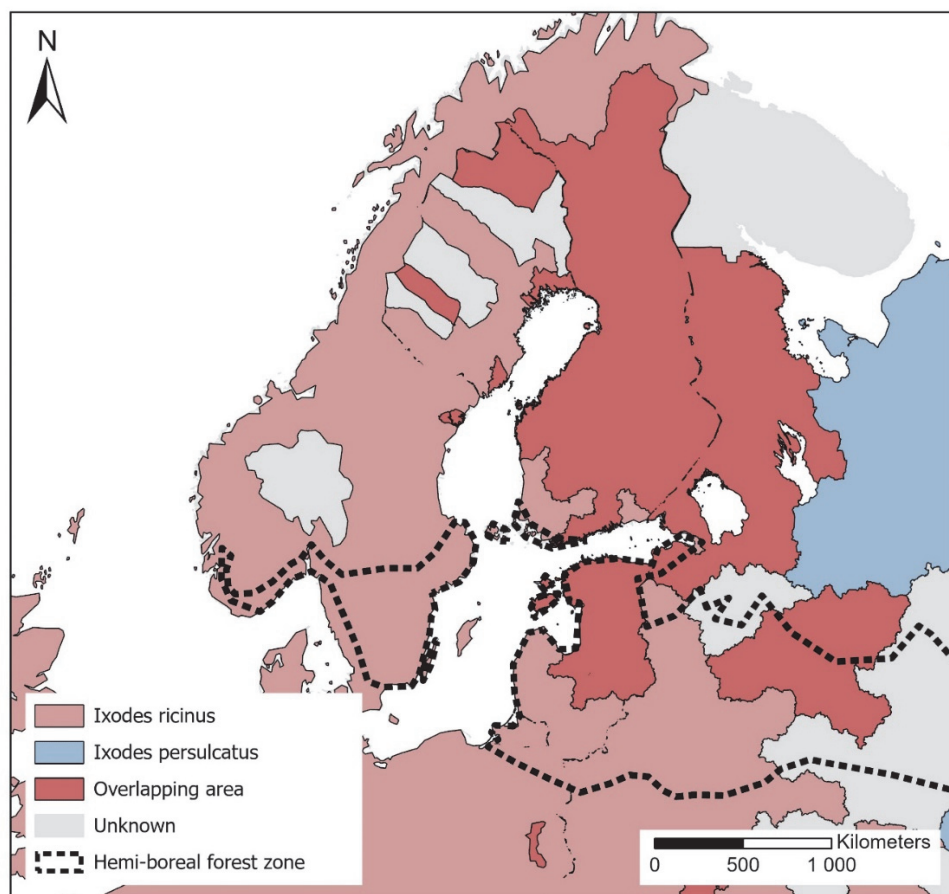


## Materials and methods

This section describes the basic principles behind the methods and techniques used in this doctoral thesis. The selection of specific methods was guided by the eco-epidemiological theoretical framing and the Eco-Epi model. To study tick abundance, pathogen prevalence and public health risk of tick-borne diseases, mixed methods, including quantitative and qualitative methods, were used. This thesis comprises three field studies in which ticks and field data were sampled from green spaces across a natural-urban gradient (papers I, II, and IV). Tick and environmental data were collected and analyzed with statistical methods to determine the effect of landscapes on ticks and tick-borne pathogens. Qualitative interviews with visitors to urban green spaces were also conducted to identify individual behaviors and the use of protective measures against ticks to analyze the risk of tick-borne diseases in urban green spaces. Additionally, one study involved a retrospective analysis of Equine Granulocytic Anaplasmosis (EGA) cases in Stockholm County utilizing data extracted from the Swedish Veterinary Agency's (SVA) database (paper III). Detailed descriptions of the individual methods used are available in the corresponding papers.

### Study area

The study area is located within the European hemi-boreal forest, a transitional zone between the boreal and temperate forest zones. The hemi-boreal forest zone is distinguished by the simultaneous presence of boreal coniferous species common in nutrient-poor soils and temperate broadleaved tree species common in fertile soils. The hemi-boreal forest zone spans southern Norway and Sweden, and on the opposite eastern side of the Baltic Sea, it covers a large part of the Baltic States and reaches the Russia Federation (Figure 4). Forests in the hemi-boreal zone are dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) mixed with broadleaved trees, which include birches (*Betula* spp.), aspen (*Populus tremula*) and alders (*Alnus* spp.). Temperate broadleaved species such as pedunculate oak (*Quercus robur*), lime (*Tilia cordata*), ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*) and elms (*Ulmus* spp.) are also common. The abundance of broadleaved trees has strongly declined over time in many areas due to anthropogenic landscape changes. The case studies in this thesis are located along a natural-urban gradient within the hemi-boreal forest zone, in landscapes that serve multiple purposes, including residential areas, recreational areas and farmland.



**Figure 4.** The study area of this thesis is located within the hemi-boreal forest, a transitional forest zone that extends across the Baltic Sea. Within this region, two medically important *Ixodes* tick species are increasing in range and abundance. The 2023 tick distribution is modified from the European Centre for Disease Prevention and Control, 2023. The border of the hemi-boreal forest is modified from Rivas-Martínez et al. (2017).

## Site selection along the urbanization gradient

To assess tick abundance and pathogen prevalence across the natural-urban gradient, field inventories were performed at random sampling sites in Stockholm County. One hundred coordinates were randomly selected with ArcGIS Pro (version 2.5.0, ESRI Redland, USA). Land cover maps based on satellite images (Svenska marktäckedata (SMD), Naturvårdsverket, 2014), was used to calculate an urbanization index in a buffer zone with a 1km radius around each random coordinate. The urbanization index is equal to the proportion of *Artificial surfaces* surrounding each coordinate. Since Stockholm County is surrounded by water, adjustments were made by subtracting the proportion of *Open water* to account for non-tick habitats (Eq. 1).

$$\text{Urbanization index} = \text{Artificial surfaces (\%)} / (100 - \text{Open water (\%)}) \times 100 \text{ (Eq. 1)}$$

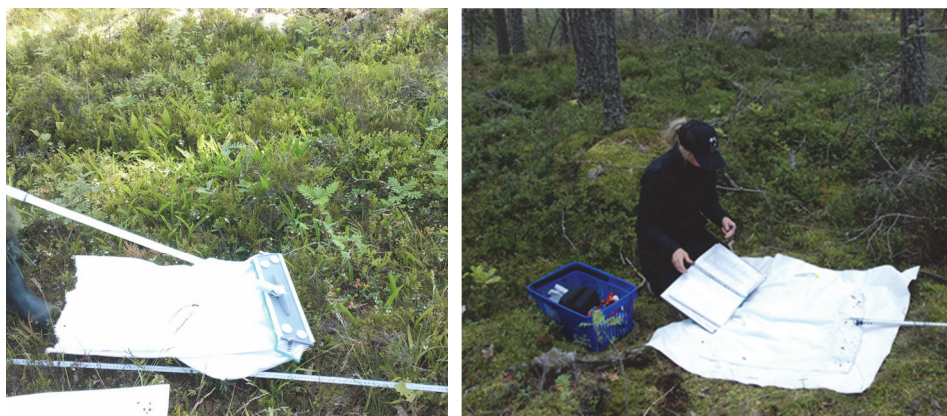
The urbanization index ranges from 0 to 100, with 0 indicating a completely natural or semi-natural site and a value of 100 indicating a landscape with only artificial surfaces. Sites with more than 50% *Artificial surfaces* were categorized as urban core areas and were therefore excluded from the site selection. From all coordinates with an urbanization index  $\leq 50\%$  we randomly selected 35 sites.

## Sampling design and field methods

The randomly selected sampling sites, ranged from large natural and semi-natural green spaces in rural settings to parks and small patches of vegetation in highly urbanized areas close to the city center. Field sampling also adhered to a stratified randomized order, where sites from natural and semi-natural rural landscapes, and peri-urban and urban areas were visited during the same day, mitigating potential spatial-temporal confounding effects. During each site visit, all questing ticks were sampled, and microhabitat conditions were recorded.

### Questing tick sampling

To study tick population dynamics and pathogen prevalence, representative sampling of all questing ticks is desirable. Blanket dragging or flagging are the most common methods used for tick sampling. Blanket dragging uses a wooden stick attached to a flannel blanket that is dragged over the vegetation using a rope tied to both ends of the stick (Lindström & Jaenson, 2003). Flagging is a technique that involves waving a cotton flag over vegetation (Schultz et al., 2014). To sample questing ticks, contact between ticks and the blanket is critical, which can be challenging for different vegetation structures. The mopping technique was previously developed at Södertörn University (Ashgar et al., 2016). The mopping technique involves a white flannel blanket measuring 0.7 m  $\times$  0.7 m attached to a mop (Figure 5). In contrast to the common dragging technique, the mop is held in front of the user and is moved anteriorly over the vegetation. The mop handle permits easy adjustments to different vegetation structures and field layer heights.



**Figure 5.** Mopping technique for tick sampling. For each 2 m × 2 m plot, all questing ticks attached to the blanket were collected and microhabitat features including temperature, vegetation height and tree stem density, were documented.

Sampling was performed between 9:00 a.m. and 6:00 p.m. but was avoided on days with heavy precipitation. At each sampling site, we randomly selected five or ten 2 m × 2 m plots that were mopped and inventoried for ticks. In addition, we used equal sampling effort in each sampling, which allowed us to compare factors affecting tick abundance and pathogen prevalence among sampling sites as long as we controlled for the number of plots per site. To increase the validity of the pathogen prevalence estimates at each site, we additionally sampled nymphs and adult ticks from the vegetation surrounding the sampling plots at each site. The surrounding vegetation was mopped for a specific time, close to 2 minutes, which covered approximately 700m<sup>2</sup>–1000m<sup>2</sup> per site depending on the time used. All questing ticks attached to the blanket were collected with tweezers, put into tubes, categorized according to life stage, and later stored at -80°C. Tick life stage categorization was later confirmed in the laboratory.

### Microhabitat data collection

Microhabitat data, including the variables *time*, air *temperature*, *weather* conditions, and *vegetation height* were systematically recorded for each 2 m × 2 m sampling plot. *Tree stem density* surrounding each plot was estimated using the Bitterlich sampling technique. Each of the sampling plots was also photo-documented. These photos were processed using a 16-square grid layer in Power Point to assess the *general field layer* composition and to identify plant species.

### Retrospective data collection

Published clinical cases of HGA in Europe are rare compared to those worldwide, but the Swedish Veterinary Agency (SVA) has data on *A. phagocytophilum* infections in animals. In a retrospective analysis utilizing 1030 diagnostic test results for Equine

Granulocytic Anaplasmosis (EGA) data were extracted from the SVA laboratory information system from 2002–2015. All clinical samples were sent to the SVA by horse owners or veterinarians after suspected infection with *A. phagocytophilum*. We used the proportion of positive results for EGA among all horses that were tested for symptoms of acute infection as an estimator of incidence.

## Molecular analyses

### Real-time TaqMan PCR

Tick-borne pathogen prevalence estimates are essential for implementing effective prevention and control measures against tick-borne diseases. Polymerase chain reaction (PCR) is a standard method for direct detection of tick-borne pathogens and yields qualitative (conventional, nested PCR) or quantitative (real-time PCR) results. The SYBR Green assay and TaqMan assay are widely used real-time PCR techniques for monitoring amplification. Both methods generate fluorescence in “real-time”, with TaqMan assays requiring a dual-labeled probe for enhanced specificity compared to SYBR Green. The rapid speed, high sensitivity and specificity of real-time TaqMan PCR, makes this the method of choice for detection of bacterial pathogens in ticks and horses as well as for the molecular detection of tick species.

For the detection and quantification of *A. phagocytophilum* infection in horses, DNA extraction was performed on 200 microliters of EDTA blood, which served as a template in the real-time TaqMan PCR assays. The assessment of pathogen prevalence in questing ticks, involved screening medically important tick stages (nymphs and adults) for bacterial infection. To disrupt the exoskeleton and expose internal tissues, ticks were cut open, and subsequently, DNA was extracted and purified from the tissues. The detection of tick-borne bacterial pathogens, including *B. burgdorferi* (s.l.), *B. miyamotoi*, and *A. phagocytophilum*, was carried out using TaqMan real-time assays. Furthermore, tick species were confirmed by using a species-specific duplex TaqMan real-time PCR assay for *Ixodes ricinus* and *I. persulcatus*.

### Nested PCR

Nested PCR is a modified version of standard PCR that allows highly specific amplification of the target sequence. The procedure usually involves two sequential amplification reactions, each of which utilizes a different pair of primers. The product of the first amplification reaction was used as a template for the second PCR, which was primed by oligonucleotides that were placed internal to the first primer set to generate a shorter and more specific PCR product. Nested PCR amplification contributes to increased sensitivity and specificity. For molecular testing of *B. burgdorferi* (s.l.) genospecies, the final PCR product was sent for sequencing.

## Sequencing

Knowledge of *Borrelia* genospecies prevalence is important for defining the risk of infection and for medical authorities to formulate appropriate strategies and guidelines for the diagnosis and treatment of *Borrelia* diseases. Nucleotide sequencing of the nested PCR products to determine *B. burgdorferi* (s.l.) genospecies was performed by Macrogen Inc. (Amsterdam, The Netherlands). All the sequences were analyzed using both strands and were examined using the Basic Local Alignment Tool (BLAST).

## Habitat and landscape characterization

The use of GIS and satellite data maps in tick research involves the analysis of high spatial resolution images to quantify landscape elements that favors tick abundance. A common procedure for identifying the effect of different landscape scales is to establish different buffer zone sizes around each sampling location (Jackson and Fahrig, 2015). Landscape realizations were based on information obtained from the Swedish CORINE Land Cover Database (Nationella Marktäckedata (NMD), Naturvårdsverket, 2019). The land cover data maps have a spatial resolution of 10 m and include the following six main categories: 1) *Forest and seminatural areas*, 2) *Open areas*, 3) *Arable land*, 4) *Wetlands*, 5) *Artificial surfaces* and 6) *Inland and marine water*. We established buffer zones with increasing radii around the centroid of all the sampling plots at each sampling site. The smallest buffer zones (100 m) represent the local habitat land cover at the different sampling sites. Larger buffer zones (200 m–1000 m) represent the land cover distribution of the adjacent landscape around each sampling site. Landscape configuration metrics were estimated with FRAG-STATS version 4 (McGarigal, 1995). For landscape heterogeneity, we used the *Shannon diversity index (SHDI)*, which estimates the diversity of all included land cover classes at each sampling site weighted by their proportional coverage. The *contagion (CONTAG)* of land cover types was used to measure the aggregation of landscape attributes that can influence the suitability of sites for different tick host species. As measures of forest configuration, we used *percent forest cover (PLAND)* and *total forest edge length (TE)*.

## Wildlife host data collection

The Swedish Species Observation System (Artportalen) is a citizen science-based web portal and database where species observations are reported. The main reporting group is the general public, but the system is also integrated with the authorities reporting survey-based biodiversity data. The Species Observation System integrates the use of computer software, map observations and GIS-tools to determine time and place, and validation committees to develop trust in the observations. Currently, the Swedish Species Observation System is one of the largest collections and calculating

center for citizen data in the world, used extensively by public authorities in Sweden (Kasperowski et al., 2022).

The distribution of tick-borne pathogens is directly linked to the home ranges of wildlife hosts that feed, infect and transport ticks. The main limitation of our data is that there is a large bias in inventory effort for the different inventory sites. Therefore, we cannot estimate the relative abundance of individual species. Instead of only using presence absence data for each site, we estimated the proportion of small-, medium-, and large-sized mammals of all mammal observations and the proportion of ground feeding Thrushes of all bird observations. This allows us to compare the relative wildlife host size class distribution among the different sites.

### Exposure data collection

Risk assessment for tick-borne diseases includes a combination of factors related to the identification of tick hazards and the characterization of human exposure. To assess the magnitude of public exposure to tick hazards in urban green spaces, we extracted residential census data available from Statistics Sweden (Statistiska centralbyrån, SCB). The data on the number of residents are available in raster format with a resolution of 1km<sup>2</sup> in the open Geodata section of the SCB. Population density provides an estimate of the number of residents living next to green spaces inhabited by infected ticks, but not the activity of residents in the urban green space. The visitor data information from the six public count boxes in an urban green space was provided by the City of Stockholm.

### Individual exposure

To estimate the risk of infection due to ticks and tick-borne pathogens at the individual level, visitors were interviewed onsite in an urban green space. The survey included questions about visitors' motives, behaviors, and movement patterns in different green spaces and, their knowledge about ticks. Each interview was conducted face-to-face, consisted of 17 questions, and lasted approximately 5 minutes per interviewee. The questionnaire covered 4 thematic areas, namely demographic and recreational risk factors, previous experiences with ticks and tick-borne diseases, usage of commonly recommended prevention behaviors, and knowledge of ticks and tick-borne diseases.

Demographic and recreational behaviors were assessed to determine the overall behaviors and recreational activities in urban green spaces. In addition to age and gender, recreational risk factor information was obtained by asking the visitors if they lived close to the nature reserve, how often they visited the green space and what activities they usually engaged in. The respondents were also asked about the frequency of tick bites and their experiences with infections involving tick-borne diseases. To determine the extent of preventative behaviors, the visitors were asked whether they used insect repellents other repellents, or whether they engaged in any

other behaviors to prevent tick bites. Finally, to assess the knowledge and awareness of ticks, visitors were asked to identify a *I. ricinus* nymphal tick from photos of one tick and two other arthropods. This survey was exempted from ethical approval from the Swedish Ethical Review Authority since no personal information was collected as part of the study.

## Statistical methods

By using multisite datasets, the objective was to investigate the eco-epidemiological aspects of ticks and the risk of tick-borne pathogens in different green spaces. Generalized linear mixed models (GLMMs), frameworks that can account for sample dependencies, random variation, response distribution, and overdispersion, and are commonly used when analyzing the complexities of ticks and land cover data. These models were used when analyzing the associations between ticks and tick-borne pathogens and different land cover characteristics.

To analyze the effect of factors associated with tick abundance in green spaces across the natural-urban gradient, we used generalized linear mixed models assuming Poisson distributed residuals. The dataset used for analyzing factors affecting tick abundance across the urbanization gradient contained a larger proportion of zeros than would be expected according to a Poisson or a negative binomial distribution causing overdispersion (Zuur et al., 2009). We fitted zero-inflated Poisson models using the package *glmmTMB* (generalized linear mixed models using Template Model Builder) (Brooks et al., 2017). To analyze the factors responsible for pathogen prevalence, a Gaussian distribution of residuals was applied. To analyze the change in the odds of obtaining a positive EGA sample, we applied logistic regression with quasi-binominal error distribution to correct for overdispersion. To analyze the relationships between bacterial pathogens and environmental factors, site was included as a random factor, and the models were analyzed assuming a Poisson distribution. Correlations among population size, visitor counts, tick densities, and pathogen prevalence were analyzed using Pearson's correlation coefficients.

All models were tested for multicollinearity using the variance inflation factor (VIF) (O'brien, 2007). To provide an indication of the final model's goodness-of-fit, we estimated the variance explained by the fixed factors (marginal  $R^2$ ) and the variation explained by both the fixed and random factors (conditional  $R^2$ ). Model fit was assessed by the residual distribution of each model using the package DHARMA (Hartig, 2020). All analyses were performed with the statistical program R (R core Team, 2021).

## Key results of the papers included in this thesis

### I. Factors responsible for *Ixodes ricinus* presence and abundance across a natural-urban gradient

This study examined the impact of local site factors and landscape characteristics on tick presence and abundance in different green spaces along the natural-urban gradient in Stockholm County, Sweden. Ticks of the species *Ixodes ricinus* were present at 41 of the 47 green spaces. The highest tick abundance was observed in rural areas and natural and semi-natural habitats, but ticks were also present in highly urbanized areas including parks and gardens. Results from the generalized linear mixed models showed that Conditional R<sup>2</sup> was higher than marginal R<sup>2</sup>, indicating that even if we found significant effects from the studied environmental variables, a substantial part of the explained variance of tick presence and abundance was due to differences among sampling sites not accounted for by the fixed factors. The conditional and the zero-inflated model components of the glmmTMB models, show that the environmental factors affecting tick presence can be different from those affecting tick abundance. In general, local sampling plot factors were important for tick abundance, especially the significant negative effect of vegetation height. While landscape characteristics affected both tick presence and abundance, with significant negative effects of urbanization and mixed effects of open areas and forests depending on tick life stage and forest type. Forest stands with mixed coniferous forest in intermediate and large buffer zones showed a significant positive effect on nymph abundance. Presence and abundance of larvae were instead significantly positively affected by broadleaved forest and broadleaved hardwood forest. In addition, there was a significant curvilinear effect of the factor Month with a peak in late summer for abundance of both larvae and nymphs.

### II. *Ixodes*-borne bacterial pathogens distribution across a natural-urban gradient

This study extended the eco-epidemiological investigations and aimed to understand how tick densities and pathogen prevalence is related to green space characteristics and wildlife communities across the natural-urban gradient in the hemi-boreal zone in the Baltic Sea area. Infected ticks were present at 25 of the 35 sites with approximately one-third of the examined ticks infected with at least one bacterial pathogen. Both microhabitat and habitat characteristics explained significant parts of the variation in the occurrence patterns of the different pathogens. *Borrelia burgdorferi*

sensu lato prevalence was significantly positively associated with tick abundance. *B. burgdorferi* (s.l.) was also significantly positively affected by *Tree stem density* surrounding the sampling plots, and negatively affected by air temperature. For *A. phagocytophilum*, none of the microhabitat conditions showed any significant effects on the prevalence. On the other hand, sampling site habitats with *Broadleaved forests*, was significantly positive for *A. phagocytophilum*. Ticks infected with *B. miyamotoi* was found at seven sites and the mean prevalence was 0.1%. All ticks were identified with molecular methods as *I. ricinus*. Small sized mammals such as rodents and shrews had large relative distribution in urban areas (Figure 3). Medium sized mammals such as hares or foxes had fairly equal relative distribution in both urban and rural areas. Large sized mammals such as moose and roe deer more often showed high relative distribution in rural and peri-urban areas, but they were also present in highly urbanized areas. There were no significant effects of relative mammal distribution on pathogen prevalence.

### III. Equine Granulocytic Anaplasmosis in Southern Sweden: associations with coniferous forest, water bodies and landscape heterogeneity

The aim of this study was to identify spatial risk factors by investigating landscape features related to EGA. Specifically, assessing at which classification level, and at which spatial scale, different types of habitats affect EGA. The temporal variations of EGA in Stockholm County, Sweden during 2002–2015, as well as the yearly seasonal variation in clinical illness was also assessed. This retrospective analysis utilized 1030 EGA diagnostic test results obtained from the Swedish Veterinary Agency (SVA, Sweden). Thirty-two percent of all horses tested for EGA during 2002–2015 showed a positive PCR result. The proportion positive tests showed a significant increasing trend over the study period accompanied by marked differences in the seasonal distribution within each year, with the highest proportional frequency in September. The relationship between different land cover types and EGA varied among the different buffer zone sizes. However, results from the four different land cover levels were congruent. For most of the land cover variables with positive associations, the impact emerged at distance between 100–300 m from the horse farm. The association with landscape characteristics is shown by the significant positive associations between EGA and *Coniferous forest* and *Water bodies*. In addition, this study showed that EGA was positively influenced by landscape heterogeneity.

### IV. Ticks-public health risks in urban green spaces.

The aim of this study was to assess the public health risk for tick-borne diseases in an urban green space used for recreation. By using data on hazard and exposure, we evaluated how the risk for tick-borne diseases is affected by habitat characteristics, human usage, and individual behaviors at six entry points. To assess the public health risk, data on hazard and exposure were combined into an index estimating the

potential risk for tick-borne diseases. All collected nymphs and adult ticks belonged to the species *Ixodes ricinus*. The density of questing nymphs and adult ticks varied from 0.8 to 4.8 per 100m<sup>2</sup> among the different sites. High tick densities were commonly found in humid broadleaved forest with low field vegetation. The mean *Borrelia burgdorferi* (s.l.) prevalence was 26.7%, predominately represented by *B. afzelii* as the prevailing genospecies. The mean prevalence for *Anaplasma phagocytophilum* was 28.2%. Both pathogens were detected at all sampling sites, whereas *B. miyamotoi* was absent in all sampled ticks. High pathogen prevalence had a significant positive correlation with increasing proportions of artificial areas. Integrating the tick hazard with human exposure we found that the public health risk for tick-borne diseases was moderate to high at most of the studied entry points. Many of the visitors frequently used urban green spaces. Walking was as the most common activity, but visitors also engaged in activities with higher risk for tick encounters. Individual protective measures were connected to specific recreational activities such as picking berries or mushrooms.



## Discussion

The expansion of urban areas into rural landscapes combined with the surge in recreational activities is changing human and domestic animal exposure to ticks and tick-borne pathogens (Caminade et al., 2019). This doctoral thesis explores the eco-epidemiological dynamics of ticks and tick-borne pathogens along the natural-urban gradient, addressing a research gap, particularly in the Nordic countries around the Baltic Sea. This research aligns with prior studies and contributes novel insights, offering a comprehensive understanding of the eco-epidemiology of ticks and tick-borne pathogens in green spaces along the natural-urban gradient.

### Tick abundance across the natural-urban gradient

The percentage of the global population residing in urban areas will continue to increase, and tick-borne diseases will continue to emerge and increase in prevalence in urban areas (Grochowska et al., 2020). Consequently, more of the human population faces an elevated risk of contracting tick-borne diseases than they did before (Connolly et al., 2021). This study systematically analyzed patterns of tick abundance and pathogen prevalence in relation to urbanization. The findings suggest that we can use population densities and landscape characteristics to estimate the public health risks due to ticks and provide insight into habitat features that may drive tick-borne disease risk across the natural-urban gradient.

The periphery around cities constitutes an environmental gradient ranging from natural and semi-natural to highly modified urbanized areas. In urban landscapes, the requirement of high relative humidity constrains tick abundance in green spaces such as forest patches, parks and gardens (Pfäffle et al., 2013). The findings showed that *Ixodes ricinus* was present across the entire natural-urban gradient but was more abundant in rural areas and large natural and semi-natural green spaces (paper I). However, *I. ricinus* ticks were also sampled in parks and small pockets of vegetation in highly urbanized areas (papers I and IV). In Stockholm County, large green wedges stretch from rural areas to city centers. This suggests that ticks are regularly transported to urban habitats by wildlife, and that ticks can access hosts capable of feeding all tick stages also within urban environments (Kowalec et al., 2017).

Knowledge about circulating ticks is important for public health, as different tick species serve as vectors for pathogens that cause more severe diseases (Wang et al., 2023). The prevalence and distribution of two medically important *Ixodes* tick species are increasing in the Baltic Sea region including Sweden, Finland, and western Russia (Tokarevich et al., 2011; Bugmyrin et al., 2013; Kulha et al., 2022). In particular, the westward expansion of *I. persulcatus* which originated from western Russia, appears

to be a relatively recent and rapid phenomenon (Kulha et al., 2022). The first evidence of *I. persulcatus* occurrence in northern Sweden was in 2015, and within a few subsequent years, tick populations were considered to have been established (Jaenson et al., 2016; Jaenson et al., 2019). Nevertheless, all the nymph and adult ticks analyzed in this thesis were conclusively identified as *I. ricinus*, and no evidence of *I. persulcatus* presence in Stockholm County was observed (papers I, II and IV).

### Bacterial pathogen prevalence across the natural-urban gradient

Bacterial pathogens were present at a majority of the sampling sites, with approximately one-third of the collected ticks carrying at least one bacterial pathogen. While tick densities decreased along the natural-urban gradient, the prevalence of bacterial pathogens did not follow the same pattern (paper II). Specifically, urbanization did not have any impact on the prevalence of *Borrelia burgdorferi* (s.l.) (paper II), aligning with previous research demonstrating comparable prevalence rates between urban and rural landscapes (Heylen et al., 2019; Peralbo-Moreno et al., 2022; Remesar et al., 2023). The mean prevalence of *B. burgdorferi* (s.l.) was 24%, with *B. afzelii* as the predominant genospecies (paper II). Additionally, the emerging pathogen *B. miyamotoi*, associated with tick-borne relapsing fever, was sporadically detected in a limited number of ticks (paper II). The mean prevalence of *Anaplasma phagocytophilum* in questing ticks was 7.5%, with infected ticks observed even in highly urbanized areas, including maintenance parks (papers II and IV). These findings highlight the importance of promoting awareness of tick-borne diseases across the urbanization gradient, particularly in urban parks where citizens may generally still believe that tick risk is minimal (Klemola et al., 2019).

The prevalence of pathogens in questing ticks across various sites may be explained by the presence of important pathogen reservoir hosts along the natural-urban gradient. Green wedges extending from rural landscapes toward the city center of Stockholm form a network utilized by wildlife, and urban forests, parks and gardens offer shelter and nesting sites (Wang et al., 2020). The citizen science project reporting wildlife observations showed that small, medium and large mammals are present across the urbanization gradient (paper II). Small mammals such as rodents were more commonly reported in highly urbanized areas, and large mammals more commonly reported in rural landscapes, but also frequently reported in highly urbanized areas (paper II). Although we did not find any effect of the proportion of wildlife species on pathogen prevalence at each site, we showed that mammals and birds are common in green spaces across the urbanization gradient (paper II).

Small mammals, which act as reservoir hosts for many tick-borne pathogens, may experience lower predation in urban landscapes, than in natural and semi-natural areas (Rizzoli et al., 2014; Takumi et al., 2019). The dominance of *B. afzelii* among the *Borrelia* species suggests that rodents primarily serve as hosts for *Borrelia* infection in ticks in Stockholm County (papers II and IV). Knowledge of *Borrelia* genospecies prevalence in ticks holds significance not only for research studies but also for public

health, as distinct genospecies have been linked to different clinical manifestations (Chiappa et al., 2022). Domination of the human pathogen *B. afzelii* among the infected ticks suggested that individuals infected with *Borrelia* in Stockholm County develop the skin symptom Erythema migrans. However, despite the low prevalence of *B. miyamotoi* in questing ticks (paper II), this tick-borne infection should be considered for patients with symptoms of relapsing fever.

Various large and small mammals are considered reservoir hosts for *A. phagocytophilum* (Stuen et al., 2013). Recent speculation suggests that domestic animals, such as dogs and horses, may act as superspreaders of ticks and potentially *A. phagocytophilum*, contributing to amplification cycles by feeding large numbers of ticks (Jaarsma et al., 2019). Consequently, domestic animals may play a role in *A. phagocytophilum*-infected ticks in peri-urban and urban green spaces (papers II and IV). Despite the apparent ubiquitous presence of *A. phagocytophilum* in ticks across Europe (Svitáková et al., 2015), documented clinical cases of HGA are relatively rare compared to those in the rest of the world (Azagi et al., 2020). It remains uncertain whether this reflects the epidemiological dynamics of human infection in Europe or whether the disease is underdiagnosed or underreported. Since HGA is not a notifiable disease in Sweden, its importance as a human pathogen in Sweden is still uncertain. Given the distribution and increasing number of cases of EGA in Stockholm County, the authors concluded that the risk of encountering infected ticks is omnipresent during recreational activities and highlighted the need to promote public awareness, including HGA (papers II and III).

### Influence of habitat and landscape features on tick abundance

The analytical approach provided a model for analyzing both landscape characteristics and site-specific variation in the presence and abundance of tick populations. A main finding of this thesis is that while landscape features contribute significantly to the presence of *I. ricinus*, the variation in tick abundance across sampling sites is predominantly influenced by microhabitat features (paper I). Given the sensitivity of ticks to desiccation, habitat features are known to be important determinants of tick establishment and abundance (Piedmonte et al., 2018). It is well established that *I. ricinus* ticks need a humid microclimate, which is produced by ground vegetation and the litter layer that protects the ticks from desiccation during off-host periods and questing (James et al., 2013). Consequently, the lowest tick densities were observed in drier microhabitats, such as those characterized by bare ground or forest floors dominated by plant species such as heather or lichen (paper IV). Nevertheless, along the urbanization gradient, ticks were observed in a diverse range of microhabitat types, including highly urbanized maintenance parks (papers I and paper IV). This information is also relevant to public health, considering that humans and their companion animals are more likely to spend more time and make closer skin contact with low vegetation in parks or along trails than with tall rough vegetation in large and remote green spaces.

Habitat features, which are intricately linked to the characteristics of the surrounding landscape, define ecosystem arrangement and interactions (Jeanneret et al., 2003). Forests play a critical role in influencing tick survival by creating a humid microhabitat as well as determining habitat suitability for wildlife hosts. Broadleaved forests and mixed forests harboring diverse fauna are generally considered ideal habitats for *I. ricinus* and their associated hosts (Jaenson et al., 2009). Coniferous forests in areas with high rainfall and a thick moist litter layer can also support high tick densities (Walker et al., 2001). Within the Stockholm County region, the predominant land cover type in the surrounding landscape promoting *I. ricinus* abundance in different green spaces is mixed coniferous forest (paper I). *I. ricinus* was also present in landscapes with a high proportion of broadleaved hardwood forests, consistent with findings from previous studies (Estrada-Peña, 2001; Pfäffle et al., 2013). However, in Stockholm County, broadleaved hardwood forests are extremely scarce except for maintained parks and small remnants of the old farming landscape. In many parts of Europe, climate change is altering the growth and development of forest types, with a decrease of coniferous forests and an increase in mixed and broadleaved forests. Such changes in forest composition and structure might increase the proportion of habitats suitable for ticks in this region, consequently influencing the epidemiology of tick-borne diseases (Tack et al., 2012)

### Influence of habitat and landscape features on bacterial pathogen prevalence

Along the natural-urban gradient, the density of trees had a positive effect on the number of *Borrelia*-infected ticks (paper II). We interpret this as questing ticks infected with *B. burgdorferi* (s.l.) being present in a range of different habitats, provided that there are trees covering the ground that provide suitable microhabitats for ticks and reservoir hosts. The prevalence of local pathogens in questing ticks depends on the presence of multiple hosts in a suitable tick habitat throughout the urbanization gradient (Mackenstedt et al., 2015). While the transmission of pathogens is confined within ticks and their hosts, the mobility and presence of these hosts are shaped by the availability and spatial structure of their habitats. Given the high fragmentation of urban landscapes, the movement of wildlife can both be constrained and facilitated (Heylen et al., 2019; Răileanu et al., 2021).

For ticks infected with *A. phagocytophilum*, there were distinct positive effects of broadleaved forests both within the local habitat and in the surrounding landscape (paper II). The role of wildlife species in the circulation of *A. phagocytophilum* has yet to be fully understood, but several wild ruminants are thought to be important reservoir hosts (Jaarsma et al., 2019). Broadleaved forests may serve as favorable habitats by offering good sources of diet preferences, including leaves and shoots of broadleaved trees, for reservoir hosts of *A. phagocytophilum* (Kamler & Homolka, 2005). Given the scarcity of studies examining the spatial associations of clinical anaplasmosis, our study on Equine Granulocytic Anaplasmosis (EGA) provides a

contemporary perspective on the risk for *A. phagocytophilum* infection in Stockholm County (paper III). There was a significant increase in the proportion of EGA cases from 2002 to 2015. Our findings suggest that EGA cases increase in areas with high proportions of young humid coniferous forest and in areas with water bodies in the surrounding landscape (paper III). The results from this study also hold potential significance for the public health field, since the agent causing EGA is identical to the agent causing human granulocytic anaplasmosis (HGA) (Egenvall et al., 2001).

### Public health risks in urban green spaces

Risk assessments for tick-borne diseases include a combination of factors related to the identification of tick hazards and the characterization of human exposure (Hassett et al., 2022). Urban green spaces used for recreation have been identified as high-risk environments for exposure to infected ticks (Beauté et al., 2016; Gregory et al., 2022; Mols et al., 2022). Both ticks and a high prevalence of bacterial tick-borne pathogens were found at entry points into an urban green space in Stockholm County (paper IV). Previous research has shown that tick densities generally decrease with increasing urbanization (Heylen et al., 2019). Similar tendencies were observed in this study, where despite ticks being present at all entry points to the green space, lower tick densities were observed in highly urbanized areas. However, low tick densities were also recorded at the least urban entry point, suggesting that tick densities also depend on the local properties of the habitat. Ticks infected with bacterial pathogens were found at all entry points, with a high prevalence in the highly urbanized part of the green space (paper IV).

Conducting a comprehensive risk assessment for tick-borne diseases requires not only knowledge about tick hazards but also acquiring information about human exposure to infected ticks (Kubiak et al., 2022). Public health strategies to mitigate the impact of tick-borne diseases require surveillance of ticks and tick-borne pathogens in urban green spaces frequently visited by the public. The estimates of human activity varied across the different entry points of the urban green space. Unsurprisingly, at entry points located close to highly urbanized areas, the largest human population lived in the surrounding areas and many visitors entered the green space (paper IV). The highest risk factor for tick-borne disease was at the entry point, which is associated with a high surrounding human population, many visitors, high densities of ticks, and a high prevalence of tick-borne pathogens (paper IV). Additionally, understanding individual risk factors such as behavior and movement patterns is important for implementing public health measures to prevent tick-borne diseases.

Outdoor recreational activities expose visitors to the possibility of encountering infected ticks if these activities are performed in hazardous tick habitats (Hassett et al., 2022). Nevertheless, outdoor recreational activities are continuously increasing among Europeans, and have resulted in increased contact with ticks and increased risk of disease infection (Sanongo et al., 2003; Sormunen et al., 2020). However, few studies have analyzed how different recreational activities may influence tick-borne

disease risk (Bayles et al., 2013; Omodior et al., 2021). Visitors to urban green spaces engage in a diverse range of activities, with walking being the predominant activity (paper IV). Most of the visitors also reported that they regularly enjoyed foraging in the forest beyond the established trails, a behavior that increases the risk of tick encounters, especially if protective measures are not applied (Hassett et al., 2020).

While visitors to urban green spaces had a very high level of knowledge about ticks in urban green spaces, we found a large discrepancy between their knowledge of ticks and their usage of preventative measures (paper IV). Regarding the use of protective clothing, most visitors reported that their attire was primarily dictated by weather conditions or recreational activity rather than being a deliberate preventative behavior to avoid ticks. Repellents were used sporadically but first and foremost to protect against mosquitoes and not ticks. Some visitors reported resorting to alternative repellents such as coconut oil or lavender spray (paper IV). Notably, visitors with a prior history of tick-borne disease also reported frequent weekly visits to green spaces and multiple tick bites every year (paper IV). The challenge for public health authorities is to promote increased awareness and use of protective measures without causing a negative impact, so that residents, rather than avoiding of recreational activities, continue spending time in urban green spaces.

## Concluding remarks and future directions

This doctoral thesis aimed to study the eco-epidemiological dynamics and mechanisms of ticks and tick-borne pathogens along the natural-urban gradient. Eco-epidemiology, an emerging field in which biological and ecological factors impact infectious diseases are investigated, is especially important when studying the ecological factors affecting tick abundance, pathogen prevalence and risk for tick-borne diseases. This thesis provides important information on tick abundance and pathogen prevalence in green spaces across the natural-urban gradient, addressing a notable knowledge gap in many regions, particularly in the hemi-boreal forest zone within the Baltic Sea region.

The systematic random tick sampling approach is useful for comparisons among sites and also enables comparisons with other studies using similar procedures. The results showed that ticks and tick-borne pathogens were present all along the natural-urban gradient. Within the hemi-boreal forest zone, tick abundance was positively associated with mixed coniferous forests in the surrounding landscape and with habitats characterized by broad-leaved forests. While the conditions for suitable habitats may be region specific to hemi-boreal forests in the Baltic Sea region, the readily accessible CORINE landscape descriptions offer a valuable resource and can be used for further explanations of different tick species and tick-borne pathogens in different habitats. A clear and explicit definition of the study elements, as well as the measurement of multiple landscape features and disease risk metrics, would be helpful in future studies.

Bacterial tick-borne pathogens are subjected to notification requirements in very few European countries. This thesis contributes to the broader understanding of ticks and the bacterial pathogens they may transmit, including the prevalence of *Borrelia* genospecies, which is important for treating and diagnosing patients. Published cases of human granulocytic anaplasmosis (HGA) are rare in Europe and the disparity between tick pathogen prevalence and the relatively low number of HGA cases may be attributed to factors such as a low transmission rate, asymptomatic cases, or undiagnosed mild infection in humans. Nevertheless, the findings presented here show that HGA should be considered a possible diagnosis if patients present with HGA symptoms coupled with a history of tick bites.

This thesis demonstrated that residents are at risk of tick-borne diseases when visiting urban green spaces. Visitors to urban green spaces generally possessed good knowledge of ticks, while the use of protective measures was restricted, especially during everyday leisure activities. This information can be used to inform visitors to urban green spaces made accessible by clear signage at the entrance, reminding the

public about the presence of ticks and the importance of protective measures. Future research is needed to unravel the factors integral for behavioral decision making regarding protective measures. This includes an exploration of recreational activities and the perceived risk in terms of susceptibility to and severity of tick-borne diseases and the perceived efficacy of different protective measures.

This research should be considered exploratory and not as a complete portrayal of all factors influencing the risks due to ticks in urban green spaces. In an ongoing study, interviews with visitors to urban green spaces in Latvia were conducted, employing identical inquiries about behavior and movement patterns as in this thesis. That study aims to facilitate a comparative analysis of national and cultural differences in recreational behavior and individual protective usage within the Baltic Sea region. In a collaborative project with the *Borrelia* group on the Åland Islands, there will be additional information regarding the eco-epidemiology of tick-borne disease in the hemi-boreal zone in the Baltic Sea region. Findings from these projects should be integrated with established biological, epidemiological, and ecological understandings of the public health risks due to ticks and operationalized in future practice.

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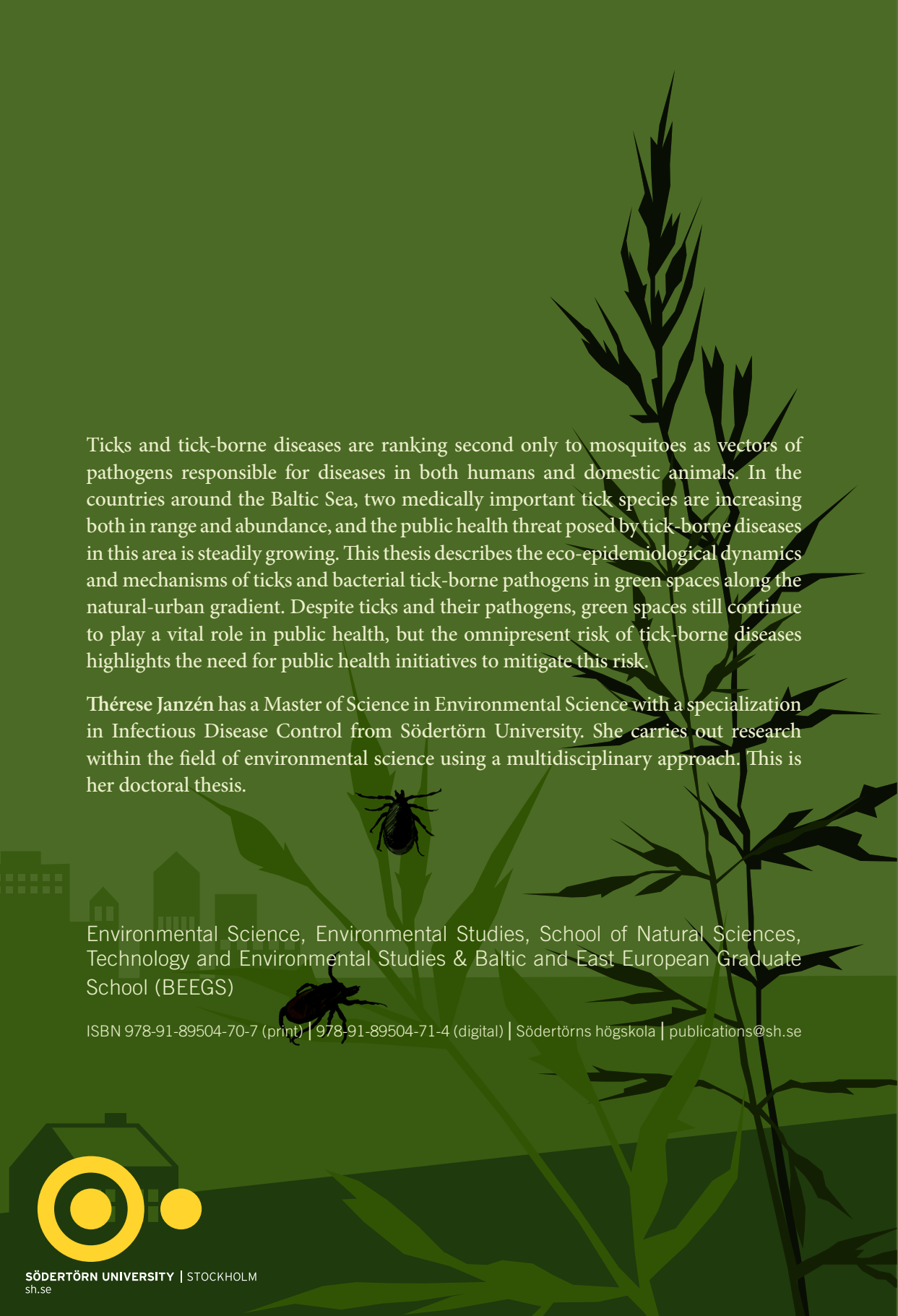
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Ticks and tick-borne diseases are ranking second only to mosquitoes as vectors of pathogens responsible for diseases in both humans and domestic animals. In the countries around the Baltic Sea, two medically important tick species are increasing both in range and abundance, and the public health threat posed by tick-borne diseases in this area is steadily growing. This thesis describes the eco-epidemiological dynamics and mechanisms of ticks and bacterial tick-borne pathogens in green spaces along the natural-urban gradient. Despite ticks and their pathogens, green spaces still continue to play a vital role in public health, but the omnipresent risk of tick-borne diseases highlights the need for public health initiatives to mitigate this risk.

**Thérèse Janzén** has a Master of Science in Environmental Science with a specialization in Infectious Disease Control from Södertörn University. She carries out research within the field of environmental science using a multidisciplinary approach. This is her doctoral thesis.

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