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Studies on species distribution, pathogen prevalence, and historical *Borrelia* seroprevalence

Maija Lamppu

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To my family

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ABSTRACT

Ticks and tick-borne diseases are an increasing public health concern in Finland and other Nordic countries, as cases of Lyme borreliosis (LB) and tick-borne encephalitis (TBE) continue to rise. A decade ago, tick research in Finland was still scarce, and the last nationwide study on tick distribution had been published in 1961.

The aim of this doctoral research was to update the distribution ranges of the medically important *Ixodes* ticks in Finland, compare the pathogen prevalence of *I. ricinus* and *I. persulcatus*, and examine changes in the prevalence of *Borrelia burgdorferi* sensu lato (Bbsl) antibodies in the Finnish population over a 50-year period.

By using a national citizen collection, the distribution of *I. ricinus* was updated, and for the first time, a comprehensive mapping of *I. persulcatus* occurrence in Finland was conducted. The results suggested a northward shift in tick distribution. *Ixodes ricinus* was the dominant species in southern coastal regions, while *I. persulcatus* proved to be more common than previously assumed, even appearing to dominate in certain areas, especially in north-western coast. Pathogen prevalence and diversity were higher in *I. ricinus*, yet *I. persulcatus* had a higher prevalence of Bbsl bacteria and TBE virus, the causative agents of the two most important tick-borne diseases. The highest pathogen prevalence overall was observed in ticks from southern Finland. In addition, this research detected rare and potentially harmful pathogens not previously reported in Finnish ticks. Antibody measurements from four cross-sectional surveys of the Finnish population collected between 1966 and 2017 showed a significant decrease in Bbsl seroprevalence over a 50-year period. Possible explanations include improved diagnostics, effective and prompt antibiotic treatment, increased public awareness, and societal and economic changes.

The results of this thesis provide new information about the two medically important tick species occurring in Finland, the pathogens they carry, and changes in Bbsl exposure in the population. Moreover, it highlights the importance of continuous surveillance and public awareness in managing the risks of tick-borne diseases.

KEYWORDS: ticks, *I. ricinus*, *I. persulcatus*, *Borrelia*, distribution, tick-borne pathogens, crowdsourcing, seroprevalence, Finland

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TIIVISTELMÄ

Puutiaiset ja niiden levittämät taudit ovat kasvava kansanterveydellinen huolenaihe Suomessa ja muualla pohjoismaissa, mikä näkyy Lymen borrelioosin (LB) ja puutiaisaivotulehduksen (TBE) tapausmäärien lisääntymisenä. Vielä vuosikymmen sitten puutiaistutkimus oli vähäistä Suomessa ja viimeinen puutiaisten levinneisyyttä koskeva tutkimus oli julkaistu vuonna 1961.

Väitöskirjatyön tavoitteena oli päivittää ihmisille terveydellisesti merkittävien *Ixodes*-puutiaisten levinneisyysalueet Suomessa, vertailla puutiaisen (*I. ricinus*) ja siperianpuutiaisen (*I. persulcatus*) patogeenimääriä sekä tutkia *Borrelia burgdorferi* sensu lato (Bbsl) -bakteerin vasta-aineiden esiintyvyydessä tapahtuneita muutoksia suomalaisessa väestössä 50 vuoden aikana.

Valtakunnallisen kansalaiskeräyksen avulla *I. ricinus* -puutiaisen levinneisyys päivitettiin, ja ensimmäistä kertaa saatiin kattava kartoitus *I. persulcatus* -puutiaisen esiintymisestä Suomessa. Tulokset viittasivat puutiaisten levinneisyysalueen siirtyneen pohjoisemmaksi. *Ixodes ricinus* oli valtalajina eteläisillä rannikkoalueilla, kun taas *I. persulcatus* oli odotettua yleisempi ja paikoin jopa vallitseva laji tietyillä alueilla, erityisesti luoteisrannikolla. Patogeenien esiintyvyys ja monimuotoisuus olivat suuremmat *I. ricinus* -puutiaisilla, mutta *I. persulcatus* -puutiaisilla havaittiin korkeampi esiintyvyys kahden tärkeimmän puutiaistaudinaiheuttajan, Bbsl-bakteerin ja TBE-viruksen osalta. Korkein patogeeniprevalenssi oli eteläisen Suomen puutiaisilla. Lisäksi tutkimus havaitsi harvinaisia ja ihmiselle mahdollisesti haitallisia patogeeneja, joita ei oltu aiemmin raportoitu suomalaisista puutiaisista. Vasta-aineiden määritys neljästä vuosien 1966–2017 aikana kerätystä poikki-leikkausotoksesta suomalaisesta väestöstä osoitti, että Bbsl seroprevalenssi on laskenut merkittävästi väestössä 50 vuoden aikana. Mahdollisia selityksiä ovat diagnostiikan kehittyminen, tehokas ja varhainen antibioottihoito, lisääntynyt tietoisuus sekä yhteiskunnalliset muutokset.

Väitöskirjan tulokset toivat uutta tietoa kahdesta Suomessa esiintyvästä ihmisen kannalta merkittävästä puutiaislajista, niiden kantamista taudinaiheuttajista sekä muutoksista väestön Bbsl-altistuksessa. Tutkimus korostaa jatkuvan seurannan ja kansalaistietoisuuden merkitystä puutiaislevitteisten tautien hallinnassa.

ASIASANAT: puutiaiset, *I. ricinus*, *I. persulcatus*, *Borrelia*, levinneisyys, puutiaisvälitteiset patogeenit, kansalaiskeräys, seroprevalenssi, Suomi

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Abbreviations

ACA	acrodermatitis chronica atrophicans
Avohilmo	Register for Primary Health Care Visits
Bbsl	*Borrelia burgdorferi* sensu lato
CI	confidence interval
COI	a Cutoff-Index
DNA	deoxyribonucleic acid
ddH2O	double-distilled water
EM	erythema migrans
ELISA	enzyme-linked immunosorbent assay
Eur-TBEV	European subtype of tick-borne encephalitis virus
FE-TBEV	Far Eastern subtype of tick-borne encephalitis virus
GEE	generalized estimating equation
GLM	generalized linear models
HGA	human granulocytic anaplasmosis
HGE	human granulocytic ehrlichiosis
IgG	Immunoglobulin G
IgM	Immunoglobulin M
IGS	intergenic spacer
ITS	internal transcribed spacer
LA	Lyme arthritis
LB	Lyme borreliosis
LNB	Lyme neuroborreliosis
NIDR	National Infectious Diseases Register
Osp	outer surface protein
PCR	polymerase chain reaction
rDNA	ribosomal DNA
RF	relapsing fever
RNA	ribonucleic acid
rPCR	real-time PCR
rRNA	ribosomal RNA
RT-PCR	reverse transcriptase PCR

SFG	the spotted fever group
Sib-TBEV	Siberian subtype of tick-borne encephalitis virus
TBD	tick-borne disease
TBE	tick-borne encephalitis
TBEV	tick-borne encephalitis virus
TBP	tick-borne pathogen
THL	Finnish Institute for Health and Welfare

List of original publications

This thesis consists of the following publications and manuscripts, which are referred to in the text by their Roman numerals:

I Laaksonen Maija*, Sajanti Eeva*, Sormunen Jani J., Penttinen Ritva, Hänninen Jari, Ruohomäki Kai, Sääksjärvi Ilari, Vesterinen Eero J., Vuorinen Ilppo, Hytönen Jukka, and Klemola Tero. Crowdsourcing-based nationwide tick collection reveals the distribution of *Ixodes ricinus* and *I. persulcatus* and associated pathogens in Finland. *Emerging Microbes & Infections*, 2017; 6(5):e31.
https://doi.org/10.1038/emi.2017.17

II Laaksonen Maija, Klemola Tero, Feuth Eeva, Sormunen Jani J., Puisto Anna, Mäkelä Satu, Penttinen Ritva, Ruohomäki Kai, Hänninen Jari, Sääksjärvi Ilari E., Vuorinen Ilppo, Sprong Hein, Hytönen Jukka, Vesterinen Eero J. Tick-borne pathogens in Finland: comparison of *Ixodes ricinus* and *I. persulcatus* in sympatric and parapatric areas. *Parasites & Vectors*, 2018; 11: 1-13.
https://doi.org/10.1186/s13071-018-3131-y

III Lamppu Maija, Klemola Tero, Vesterinen Eero, Dub Timothée, Pietikäinen Annukka, Hytönen Jukka. Repeated cross-sectional surveys show a decreasing trend in *Borrelia burgdorferi* sensu lato seroprevalence over a 50-year period, Finland, 1966 to 2017. *Eurosurveillance,* 2025; 30(36):2500171.
https://doi.org/10.2807/1560-7917.ES.2025.30.36.2500171

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1 Introduction

Zoonoses are infectious diseases that are naturally transmissible between animals and humans. Arthropod vectors are responsible for transmitting many of these zoonotic pathogens to humans during blood feeding. Together with mosquitos, ticks (Acari: Ixodida) are the most important arthropod vectors of zoonoses worldwide, affecting health of both humans and our companion animals. Ticks are vectors for several severe zoonotic infections, caused by various bacterial, parasitic, and viral pathogens (Jongejan and Uilenberg 2004; Madison-Antenucci et al. 2020). Ticks can also carry several pathogens simultaneously, and co-infections in the host may lead to unpredictable clinical outcomes and increased disease severity (Diuk-Wasser et al. 2016; Swanson et al. 2006).

Surveys conducted in Northern Europe have revealed a northward shift in tick distribution and an increase in tick abundance over the past few decades (Jaenson, Jaenson, et al. 2012; Lindgren et al. 2000). At the same time, the incidence of tick-borne diseases is rising and the number of identified pathogenic microbes transmitted by ticks has increased (Gray et al. 2009; Madison-Antenucci et al. 2020). The most important tick-borne pathogens affecting on public health in Northern Europe and Finland are *Borrelia burgdorferi* sensu lato (Bbsl) bacteria causing Lyme borreliosis (LB) and tick-borne encephalitis virus (TBEV) causing tick-borne encephalitis (TBE). In Finland, tick-borne pathogens are transmitted to humans via two hard ticks (Acari: Ixodidae): the castor bean tick *Ixodes ricinus* (Linnaeus 1758) and the taiga tick *Ixodes persulcatus* (Schulze 1930). One of the northernmost tick populations in Europe and the overlapping distributional area of these two human-infesting tick species (*I. ricinus* and *I. persulcatus*) both locate in Finland. The last nationwide mapping of the geographical distribution of *I. ricinus* in Finland is six decades old (Öhman 1961) and the distribution of *I. persulcatus* was never studied in Finland before.

1.1 Hard ticks (Acari: Ixodidae)

Ticks are blood-feeding arachnids of the order Ixodida. The order Ixodida is divided into two major families: hard ticks (Ixodidae) and soft ticks (Argasidae). The third family, Nuttalliellidae, comprises of only one species. Hard ticks are differentiated from soft ticks by the hardened plate on the dorsal side of the body called a scutum, as well as their prominent mouthparts called a capitulum (consisting of hypostome and palps) (Hillyard 1996). Ixodidae is the largest family in the order, consisting of over 700 species among 14 genera, with *Ixodes* being the largest genus, containing roughly 250 species (Guglielmone et al. 2020).

Six *Ixodes* tick species that are considered endemic to Finland have been identified: *I. ricinus*, *I. persulcatus*, *I. trianguliceps*, *I. lividus*, *I. arboricola* and *I. uriae* (Jääskeläinen et al. 2006; Laakkonen et al. 2009; Sormunen, Klemola, and Vesterinen 2022; Ulmanen 1972; Ulmanen et al. 1977). The latter four of these ticks are nidicolous (endophilic) species, which means they are usually encountered only inside their hosts' nest feeding on them, thus being more host specific. Only two of these species are significant concerning human health: *Ixodes ricinus* and *I. persulcatus*. These two are non-nidicolous (exophilic) species, which means they are actively seeking hosts when weather conditions are suitable (Hillyard PD 1996). Moreover, they are opportunistic generalists, feeding on almost any terrestrial vertebrate, that indicates its suitability to act as a host (Estrada-Peña, Guglielmone, and Nava 2023; Kahl and Gray 2023). Therefore, *I. ricinus* and *I. persulcatus* will feed on humans as well, if the opportunity arises, potentially transmitting multiple pathogens in the process.

1.2 Study species – *Ixodes ricinus* and *Ixodes persulcatus*

1.2.1 General morphology and identification

Ticks have four life stages: egg, larval stage, nymphal stage and adult stage. Larvae are typically less than 1 mm in length, nymphs range approximately between 1-2 mm, and unfed adults are between 2 and 4 mm in length. However, adult females may reach a length of over 10 mm and 100-fold increase in total volume, when engorged (Starck et al. 2018). As typical arachnids, nymphs and adults have four pairs of legs. Larvae have only three pairs, but the fourth leg pair appears when they moult to nymphs. The scutum extends over the whole body in male ticks, whereas in females and immature stages, it only covers the anterior part. When feeding, the body, called the idiosoma, becomes engorged allowing the tick to take a large blood meal. However, on adult males, the scutum limits their feeding ability, and while they may take small blood meals, their main interest on the host is to mate with females. The mouthparts are located on the capitulum and consist of the chelicerae and hypostome, which together enable penetration of the skin and secure attachment to the host (Richter et al. 2013). A pair of sensory structures called as palps are located around the mouthparts. Ticks also have a unique sensory structure called Haller's organ, which is located on the tarsus of the forelegs. This organ is critical in questing for hosts and finding a mate, since tick uses it to sense humidity, temperature, carbon dioxide, and pheromones (Hillyard 1996; Sonenshine and Roe 2014).

Ixodes ticks can be identified to species level under a microscope, using several key morphological features distinguishing *I. ricinus* from *I. persulcatus* (Estrada-Peña et al. 2018; Filippova NA 1977; Hillyard 1996): In females the length of alloscutal setae is longer and more segregated in *I. ricinus* compared with *I. persulcatus*; the posterior marginal groove is clearly visible in *I. persulcatus*, unlike in *I. ricinus*; the concave in dorsal posterior margin of the basis capitula is V-shaped in *I. ricinus* and straight in *I. persulcatus*; a syncoxae is visible on first coxa in *I. ricinus*, but not in *I. persulcatus*; the genital aperture is arched (5-6:1) in *I. ricinus* and straight (1.5-2:1) in *I. persulcatus* (**Figure 1**). In males, species-specific characteristics include setae length and syncoxae. The general dorsal features of both sexes of *I. ricinus* and *I. persulcatus* are shown in **Figure 2**.

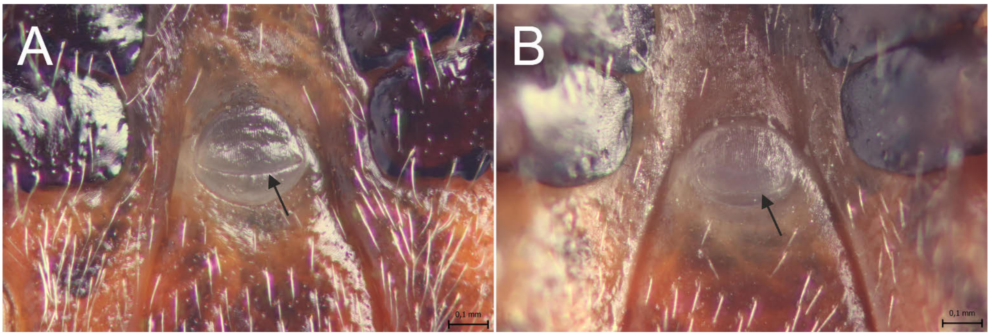

Figure 1. A) Genitals of *Ixodes persulcatus* female; B) genitals of *I. ricinus* female.

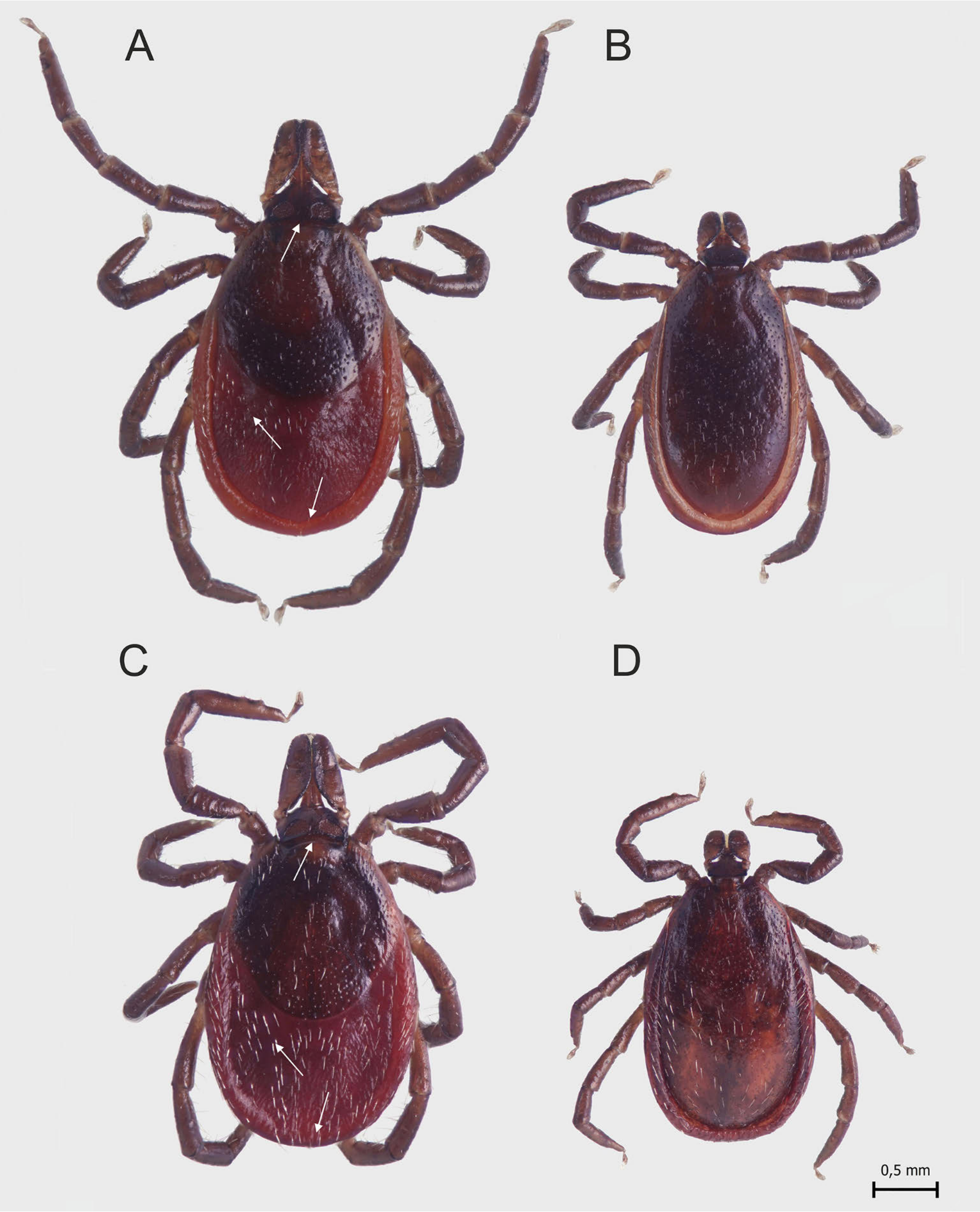

Figure 2. A) *Ixodes persulcatus*, female; B) *I. persulcatus*, male; C) *I. ricinus*, female; D) *I. ricinus*, male.

1.2.2 Distribution in nature

Environmental factors and availability of host animals affect tick host-finding and seeking possibilities, rate of tick development and mortality, thus the density and distribution in nature (Medlock et al. 2013; Sirotkin and Korenberg 2018). *Ixodes* *ricinus* and *I. persulcatus* inhabit a variety of forest types throughout the ranges of their host animals in the temperate zone of Eurasia and they both appear to have a high ecological flexibility (Sirotkin and Korenberg 2018). *Ixodes ricinus* is distributed throughout Europe, extending to Fennoscandia in North, north Africa in South and the Urals in East (Estrada-Peña edat al. 2018), while the distribution of *I. persulcatus* extends from Fennoscandia to Japan (Wang et al. 2023). However, because ticks have limited mobility, the range within which they can seek a host is relatively small. The small habitat also makes them more vulnerable to changing climatic conditions, such as dryness. Hard ticks are relatively sensitive to desiccation and require high humidity to survive when they are not on a host (Sirotkin and Korenberg 2018). When not searching for a host, *I. ricinus* and *I. persulcatus* remain in sheltered, humid environments such as the litter layer (Hillyard 1996; Sonenshine and Roe 2014). Under conditions of low moisture, ticks will quest for shorter periods (Perret, Rais, and Gern 2004) and if desiccating conditions are lasting too long, tick mortality is increased (Perret et al. 2000, 2004). Generally, higher relative humidity and mean air temperature increase tick densities (Gray et al. 2009; Sirotkin and Korenberg 2022; Sormunen, Klemola, et al. 2016), while extremely high temperatures together with lower humidity may reduce tick densities (Brown et al. 2014; Ogden et al. 2021). Climatic requirements of *I. persulcatus* and *I. ricinus* seem to differ from each other, as *I. persulcatus* appears to be adapted to habitats that are slightly drier and colder than those preferred by *I. ricinus* (Jaenson et al. 2016; Sirotkin and Korenberg 2018). In nature, questing ticks are also shown to aggregate. Especially, aggregations of larvae are commonly observed after hatching from a single egg batch and due to limited mobility (Healy and Bourke 2008). When seeking a host, different life stages typically quest at different heights in vegetation. Larvae are questing at the lowest parts, nymphs slightly higher, and adults climb to the highest parts of ground vegetation in order to reach the larger host animals (Sonenshine and Roe 2014). Ticks can uptake relatively large blood meals, enabling them to survive long periods without a host, even years, spending approximately 90% of their lifetime off the host (Hillyard 1996; Sonenshine and Roe 2014). When blood feeding, adult ticks can stay attached to a host even up to two weeks, which enable the dispersal of ticks to new environments (Estrada-Peña and De La Fuente 2014).

It appears that the populations of both tick species have increased and they have expanded their distributional ranges towards northern latitudes and higher altitudes over the last decades (Bugmyrin et al. 2013; Jaenson, Jaenson, et al. 2012; Jore et al. 2011; Lindgren et al. 2000; Sormunen, Klemola, et al. 2016; Sormunen, Sääksjärvi, et al. 2023). The distribution of tick species in Finland is interesting because the country is one of the northernmost areas of tick occurrence in Europe, and because it is located within the overlapping distribution range of *I. ricinus* and *I. persulcatus.*

The last nationwide distribution map of *Ixodes* ticks in Finland was based on a survey published in 1961 (Öhman 1961) and at that time *I. persulcatus* was not yet found from Finland. Since the early 21st century, sporadic reports (Alekseev et al. 2007; Jääskeläinen et al. 2006, 2011) had confirmed the presence of *I. persulcatus* in some parts of Finland, yet its overall distribution remained unclear.

1.2.3 Seasonal activity

The tick activity in different parts of its living range is affected by microclimatic and weather conditions, with the timing of activity peak varying by life stage and regional conditions in a given year (Hancock et al. 2011). In northern Europe, both the unimodal (one activity peak per year) and bimodal (two activity peaks per year) activity patterns have been reported for *I. ricinus* (Gray 2008; Mejlon and Jaenson 1993; Sormunen, Klemola, et al. 2016). Ticks survive the coldest months by overwintering and become active in spring once temperatures rise above 5–7°C (Gray et al. 2009; Perret et al. 2000; Sonenshine and Roe 2014). Larval activity starts later when temperature exceed ~10°C (Randolph 2004). In northern Europe, the first activity peak of questing *I. ricinus* usually takes place in May-June and the second activity peak in the August-September (Cayol et al. 2017). The activity pattern of *I. persulcatus* is different, as the activity of *I. persulcatus* accelerates rapidly to a peak in April-May followed by a sharp decline later in the summer, resulting a shorter questing period than in *I. ricinus* (Bugmyrin and Bespyatova 2023; Uspensky 2016).

1.2.4 Host interactions

Ticks need a blood meal from a suitable vertebrate host animal for survival, for development from one life stage to the next, and for reproduction. Ticks will need three hosts to finish its life cycle, and in northern Europe, the completion of the whole life cycle usually takes from two to four years, though it can range from one to six years (Hillyard 1996; Sonenshine and Roe 2014). Under suitable weather conditions, *Ixodes* ticks seek hosts by climbing on vegetation to await passing animals. This host seeking activity is called questing (Hillyard 1996). Animals signal their suitability to act as hosts through host-produced substances (kairomones) such as carbon dioxide and body heat, and through physical disturbances in the environment, which attract ticks (Carr and Roe 2015; Leonovich 2020; Zhang et al. 2024). On the host, ticks may look for a suitable attachment site for several hours before attaching. Feeding can last from a few days in larvae and nymphs to up to two weeks in adult females (Estrada-Peña and De La Fuente 2014). Tick uses its mouthparts to penetrate the skin of the host and anchor itself with a ratchet-like process (Richter et al. 2013). The feeding process involves a finely coordinated and dynamic exchange of fluids between the tick and its host, regulated by the tick (Kahl and Gray 2023). Tick saliva contains a large number of molecules that ensure the free flow of nutrients from the host to the tick, minimize pain and itch in the host, prevent immune damage to the tick, and at the same time, facilitate the transmission of pathogens from the tick to the host (Nuttall 2019). Once ticks have fed, they detach and drop off the host to moult to the next life stage or to lay eggs (Hillyard 1996). Moulting of larvae and nymphs occurs either within a few weeks after detachment, or following 9-10 months of winter diapause (Gray et al. 2016; Kahl and Gray 2023). Adult females die shortly after laying their eggs, whereas adult males continue to copulate until they exhaust their energy reserves. The copulation takes place in the field, or, in most cases, on the host while females feed (Buczek et al. 2023).

Ixodes ricinus and *I. persulcatus* are generalists, having a similar wide range of hosts (reported from hundreds of vertebrate species) that may vary somewhat across different parts of their distribution (Gern 2008). The main hosts of the *Ixodes* larvae and nymph are small animals such as rodents and ground-feeding birds, while adults feed more often on medium to large-sized animals, such as deer (Estrada-Peña and De La Fuente 2014; Jaenson et al. 1994; Randolph et al. 1999; Uspensky 2016). Humans are considered incidental hosts for ticks, but these attachments can still lead to the transmission of tickborne pathogens.

1.2.5 Ticks as pathogen vectors

Ticks are significant vectors of numerous pathogens to humans and animals around the world. Enzootic cycles of most pathogens rely on reservoir hosts that act as amplification sources for the pathogen, and vector species, such as ticks, that transmit the pathogen between reservoir hosts (Dantas-Torres et al. 2012). The ability of ticks to transmit several different pathogens is closely linked to their life cycle, as they take a blood meal at each developmental stage, providing multiple opportunities to acquire or transmit pathogens, which are retained through repeated moulting events (Kahl 2018; Kurtenbach et al. 2006). Moreover, since the blood meals of *Ixodes* ticks are long-lasting, this further enhances the opportunity for pathogen transmission. Individual ticks can also be simultaneously infected with multiple pathogens. Ticks themselves usually hatch from eggs uninfected and acquire pathogens from the reservoir hosts during blood meals. Thus, adult ticks often have a higher pathogen prevalence rate than nymphs, since adults have accounted hosts animals already twice. However, nymphs are often responsible for transmitting pathogens to humans due to their small and unnoticeable size (Huegli et al. 2011; Rudenko et al. 2011). Beside horizontal transmission during the blood meal, vertical or transovarial transmission (from mother to egg) has also been observed for some pathogens, such as *Borrelia miyamotoi*, some *Rickettsia* and *Babesia* species and TBEV (Chitimia-Dobler 2024; Hauck et al. 2020; Moore et al. 2018; Ravindran et al. 2023; Wilhelmsson et al. 2021).

1.3 Tick-borne pathogens (TBPs)

1.3.1 *Borrelia burgdorferi* sensu lato complex (Bbsl) and Lyme borreliosis (LB)

Spirochetes of the *B. burgdorferi* sensu lato complex (Bbsl) are the most commonly reported and significant tick-borne pathogens in Europe. Bbsl is a genetically diverse group of bacteria, including over 20 named genospecies, and new genospecies and variants continue to be recognised (Stanek et al., 2012; Wolcott et al., 2021). The most important Bbsl genospecies that commonly infect people are *B. burgdorferi* sensu stricto, *B. afzelii* and *B. garinii*. Moreover, *B. spielmanii*, *B. bavariensis* and *B. mayonii* are often associated with LB. Other potentially pathogenic genospecies are *B. lusitaniae*, *B. bissettiae*, *B. kurtenbachii* and *B. yangtzensis*, but their importance as human pathogens is not clearly established (Mead 2022; Steinbrink et al. 2022). The pathogenicity of *B. valaisiana* has been discussed for many years but currently it is considered not to be human pathogenic (Margos et al. 2017). Moreover, there are several identified Bbsl genospecies that have not yet been reported from humans (Mead 2022; Pritt et al. 2016; Rudenko et al. 2011; Stanek et al. 2012; Stanek and Reiter 2011; Steinbrink et al. 2022). Many of the identified Bbsl genospecies circulate in Europe, where the most common genospecies causing LB are *B. afzelii* and *B. garinii* (Rauter and Hartung 2005). Moreover, particular groups of reservoir hosts seem to harbour different genospecies of Bbsl (Hanincova et al. 2003; Wolcott et al. 2021).

Ticks acquire Bbsl spirochetes either through a blood meal from an infected host or by co-feeding near an infected nymph (Gern and Rais 1996). Most of the Bbsl spirochetes remain colonized in the tick midgut as it moults to the next life stage (Radolf et al. 2012). During the following feeding, spirochetes migrate to the salivary glands from where they are transmitted through the saliva to the new host (Kurtenbach et al. 2006). Delayed transmission has been demonstrated for Bbsl (Piesman et al. 1987), with transmission from tick to host typically occurring after 12 to 24 hours of feeding (Cook 2014; Sertour et al. 2018). Thus, for humans the risk for getting infected is very low if the tick is removed within the first day. Transovarial transmission has not been demonstrated for Bbsl (Richter et al. 2012). In Europe, *I. ricinus* and *I. persulcatus* are the main vectors of Bbsl. Significant reservoir host species for Bbsl are small rodents, like *Apodemus* mice, and various bird species (Gern et al. 1998; Gern and Humair 2002; Marsot et al. 2012; Newman et al. 2015). Moreover, migratory birds have an important role in dissemination of infected ticks (Comstedt et al. 2006; Olsen et al. 1995). Some hosts, such as humans and pet animals, do not contribute to the maintenance of tick or Bbsl populations, and are thus considered incidental, dead-end hosts (Kurtenbach et al. 2006). Large sized mammals, like ungulates, have no reservoir host competence for Bbsl either, although their role as hosts for ticks, particularly adult ticks, is considerable (Pearson et al. 2023; Talleklint and Jaenson 1994). The enzootic cycle of Bbsl is presented in **Figure 3.**

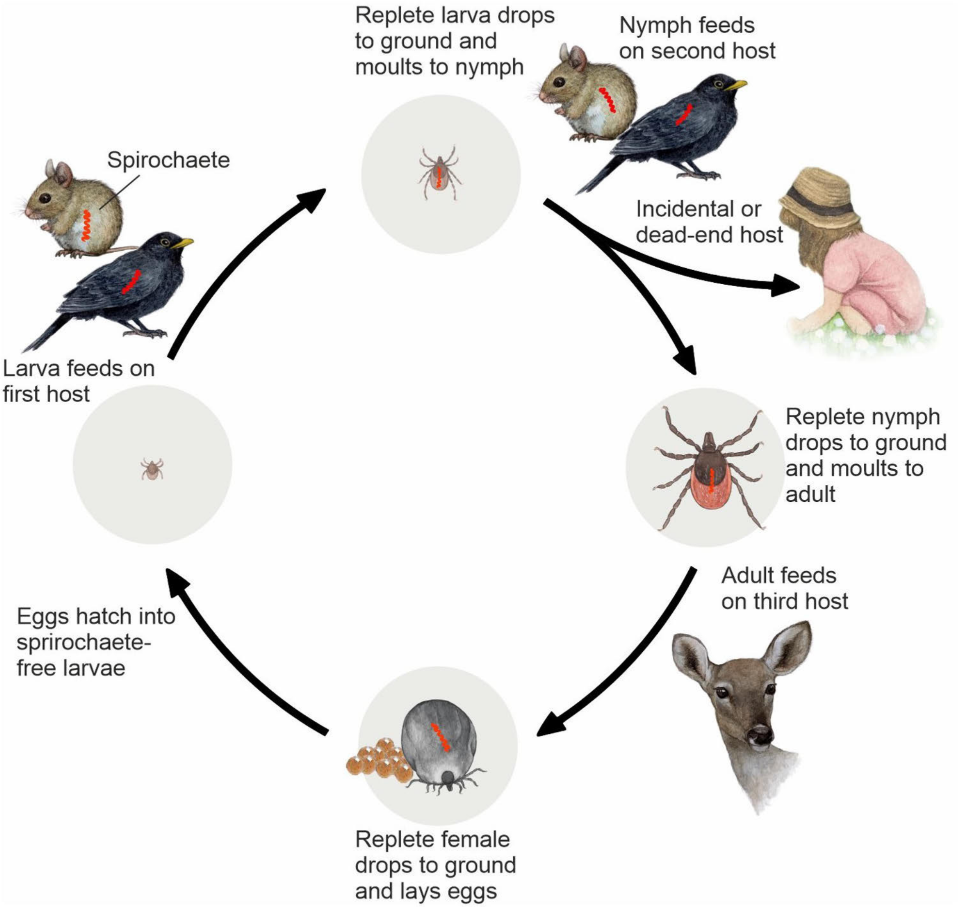

Figure 3. The enzootic cycle of *Borrelia burgdorferi* sensu lato spirochetes. Modified from Radolf et al. (2012).

Bbsl spirochetes are the causing agents of LB, which is the most common tick-borne disease in the Northern Hemisphere (Stanek et al. 2012). LB is a multisystemic disorder manifesting as a range of clinical signs affecting several organs. The most common clinical manifestation is erythema migrans (EM), which typically appears within 1-2 weeks at the tick bite site and eventually resolves, even without antibiotic treatment (Stanek et al. 2012). However, without a treatment in the early localized phase, the risk for developing disseminated disease increases, since the spirochetes can spread to other tissues and organs, causing more severe manifestations affecting skin (Acrodermatitis chronica atrophicans, ACA), nervous system (Lyme neuroborreliosis, LNB), joints (Lyme arthritis, LA), or heart (Stanek et al. 2012; Steere et al. 2016). Only rare cases of LNB present as chronic late LNB, with duration of symptoms for more than six months (Hansen et al. 2013). Studies suggests that infections with different pathogenic genospecies of Bbsl are associated with different clinical manifestations of LB. Although each pathogenic genospecies can cause any of the clinical manifestations of LB, LNB is strongly associated with *B. garinii* infection, *B. afzelii* causes predominantly different skin manifestations, including ACA, whereas LA is primarily associated with *B. burgdorferi* s.s. (Borchers et al. 2015). It has been suggested that the genetic diversity, at intragenospecies and intergenospecies level, is the reason for variety of clinical manifestations that Bbsl infection can display (Dykhuizen et al. 2008; Strle et al. 2011; Wormser et al. 2008). Moreover, in some cases, co-infections with different pathogens may cause diversity in the observed symptoms (Horowitz et al. 2013; Krause et al. 2002).

The number of reported LB cases has been increasing steadily during the past decades (Lindgren and Jaenson 2006; Sajanti et al. 2017; Schotthoefer and Frost 2015), but the reported national incidence rates of LB are rough estimations due to the absence of standardized surveillance systems across countries. In Europe, Finland is one of the countries with the highest reported incidence of LB (>100 cases per 100,000 population per year) (Burn et al. 2023). In 2024, almost 10,000 LB cases were reported in Finland according to the National Infectious Diseases Register (NIDR) and the Register for Primary Health Care Visits (Avohilmo) maintained by the Finnish Institute for Health and Welfare (THL; https://thl.fi/en/). Cases of LB are reported from all over country, but the highest incidence rate in Finland are in the Åland Islands and in the coastal areas (Sajanti et al. 2017). The reasons for increasing LB incidence rates are diverse and include climate change affecting surviving of vector ticks and host animals, increased public awareness of LB and improvement in diagnostics. However, reported incidence figures of LB do not directly reflect the actual infection rates of LB. Population-based seroprevalence surveys, measuring immunoglobulin (Ig) levels in the serum, provide a more reliable estimate of exposure to Bbsl. However, serological testing also has certain challenges that limit its usability, such as the inability to distinguish recent from past infections and its sensitivity depending on the stage of the disease, especially the limitation to detect early localized LB (Marques 2015). Immunoglobulin M is typically present in the early stages of infection, while IgG increases as the disease progresses. Therefore, IgM is usually measured for diagnostic purposes in acute infections, while IgG is more suitable for epidemiological or seroprevalence studies, since it reflects past exposure and may remain elevated for decades, even after successful treatment (Kalish et al. 2001). However, the concentration of antibodies declines after antibiotic treatment (Marangoni et al. 2006; Pietikäinen et al. 2022) and in cases where treatment is initiated early in the infection, seroconversion may not occur at all (Horn et al. 2025). Antibodies may also degrade over time. On the other hand, seroconversion can occur in asymptomatic Bbsl infections as well. Finally, seroprevalence estimates vary depending on the serological method used.

1.3.2 Other tick-borne pathogens and associated diseases

Tick-borne encephalitis virus (TBEV) is a flavivirus causing the other well-recognised tick-borne disease in addition to LB, namely tick-borne encephalitis (TBE). Five subtypes of TBEV have been identified, of which three subtypes circulate in European ticks; the European (Eur-TBEV), Siberian (Sib-TBEV), and Far-Eastern (FE-TBEV) subtypes (Deviatkin et al. 2020; Süss 2003; Worku 2023). Most of the human TBEV infections are considered to be asymptomatic (Gritsun et al. 2003; Larsen et al. 2014; Marvik et al. 2021; Thortveit et al. 2020). However, in rare cases, severe symptoms and even death is possible. Mortality rates are suggested to vary among different TBEV subtypes, with Eur-TBEV infections typically presenting as milder with lower mortality rate (0–2%), while Sib-TBEV infections are associated with more severe diseases and higher mortality (0–8%) (Gritsun et al. 2003). TBEV resides in the ticks' salivary glands, allowing transmission to the host within just a few minutes after attachment (Haglund and Günther 2003; Lindquist and Vapalahti 2008). Therefore, even a quick tick removal is not sufficient to prevent TBEV infection. While in some European countries the number of TBE cases has been constant or even decreasing, the incidence has increased over the last decades in many countries (Chiffi et al. 2023; Jaenson et al. 2018; Skudal et al. 2024; Slunge et al. 2022) including Finland (Tonteri et al. 2015), even though a successful vaccination campaign against TBEV has been ongoing in certain risk areas since the early 21th century. In Finland, high-risk areas for TBEV transmission are in the coastal regions in southern and western Finland (e.g. the Åland Islands), some regions in central and eastern Finland, and coastal areas in southern Lapland (Tonteri et al. 2015; Uusitalo et al. 2020). According to NIDR, fewer than 100 microbiologically confirmed cases (incidence ~1/100 000 population) were reported annually in Finland before 2020. However, nearly 200 cases were reported in both 2023 and 2024, and over 200 cases in 2025.

A species of *Borrelia* not belonging to the Bbsl species complex, but to the relapsing fever group of *Borrelia*, *B. miyamotoi*, have been reported from European hard ticks since the early 21st century (Fraenkel et al. 2002). Human patient cases linked to *B. miyamotoi* were first reported in 2011 (Platonov et al. 2011), and since then, different types of clinical symptoms have been described (Hoornstra et al. 2022). Unlike Bbsl spirochetes, *B. miyamotoi* also exhibits transovarial transmission (Scoles et al. 2004). Symptoms include non-specific manifestations, though in more severe cases it may develop into meningoencephalitis (Balážová et al. 2024; Gugliotta et al. 2013; Hoornstra et al. 2022).

Anaplasma phagocytophilum is the pathogen responsible for human granulocytic anaplasmosis (HGA, previously called human granulocytic ehrlichiosis, HGE). The reported prevalence in *Ixodes* ticks in Europe has ranged from 0% to 67% (Dumler et al. 2005; Henningsson, Hvidsten, et al. 2015; Severinsson et al. 2010; Sormunen, Penttinen, Klemola, Vesterinen, et al. 2016; Stuen et al. 2013). In most cases, HGA is a mild or moderate illness, but fatal cases have also been described (Acosta-España et al. 2025). Although there are a relative low number of diagnosed cases of HGA from Europe, a seroprevalence of up to ~30% has been reported (Wang et al. 2020). Indeed, the risk of developing clinical disease following an attachment by *A. phagocytophilum* -infected tick is considered to be very low (Henningsson, Wilhelmsson, et al. 2015). While the most important vectors of *A. phagocytophilum* in Europe are thought to be *I. ricinus* and *I. persulcatus*, various genetic variants of the pathogen circulate among different vector and host animals and can differ in their ability to cause disease (Doudier et al. 2010; Dugat et al. 2017; Portillo et al. 2011; Rymaszewska and Grenda 2008).

A close relative of *A. phagocytophilum*, *Neoehrlichia mikurensis*, has been detected in many European countries, with the prevalence in ticks ranging from 1% to over 20% (Derdáková et al. 2014; Silaghi et al. 2016). The first reported human infection in Europe was from Sweden (Welinder-Olsson et al. 2010), and since then, several cases have been documented in immunocompromised patients across Europe (Silaghi et al. 2016). The first case in Finland was reported in 2024 (Hohenthal et al. 2025).

Rickettsia is a bacterial genus including the spotted fever group (SFG) and the typhus group (Paris and Dumler 2016; Parola, Davoust, and Raoult 2005). Particularly, SFG *Rickettsia*, such as *R. helvetica* and *R. monacensis*, are often reported from *Ixodes* ticks in Europe (Jensen et al. 2023; Katargina et al. 2015a; Raulf et al. 2018; Sprong et al. 2009). In Finland, *Rickettsia* spp. was first detected in *I. ricinus* ticks from south-western coast, with the overall prevalence of 1.5% (Sormunen, Penttinen, Klemola, Hänninen, et al. 2016). Since then, higher prevalences (4% –15%) have been observed in urban areas (Sormunen et al. 2025). Diseases caused by *Rickettsia* bacteria are among the oldest-known vector-borne diseases, and several species are associated with human infections worldwide (Parola et al. 2013; Parola et al. 2005). However, to date, there are no diagnosed cases of tick-borne rickettsiosis from Finland.

Babesia is a genus of pathogenic apicomplexan parasites that infect red blood cells. More than 100 species of *Babesia* infect wild and domesticated animals, especially livestock worldwide (Homer et al. 2000). In Europe, most cases of bovine babesiosis and human babesiosis are caused by *B. divergens*, although *B. microti* and *B. venatorum* are also associated with human infections (Krause 2019; Schnittger et al. 2012). *Ixodes ricinus* is the main vector of *Babesia* spp. in Europe, although *B. venatorum* has also been found from *I. persulcatus* from Latvia (Capligina et al. 2016). Babesiosis is often asymptomatic or presents with only mild symptoms, but severe cases can occur, particularly in immunocompromised people or those who acquire the infection via blood transfusion (Krause 2019). Single case of fatal babesiosis occurred in Finland twenty years ago (Haapasalo et al. 2010).

Tularaemia is a zoonosis caused by *Francisella tularensis* bacterium, which is widely distributed over the northern hemisphere. In Europe, the subspecies *F. holarctica* is the main cause of tularaemia (Maurin and Gyuranecz 2016). In central Europe, *F. tularensis* causes sporadic cases and outbreaks, and is mainly transmitted through ticks or by contacting with animal reservoirs (Maurin and Gyuranecz 2016). However, in northern Europe, tularaemia infections are mostly vectored by mosquitos (Rossow et al. 2015). Here, incidence of tularaemia is relatively high and outbreaks with hundreds of cases are reported recurrently, reflecting cyclic population fluctuations of voles (Henttonen H 2018; Rossow et al. 2015).

Bartonella is one of the detected zoonotic bacteria in *Ixodes* ticks in Europe (Billeter et al. 2008; Nebbak et al. 2019; Reis et al. 2011), although ticks unlikely have any significant involvement in the transmission of *Bartonella* spp. and the transmission from ticks to animals has not been demonstrated (Telford and Wormser 2010). Cats are a confirmed reservoir host of *B. henselae* and can transmit this pathogen to humans through scratches or bites, leading to cat scratch disease. The disease is rare in Finland.

New microbial species, genotypes and strains with potential pathogenic properties are continually being discovered in ticks. Moreover, co-infections with these microorganisms can result in atypical or poorly understood symptoms in humans, complicating both diagnosis and treatment. However, while certain pathogens are occasionally detected in ticks, the role of *I. ricinus* and *I. persulcatus* in their transmission may be uncertain. In addition, several of these microbes are not pathogenic or have virulent properties, but may have essential roles in tick biology or facilitate the growth and transmission of other pathogens (Budachetri et al. 2018; Guizzo et al. 2023). One of these microbes is *Midichloria mitochondrii*, an endosymbiont commonly found in female *I. ricinus* ticks (Stavru et al. 2020). Other pathogens detected in *Ixodes* ticks in Europe include *Pasteurella* (Stojek et al. 2004), *Coxiella burnetii* (Körner et al. 2021), Chlamydia-like organisms (CLOs) (Hokynar et al. 2016) and *Spiroplasma ixodetis* (Binetruy et al. 2019; Lager et al. 2025). Of these pathogens, *S. ixodetis* and CLOs have been found from Finnish ticks so far. The actual vector competence of ticks for these microbes remains undetermined. In addition, the first detection of Alongshan virus, a virus capable of infecting humans, was made in 2019 in *Ixodes ricinus* ticks collected in south-eastern Finland (Kuivanen et al. 2019).

1.4 Aims of the study

The aim of this thesis was to provide novel information about human-infesting tick species in Finland, focusing on their distribution and pathogen burden, and to shed light on historical trends in human exposure to the most important tick-borne pathogen, Bbsl. The following specific aims were set:

1. To determine the distribution of *I. ricinus* and *I. persulcatus* ticks and to identify the tick-borne pathogens they carry in Finland.
2. To characterize the differences between *I. ricinus* and *I. persulcatus*, in terms of their pathogen prevalence.
3. To examine the changes in Bbsl seroprevalence in Finland over a 50-year period.

2 Materials and methods

2.1 Growdsourcing data (**I**, **II**)

A national crowdsourcing-based, nationwide tick collection campaign was organized in 2015, where citizens were asked to collect ticks across Finland from April to November, and sent them via postal mail to the University of Turku for identification and further analysis. The campaign was advertised via national newspapers, television, and the internet. Along with the ticks, citizens were asked to provide their own assessment of the collection site and date, and the species of the possible host. The species, life stage and sex of tick samples were identified by researchers based on morphological characteristics under a microscope, if possible. Almost all the received samples were recognised correctly as *Ixodes* ticks by citizens. Samples that represented other species (for example, deer keds, spiders and moss mites) were disposed. After the characterization, ticks were stored at -80ºC. Altogether, approximately 7,000 shipments were received containing a total of 19,923 individual ticks from all over Finland.

2.1.1 Tick samples used in distribution analyses (**I**)

Tick samples without adequate date information or those collected outside the campaign period (n=1,788) were excluded from the study. Of the ticks collected in 2015 (n=18,135), 17,936 could be tentatively identified to species based on morphological characteristics. Ticks that could not be identified morphologically by microscope were classified only as *Ixodes* spp. and excluded from the distribution analyses. The geographical information of the collected ticks was stored as ETRS-TM35FIN coordinates with an accuracy of 100 m. After samples lacking adequate collection site information were also excluded (=333), the remaining 17,603 coordinates were used in distribution analyses. Distribution maps were created using MapInfo Professional 12.0 software (Pitney Bowes Business Insight, Troy, NY, USA).

2.1.2 A subset of ticks for pathogen screening (**I**, **II**)

In Study **I**, a subset of 2,038 ticks (1044 *I. ricinus* and 994 *I. persulcatus*) was selected in order to investigate the prevalence of Bbsl, *B. miyamotoi*, and TBEV. In Study **II**, a total 3,465 ticks (2014 *I. ricinus* and 1451 *I. persulcatus*) were screened (including the samples analysed already in Study **I**) for *Rickettsia* spp., *Babesia* spp., *Bartonella* spp., *Anaplasma* spp., *Francisella tularensis* and *Neoehrlichia mikurensis*. Bbsl was also screened in study **II** and positive samples were further identified to genospecies level. Both subsets of samples were manually selected to roughly represent major collection areas, tick life stages and sex distribution of the whole collection. However, approximately the same number of *I. ricinus* and *I. persulcatus* samples were selected to obtain a comprehensive picture of both species, while the proportion of *I. ricinus* was four times that of *I. persulcatus* in the whole collection. Moreover, a higher proportion of *I. ricinus* samples collected in May and June was analysed for pathogens (84.1%) compared to their proportion in the whole collection (60.5%).

In Study **II**, samples were further divided into three different collection areas: 1, *Ixodes ricinus*-dominated area (southern Finland); 2, sympatric area (central Finland) and 3, *I. persulcatus*-dominated area (northern Finland) in order to investigate the prevalence of tick-borne pathogens in a sympatric area and areas dominated by a single tick species.

Samples in the subsets that could not be identified morphologically by microscope, along with uncertain samples that had been tentatively identified to species level (total of 146), were later identified by species-specific duplex real-time PCR (rPCR) assay. Of these, 57 were identified as *I. ricinus* and 41 as *I. persulcatus* in Study **I** and 38 as *I. ricinus* and 10 as *I. persulcatus* in Study **II**.

2.2 Human serum samples and health-questionnaire data (**III**)

Total subset of 3,990 serum samples was used to determine the Bbsl seroprevalence. Samples were collected from four different health surveys: Finnish Mobile Clinic Health Survey 1970 (FMC1970), Mini Finland1980 (MF1980), Health 2000 (Health2000) and Finn Health 2017 (FH2017). These surveys were aiming to gather information on the national public health through questionnaires and interviews, physical examinations, and laboratory measurements, including serum samples.

The survey FMC1970 was a nationwide cross-sectional health survey conducted over the years 1966–1972 (hereafter abbreviated as year 1970) consisting of more than 50,000 people aged 15 and over (Cuellar et al. 2020; Knekt et al. 2017). Serum samples from FMC1970 had already been analysed and the Bbsl seroprevalence reported in the previous study (Cuellar et al. 2020). However, since a different screening assay method was used in Study **III**, samples from FMC1970 were re-analysed in order to get comparable results of the seroprevalence changes between the time points. The survey MF1980, that was carried out in years 1978–1980 (hereafter abbreviated as year 1980, was part of the Finnish Mobile Clinic Survey. The survey was carried out in 40 study areas around the country. It focused on a sample of over 7,000 participants representing the Finnish population aged ≥30 years (Knekt et al. 2017). The survey Health2000 was carried out in years 2000–2001 (hereafter abbreviated as year 2000) consisting of more than 8,600 participants aged ≥18 years living in the mainland Finland (Heistaro 2008). The survey FH2017 was carried out in 2017, consisting of more than 10,000 participants aged ≥18 year from 50 localities in Finland (Borodulin and Sääksjärvi 2019).

Around 1,000 samples were selected from each survey using simple random selection. Beside serum samples, demographic and other relevant variables were analysed from each of the survey questionnaires. Approximately same number of females and males were included in the analyses. Age of the participants ranged from 15–94 years. However, only nine participants were adolescents (15–17 years old) and these samples were all collected in 1970. Samples were categorized to represent five different age groups, and each category included around 20% of participants, apart from the oldest age group (≥70 years), which included around 15% of participants. Samples were divided into five different university hospital districts: HYKS (Helsinki), KYS (Kuopio), TYKS (Turku), TAYS (Tampere), and OYS (Oulu), representing the geographical area of the residence of the participants. Around 28% of samples were collected from Helsinki district, 23% from Oulu district, 20% from Kuopio district, 17% from Turku district and 13% from Tampere district. Tampere district had missing data from 1970. Data and serum samples were obtained from the biobank administered by the Finnish Institute for Health and Welfare (THL). The samples were stored at -20°C.

2.3 Laboratory analyses

2.3.1 Analyses of tick samples (**I**, **II**)

2.3.1.1 Tick DNA and RNA extraction (**I**, **II**)

DNA and RNA were extracted sequentially from the tick samples using NucleoSpin® RNA kits and RNA/DNA buffer sets (Macherey- Nagel, Düren, Germany) following the kit protocols. DNA extracts were stored at -20ºC and RNA extracts at -80ºC.

2.3.1.2 Real-time PCR and rRT-PCR (**I**, **II**)

Real-time quantitative PCR (qPCR) assays were carried out to screen tick DNA/RNA samples for tick-borne pathogens. DNA samples were screened for Bbsl (**I**, **II**), *B. miyamotoi* (**I**), *Rickettsia* spp. (**II**), *Anaplasma phagocytophilum* (**II**), *Neoehrlichia mikurensis* (**II**) *Bartonella* spp. (**II**) and *Babesia* spp. (**II**). In addition, RNA samples were screened for TBEV (**I**).

Primers and a probe amplifying a 102-bp fragment of the outer surface protein A (ospA) gene, were used to detect Bbsl DNA as previously described (Ivacic et al. 2007). For *B. miyamotoi*, primers and a probe targeting the *B. miyamotoi* flagellin gene were used as previously described (Hovius et al. 2013) with minor modifications. For screening *Rickettsia*, *Anaplasma*, *N. mikurensis*, *Babesia*, *F. tularensis* and *Bartonella*, aliquots of original DNA samples were first pooled (10 samples per pool, 5 µl of each sample). For *Babesia, Anaplasma* and *N. mikurensis* screening, multiplex qPCR was used. Fragments of the 18S rDNA, surface protein antigen Msp2, and the chaperonin GroEL were amplified from tick lysates using the primers and probes. For *Bartonella* and *Rickettsia*, a duplex qPCR was used with primers and probes targeting *Bartonella* ssrA and *Rickettsia* gltA. Primers and a probe targeting 23 KDa gene were used to detect *Francisella tularensis* DNA. Samples were analysed in three replicate reactions carried out on 384-well plates. Original DNA samples were re-analysed if a pooled sample was found positive.

Because of the low expected prevalence, pooled RNA samples were used for TBEV screening as well. Pools were examined using real-time reverse transcription-PCR with primers, and a probe amplifying the 3′-non-coding region of the TBEV genome as previously described (Schwaiger and Cassinotti 2003; Tonteri et al. 2011). Original RNA samples were re-analysed if a pooled sample was found positive.

In addition, tick species, if unknown after morphological identification, was determined using a species-specific duplex rPCR assay as previously described (Sormunen, Penttinen, Klemola, Hänninen, et al. 2016), with primers targeting a fragment of the *Ixodes* spp. internal transcribed spacer 2 (*ITS2*) gene to amplify genus-specific segments and probes matching the *ITS2* region of each tick species.

Samples were analysed in three replicate reactions carried out on 384-well plates. DNA extracted from cultivated pathogen strains, or confirmed positive samples were used as positive controls and double-distilled water (ddH2O) was used as a negative control in each run. Samples were considered positive when successful amplification was detected in at least two replicate reactions. Assays were carried out at Finnish Microarray and Sequencing Centre (FMSC, Turku, Finland) and results were analysed using QuantStudio™ 12 K Flex Software v.1.2.2. The thermal cycling profiles, controls, primers and probes, and the mastermix contents for each assay are described in the original publications of Studies **I** and **II**.

2.3.1.3 Sequencing (**II**)

The variable 5S-23S rDNA (rrfA-rrlB) intergenic spacer region (IGS) was sequenced from samples found positive for Bbsl to identify the bacteria to genospecies level as previously described (Coipan, Fonville, et al. 2013). The 5S–23S IGS was amplified by PCR with the HotStarTaq master mix (Qiagen, Venlo, The Netherlands).

Samples that tested positive for *Rickettsia* spp., *Anaplasma* spp., and *Babesia* spp. by qPCR were subsequently sequenced. PCR primers targeting *Rickettsia* gltA, *Anaplasma* 16S rRNA, and *Babesia* 18S rRNA were used.

Electrophoresis was carried out to confirm amplification success. Purified samples were sent to Macrogen Inc. Europe (Amsterdam, Netherlands) for sequencing. The sequences were trimmed using Geneious 11.1.2, then run through BLAST (www.ncbi.nlm.nih.gov/BLAST/) and compared with reference sequences listed in the GenBank (www.ncbi.nlm.nih.gov/genbank/) nucleotide sequence database.

2.3.2 Analyses of human serum samples (**III**)

Human serum samples were analysed for Bbsl seropositivity with a two-tier testing strategy, including the first-tier screening assay using an IgG Elisa assay and second-tier confirmatory assay using an IgG bead immunoassay. Schematic overview of diagnostic assay algorithm can be seen in **Figure 4.**

2.3.2.1 First-tier screening assay (**III**)

Serum samples were first screened for lgG antibodies with Anti-*Borrelia* plus VlsE ELISA (IgG) (Euroimmun AG, Lübeck, Germany) in accordance with the manufacturer's instructions. The test is based on whole antigen extracts of the most relevant human pathogenic Bbsl strains and recombinant VIsE protein (Dessau et al. 2015). The absorbance was measured at 450 nm using Multiskan GO microplate spectrophotometer (ThermoFisher Scientific, Waltham, USA). The samples were interpreted as positive (lgG result ≥22 RU/ml), borderline (lgG result ≥16 and <22 RU/ml) or negative (lgG result <16 RU/ml) as recommended by the manufacturer.

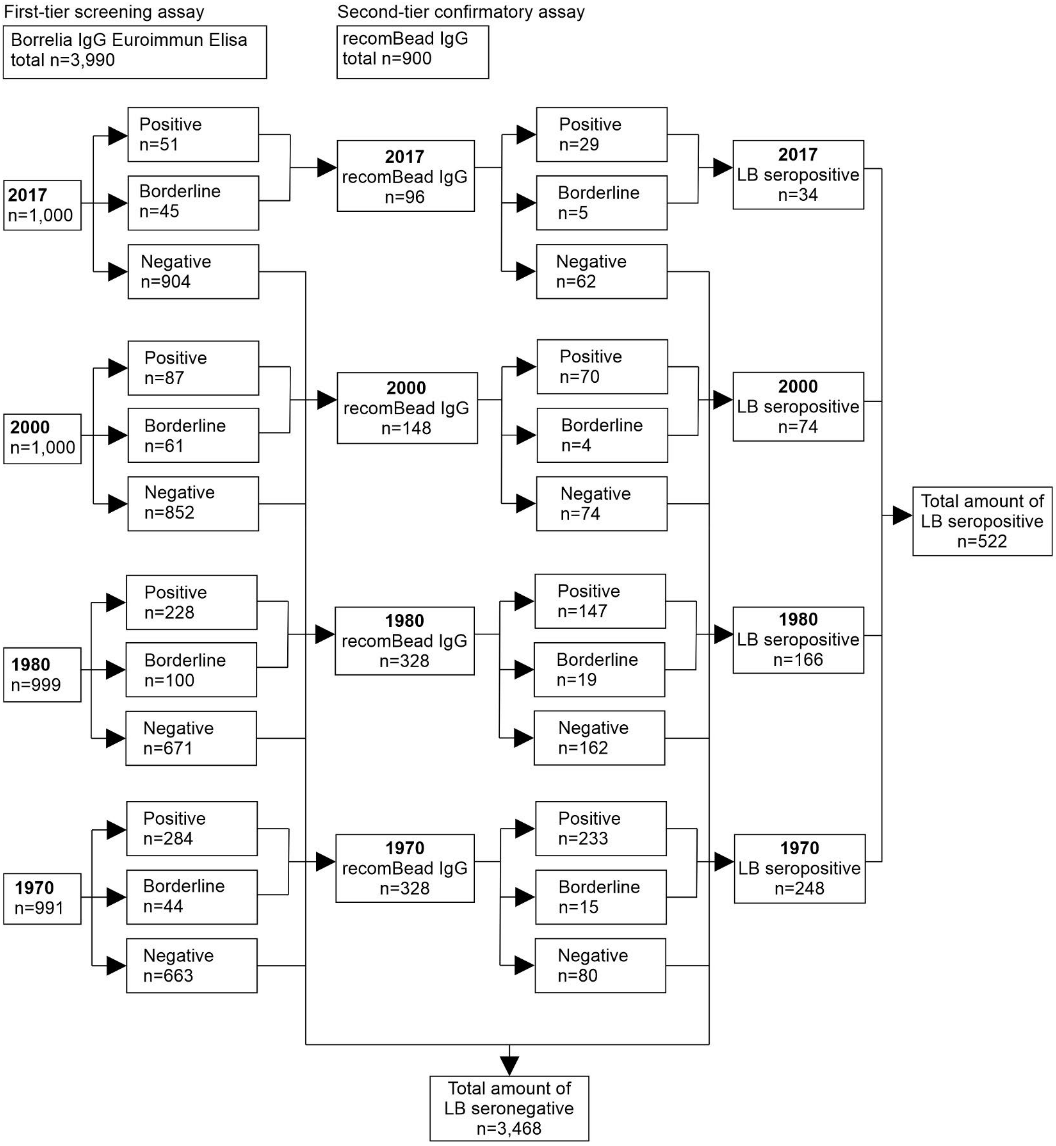

Figure 4. Schematic overview of testing algorithm for the *Borrelia burgdorferi* sensu lato seroprevalence and results in Study **III**.

2.3.2.2 Second-tier confirmatory assay (**III**)

The serum samples that were interpreted as positive or borderline (lgG result ≥16) in the Euroimmun IgG ELISA were further analysed with recomBead *Borrelia* IgG 2.0 (Mikrogen, Neuried, Germany) according to the manufacturer's instructions. The assay measures reactivity to several *Borrelia* antigens. Briefly, magnetic polystyrene beads (MagPlex beads) coated with thirteen different antigens: p100, VlsE, p58, p39, OspA, OspC of *B. burgdorferi* s.s., *B. afzelii*, and *B. garinii*, and p18 of *B. burgdorferi* s.s., *B. afzelii*, *B. bavariensis*, *B. garinii*, and *B. spielmanii*, were used to detect specific IgG antibodies from the serum samples. MAGPIX System with Luminex® xPONENT software and Mikrogen recomQuant evaluation software were used to determine the IgG levels. The serum samples were interpreted as positive (test result ≥4 points), borderline (3 points) or negative (0-2 points). The serum samples with a positive or borderline test result were considered Bbsl antibody positive. Antigen specific antibody binding signal strengths (a Cutoff-Index, COI) were considered separately in the statistical analysis.

2.4 Statistical analyses (I-III)

On many occasions, several ticks were received in one letter, and the same sender sent several letters during the collection period. These samples had often similar collection times, locations, hosts, and were often same tick species and developmental stage, in other words, samples were dependent on each other. Since the independence of observations is generally assumed by basic statistical tests, we therefore refrained from formal statistical analyses and conducted formal statistical tests only for a couple of specific cases.

A generalized estimating equation (GEE) with a binomial error distribution and logit link function was used to model the probability of an adult *I. ricinus* tick to be positive for pathogen infection in comparison with an adult *I. persulcatus*. In Study **I**, we analysed Bbsl and in Study **II**, we analysed Bbsl, *Rickettsia* spp. and total infection rate (all pathogens combined), but refrained from analysing other pathogen groups due to low infection prevalence. Larvae and nymphs were ignored as well due to their relatively low sample sizes and low numbers of positive pathogen detections in both studies. In Study **I**, the analysis was restricted to regions of sympatric occurrence of *I. ricinus* (n=527) and *I. persulcatus* (n=885) in order to exclude the effect of dissimilar environment and weather on the pathogen prevalence in ticks. This was done in practice by filtering the data according to the N coordinate of the southernmost *I. persulcatus* and northernmost *I. ricinus*. In Study **II**, we also tested whether there was a difference in pathogen prevalence between *I. ricinus*- and *I. persulcatus*-dominated areas and the sympatric area. The shipment identification was set as a clustering factor (**I** and **II**) and the species and sex of the tick were fixed explanatory factors in Study **I**, while in Study **II**, species and collection area of the tick were fixed explanatory factors in consecutive tests but never entered as fixed factors in the same model.

In order to determine whether demographic factors or self-reported health issues were associated with the Bbsl seropositivity, the laboratory results were combined with the background data of the participants. Generalized linear models (GLMs) for binomial data, with the logit link function, were used to estimate the association of possible risk factors with Bbsl seropositivity (**III**). Demographic factors included in the analyses were gender, age group, university hospital district, education, employment status, and exercise habit of the participant. In addition, some self-reported diseases, signs or symptoms, and general health-related questions were selected from the health questionnaires in order to determine whether Bbsl seropositivity was associated with conditions or symptoms known to be connected with LB. The selected health-related questions comparably presented in each survey questionnaire related to cardiovascular, rheumatic and neurological conditions. All factors and health-related questions that were studied are shown in Supplementary Table S1 of Study **III**. In our final GLM, Bbsl seropositivity was set as a dependent variable, and categorical factors sex, age group, year and university hospital district were included as fixed explanatory effects. Two-way interaction effects were studied among sex, age group and year in the first model. In addition, two-way interactions were studied with a separate model, in which Tampere district was excluded (n = 505 samples), due to missing data in 1970, to allow district-related interactions for the rest of the data. Moreover, explanatory factor, work status, was studied in a separate model, in which only data from FMC1970 and MF1980 were included (n = 1,913), since the missing information from Health2000 and FH2017. When analysing health-related questions, symptoms (binomial yes/no) possibly relating to LB were set as dependent variables and sex, age group, year, university hospital district and Bbsl seropositivity (yes/no) were set as explanatory effects.

Moreover, to assess the impact of different years on the serological response to Bbsl antigens (the concentration of IgG antibodies after Euroimmun Elisa and signal strength of IgG antibodies toward VlsE and p18 of *B. afzelii* after confirmatory immunoassay) a one-way GLM was conducted with heterogenous variances (among years), a lognormal error distribution and an identity link function.

Results were displayed using estimated marginal means with 95% confidence intervals, and the statistical significance level was considered at the 5% level. P-value adjustments for multiple comparisons in a posteriori pairwise tests in Study **III** were made with Tukey-Kramer method. The data were managed using Microsoft Excel (Redmond, WA, USA), and statistical analyses were performed with the IBM SPSS Statistics software v.23 (Armonk, NY, USA) in Study **II** and with SAS 9.4 (SAS Institute Inc., Cary, North Carolina, USA) in the Studies **I** and **III**. Graphs and figures were made with Microsoft Excel or with CorelDraw (Corel Corporation, Ottawa, Canada).

2.5 Ethics

In many cases, citizens who collected ticks for studies **I** and **II**, provided their contact information along with the tick collection details, if they wished to receive information about tick species identification. However, this contact information was removed from the dataset after participants had been informed.

In Study **III**, background data for seroprevalence study does not contain any personal information that could lead to the identification of the study participants, since data was anonymised by THL before sharing and analysing. Research authorization to access data was obtained from THL.

3 Results

3.1 The Tickbank

3.1.1 Tickbank characteristics (**I**)

Crowdsourcing-based tick collection resulted in 19,923 individual ticks, of which 18,135 were collected in 2015. From these, 17,936 ticks could be identified morphologically as *I. ricinus* (n=14,133; ~80%) or *I. persulcatus* (n=3,803; ~20%). The vast majority of the ticks were adults (95.5%), of which over 2/3 were females. The sex distribution of adult ticks was the same in both species. *Ixodes ricinus* samples contained relatively more larvae and nymphs than *I. persulcatus* (5.5% vs. 1.1%, respectively).

Most of the samples were collected from a host and only a minority (0.4%) from nature. The most commonly reported host animal was dog for both tick species (54.2% for *I. ricinus* and 62.2% for *I. persulcatus*). *Ixodes persulcatus* was detected more often in humans (19.7% vs. 14.5%) whereas *I. ricinus* was collected more often from cats (30.3% vs. 17.3%).

May accounted for the highest monthly proportion of collected samples (total of 41.2%; 36.1% of *I. ricinus* and 61.6% of *I. persulcatus*). *Ixodes persulcatus* were collected mainly from April to June (98.1%), whereas *I. ricinus* were collected more evenly from late spring to early autumn. *Ixodes persulcatus* were not collected in October and November, while almost 100 *I. ricinus* were collected during the same period.

3.1.2 Geographical distribution of *I. ricinus* and *I. persulcatus* (**I**)

Maps of the geographical distribution of *I. ricinus* and *I. persulcatus* were drawn based on the coordinates of 17,603 ticks (13,847 *I. ricinus* and 3,756 *I. persulcatus*) (**Figure 5**). Majority of tick samples were received from central Finland (the so-called Finnish Lakeland) and coastal areas, especially from the southern coast of Finland, all of which were *I. ricinus*. Whereas the distribution of *I. ricinus* largely covered central and southern Finland, especially concentrating on the proximity of large water areas, the distribution of *I. persulcatus* seemed to be clustered in three distinct areas: on the coast of the Gulf of Bothnia, in eastern Finland, and in the middle of southern Finland. The southern country below the latitude 61°N is an area dominated by *I. ricinus*, while the northern country above 65°N is dominated by *I. persulcatus*. The region between these latitudes is a sympatric zone for both species. Both tick species were received from northern Finland (north of latitude 65º N), although a vast majority of these were *I. persulcatus* (760/784; 97%). The northernmost collection sites were beyond the Arctic Circle, at latitudes of 67° N.

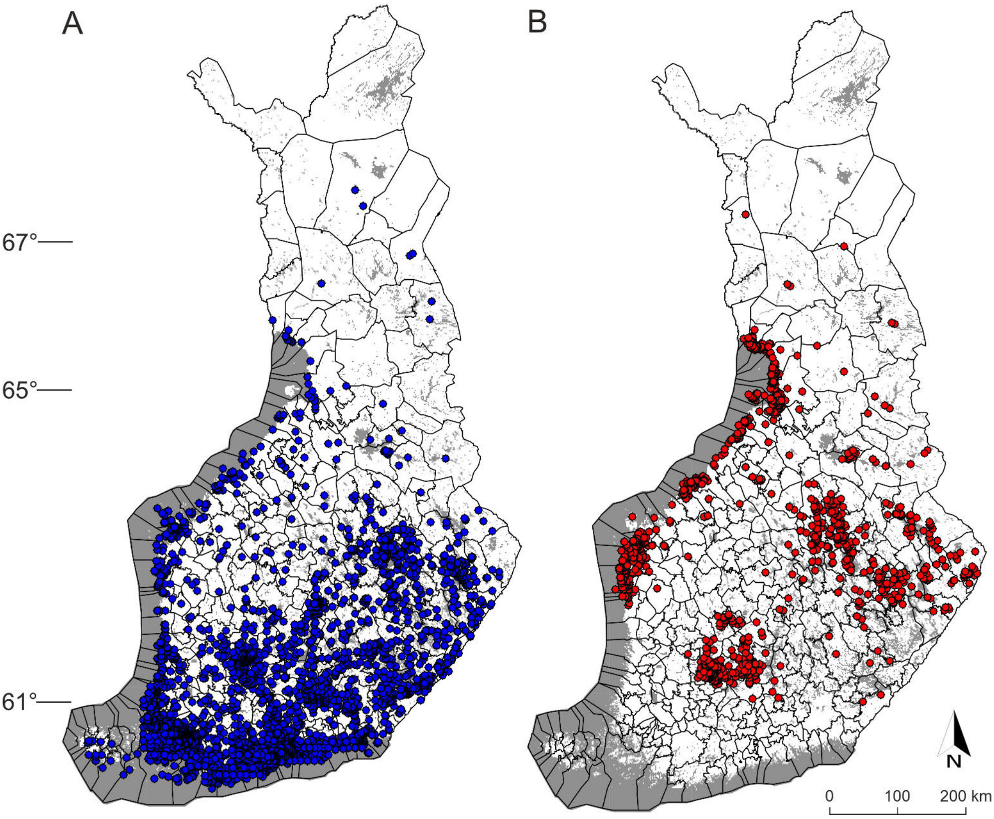

Figure 5. The geographical distribution of *Ixodes* ricinus and *I. persulcatus* in Finland based on the coordinates of 17,603 ticks collected in 2015. Blue dots indicate the collection points of *I. ricinus* (n=13,847) and red dots the collection points of *I. persulcatus* (n=3,756). Modified from the original publication of Study **I**.

3.1.3 TBPs in Finnish ticks (**I**, **II**)

A total of 3,465 tick samples, consisting of 2,014 *I. ricinus* and 1,451 *I. persulcatus* samples were analysed for the presence of pathogens in Study **II** (**Table 1**). The total infection rate and the diversity of different tick-borne pathogens was higher for

I. ricinus (30.0%, five pathogen groups) than for *I. persulcatus* (24.0%, three pathogen groups). The total prevalence of mono- and co-infected ticks were 25.7% (892/3,465) and 1.7% (60/3,465), respectively. However, TBEV and *B. miyamotoi* are not included in these numbers since they were analysed from a smaller subset (n = 2,038) in Study **I**.

Table 1. Infection prevalence (%) of pathogens in *I. ricinus* and *I. persulcatus* samples. Modified from the original publication of Study **II**.

Species	***I. ricinus***					***I. persulcatus***					**Total**
Collection area[a]	**1**	**2**	**3**	**-**[b]	**Sub-total**	**1**	**2**	**3**	**-**[b]	**Sub-total**	
No. of ticks analysed	994	998	5	17	2014	0	1160	261	30	1451	3465
No. of ticks infected	325 (32.6)	277 (27.8)	0	2	604 (30.0)	0	271 (23.4)	69 (26.4)	8	348 (24.0)	952 (27.4)
Bbsl	202 (20.3)	124 (12.4)	0	1	327 (16.2)	0	200 (17.2)	55 (21.1)	8	263 (18.1)	590 (17.0)
***Rickettsia* spp.**	126 (12.6)	152 (15.2)	0	1	279 (13.9)	0	78 (6.7)	16 (6.1)	0	94 (6.5)	373 (10.8)
N. mikurensis	11 (1.1)	6 (0.6)	0	0	17 (0.8)	0	0	0	0	0	17 (0.5)
***Anaplasma* spp.**	12 (1.2)	7 (0.7)	0	0	19 (1.0)	0	2 (0.2)	0	0	2 (0.1)	21 (0.6)
***Babesia* spp.**	7 (0.7)	4 (0.4)	0	0	11 (0.5)	0	0	0	0	0	11 (0.3)

[a] Abbreviations: 1=*I. ricinus* dominated area in south Finland, 2=sympatric area of both species in middle Finland, 3=*I. persulcatus* dominated area in north Finland.

[b] Tick samples that were not categorized into collection areas due to inaccurate collection information provided by citizens.

3.1.3.1 The prevalence of Bbsl (**I**, **II**)

The most prevalent pathogen group was Bbsl, which was detected in 17% of the screened tick samples (**Table 1**). The total prevalence of Bbsl in Study **I** was equivalent with the prevalence in Study **II** (16.9% vs. 17.0%). A significantly higher probability of Bbsl infection was found in *I. persulcatus* adults [0.22 (0.19–0.25)] compared with *I. ricinus* adults [0.16 (0.13–0.18)] (Wald statistics $\chi 2 = 8.50$, DF = 1, p = 0.004), even in the sympatric area (*I. persulcatus* adults [0.17 (0.15–0.20)], *I. ricinus* adults [0.12 (0.10–0.15)], $\chi2 = 7.68$, DF = 1, p = 0.006) (**II**). No differences in the prevalence of Bbsl were observed between females and males of either species (sex: $\chi2 = 1.03$, DF = 1, p=0.311; species× sex: $\chi2 = 0.03$, DF = 1, p = 0.872) (**I**).

In Study **II**, out of the Bbsl-positive samples (n = 590), 394 were successfully identified to genospecies level. Four different genospecies were identified: *B. garinii* (205/394; 52.0%), *B. afzelii* (151/394; 38.3%), *B. valaisiana* (25/394; 6.4%) and *B. burgdorferi* s.s. (13/394; 3.3%). Among *I. ricinus* samples, *B. garinii* (103/231; 44.6%) and *B. afzelii* (94/231; 40.7%) were the predominant genospecies, followed by *B. valaisiana* (21/231; 9.1%) and *B. burgdorferi* (s.s.) (13/231; 5.6%), while in *I. persulcatus* samples, *B. garinii* (102/163; 62.6%) was clearly the predominant genospecies, followed by *B. afzelii* (57/163; 35.0%) and *B. valaisiana* (4//263; 2.5%). *Borrelia burgdorferi* (s.s.) was not detected in *I. persulcatus*.

3.1.3.2 The prevalence of other TBPs (**I**, **II**)

The second most prevalent pathogen group was *Rickettsia* spp., which was detected in 10.8% of the screened tick samples (**Table 1**). The prevalence was 13.9% for *I. ricinus* and 6.5% for *I. persulcatus*. The GEE model also indicated a significantly higher probability of finding *Rickettsia*-positive *I. ricinus* adults [0.13 (0.10–0.17)] than *I. persulcatus* adults [0.05 (0.04–0.08)] ($\chi2 = 27.17$, DF = 1, p <0.001). Of the 373 positive samples, 254 were successfully sequenced to either *R. helvetica* (231/254, 90.9%), *Ca.* R. tarasevichiae (20/254, 7,9%) or *R. monacensis* (3/254, 1,2%). Among positive *I. persulcatus* ticks, *R. helvetica* (32/53, 60.4%) and *Ca.* R. tarasevichiae (19/53, 35.8%) were both abundant, while *R. helvetica* was clearly the most abundant species among *I. ricinus* samples (199/201, 99%). DNA of *Ca.* R. tarasevichae was detected almost exclusively in *I. persulcatus* (18/19 positive samples). Two *I. persulcatus* (3.8%) and one *I. ricinus* (0.5%) ticks were infected with *R. monacensis*.

In total, *Anaplasma* spp. was detected in 0.6% of the screened DNA samples (**Table 1**). The prevalence was 1.0% for *I. ricinus* and 0.1% for *I. persulcatus*. From 19 positive *I. ricinus* samples, 12 were identified as *A. phagocytophilum* by sequencing. Neither of the two positive *I. persulcatus* samples could be identified to species level due to a poor DNA sequence trace.

Neoehrlichia mikurensis was detected in 0.5% of the screened samples, all of which were *I. ricinus* (prevalence 0.8%, **Table 1**).

Babesia spp. was detected in 0.3% of the screened samples, all of which were *I. ricinus* (prevalence 0.5%, **Table 1**). Nine positive samples were successfully sequenced, of which seven were identified as *B. venatorum* (77.8%) and two were identified as *B. divergens* (22.2%).

Francisella tularensis and *Bartonella* spp. were not detected in either of the tick species.

TBEV and *B. miyamotoi* were analysed in Study **I** from a total of 1044 *I. ricinus* and 994 *I. persulcatus* samples. The overall prevalence of TBEV was 1.6% and the prevalence was higher for *I. persulcatus* (3.0%; 30/994) than for *I. ricinus* (0.2%; 2/1044). *Borrelia miyamotoi* was detected in six samples, of which two were *I. ricinus* (0.2%) and four *I. persulcatus* (0.4%).

3.1.3.3 Co-infection of pathogens (**I**, **II**)

Among the analysed ticks in Study **II**, 1.7% were found to be co-infected. *Ixodes ricinus* were more frequently co-infected than *I. persulcatus*: 2.4% vs. 0.8%, respectively. A higher diversity of different pathogen infections was also observed in *I. ricinus* (6 combinations) than in *I. persulcatus* (1 combination: between Bbsl and *Rickettsia* spp.) in Study **II**. However, *B. miyamotoi* and TBEV were only analysed in Study **I** and were excluded from the pathogen analyses in Study **II**. In Study **I**, eight *I. persulcatus* ticks were co-infected with TBEV and Bbsl and two *I. persulcatus* ticks were co-infected with Bbsl and *B. miyamotoi*, while no *I. ricinus* ticks were found to be co-infected. In Study **II**, most of the co-infections (68.3%) were between Bbsl and *Rickettsia* spp. pathogens. When investigating co-infections among infected adult ticks, no significant differences were observed between species or the three collection areas (species: $\chi2=1.50$, DF=1, p=0.221; collection areas: $\chi2=3.80$, DF=2, p=0.149). Co-infection prevalence for adult infected ticks was 8.1% for *I. ricinus* and 3.2% for *I. persulcatus*.

The co-infection prevalence for juvenile ticks was 2.6% (4/152) for *I. ricinus* and 3.7% (1/27) for *I. persulcatus*. Three of the four positive *N. mikurensis* nymphs were co-infected with *B. afzelii*.

3.1.3.4 Pathogens in larvae and nymphs (**I**, **II**)

In Study **II**, pathogen prevalences were investigated from 149 *I. ricinus* nymphs, 3 *I. ricinus* larvae, 26 *I. persulcatus* nymphs and 1 *I. persulcatus* larva. From the 179 samples of juvenile life stages, 33 (18.4%) were infected with Bbsl, *Rickettsia* or *N. mikurensis*. Three *I. persulcatus* nymphs (11.5%) and 31 *I. ricinus* nymphs (20.8%) were found to be infected at least one pathogen. Bbsl and *Rickettsia* prevalences in juvenile life stages (13.4% and 5.6%, respectively) were lower than in adults (17.3% and 11.1%, respectively) (**II**). In Study **I**, the prevalence of Bbsl was 17.1% (332/1,945) for adult ticks and 14.4% (13/91) for nymphs and no larvae were found to be infected. In contrast, the prevalence of *N. mikurensis* in juvenile life stages was higher than in adults (2.2% vs. 0.4%, respectively). However, three of the four *N. mikurensis* -positive nymphs were collected from the same location, and positive samples were therefore strongly correlated. One *I. ricinus* larva carried *B. garinii*, but the rest of the positive Bbsl samples from nymphs that could be identified by sequencing were *B. afzelii*. TBE was found from one *I. persulcatus* nymph in Study **I**.

3.1.3.5 Pathogen distribution (**I**, **II**)

The GEE model indicated a significantly higher probability of finding infected adults from the *I. ricinus*-dominated area compared to the sympatric area [*I. ricinus*-dominated area, 0.31 (0.27–0.35); *I. persulcatus*-dominated area, 0.28 (0.22–0.36); sympatric area, 0.25 (0.23–0.27)] ($\chi2=7.01$, DF=2, P=0.030). However, Bbsl was the only pathogen group with a significant difference in infection prevalence in adult samples between the *I. ricinus*-dominated and sympatric area [*I. ricinus* dominated area, 0.24 (0.20–0.29); *I. persulcatus*-dominated area, 0.18 (0.13–0.24); sympatric area, 0.14 (0.13–0.16)] ($\chi2=23.40$, DF=2, P<0.001). When investigating the number of infected ticks on the different latitudes in steps of one degree (approximately 110 km), the highest infection rates were found from the area below the latitude of 60°N (38.5%, n=104), between the latitudes of 60°N and 61°N (33.7%, n=808) and from the area between the latitudes of 65°N and 66°N (32.4%, n=148). In contrast, the lowest rate was from the area between the latitudes of 64°N and 65°N (21.3%, n=127).

The distribution map drawn from the positive Bbsl and *Rickettsia* samples corresponded to the distribution of the whole subset of ticks and were detected beyond the latitude of 65°N. For Bbsl, the highest prevalence of infected *I. ricinus* was observed in southern Finland (*I. ricinus*-dominated area), while the highest prevalence of infected *I. persulcatus* was observed in northern Finland (*I. persulcatus*-dominated area) (**Table 1**). *Rickettsia* spp. was the only pathogen group with a descending trend in infection prevalence towards the higher latitudes (*I. ricinus*-dominated area: 12.6%; sympatric area: 10.7%; and *I. persulcatus*-dominated area: 6.0%), even though the differences were not significant. The members of family *Anaplasmataceae* and *Babesia* spp. were not detected beyond the latitude of 65°N. The distribution of the positive *N. mikurensis* and *Babesia* samples were rather aggregated as most of the positive samples were collected from urbanized areas near the cities of Helsinki, Tampere and Turku in southern Finland. All *Babesia*-positive samples from southern Finland that were successfully identified were *B. venatorum*, whereas *B. divergens* was detected only in samples collected from central Finland. TBEV-positive samples were collected from coastal areas in the Bothnian Bay, eastern Finland and south-central Finland. *Borrelia miyamotoi* -positive ticks were collected from southwestern Finland, central Finland

and the coast of the Bothnian Bay. The distribution maps drawn from the pathogen positive samples are presented in the original publications of Studies **I** and **II**.

3.2 Bbsl seroprevalence in Finland (**III**)

A total of 3,990 human serum samples were analysed for the presence of IgG antibodies to Bbsl. Almost the same number of females (n = 2,035) and males (n = 1,955) were analysed and the age of the participants ranged from 15 to 94 years. However, only nine participants were adolescents (15–17 years old) and they were all from FMC1970 survey. The first-tier screening assay resulted in 650 positive and 250 borderline samples (total of 900 samples, 22.6%) that were further analysed with the second-tier confirmatory assay (**Figure 4**). After the confirmatory assay, 479 samples were positive and 43 were borderline (total of 522 samples, 58.0%). Thus, the overall seroprevalence of Bbsl in Finnish population from the late 1960s till 2017 was 13.1% (522/3,990; 95% CI: 12.0–14.1%).

3.2.1 Changes in Bbsl seropositivity across years (**III**)

Sampling year of the sample was statistically significantly associated with seropositivity as a main effect (GLM: $F_{3,\,3958} = 37.59$, $p < 0.001$). The probability of seropositive sample was highest in the samples gathered in 1970 (model-based [=least squares] mean estimate = 0.220) and was lower in samples gathered in 1980 (0.109), 2000 (0.036) and 2017 (0.019). As a crude percent, the seroprevalence was 25.0% in 1970, 16.6% in 1980, 7.4% in 2000 and 3.4% in 2017 (**Table 2**).

Moreover, there was a significant difference in the strength of serological responses to Bbsl antigens among study years. The highest serological responses were observed in the samples from 1970: in the concentration of antibodies in the first-tier screening assay (GLM: $F_{3,\,896} = 37.59$, $p < 0.001$ for the effect of year), and against VlsE ($F_{3,\,518} = 6.12$, $p < 0.001$) and p18 of *B. afzelii* ($F_{3,\,510} = 4.61$, $p = 0.003$) in the second-tier confirmatory assay. The concentration of the IgG antibodies of the positive samples in the first-tier screening assay varied from 16 to over 200 and the signal strength (COI-value) of IgG antibodies toward VlsE and p18 of *B. afzelii* in the second-tier confirmatory assay varied between 0 and 10. Most of the samples interpreted as positives after the confirmatory assay, had detectable IgG antibody level (COI $\geq$ 0.67) toward the p18 of *B. afzelii* (n = 385/522, 73.8%) and only minority of positives had antibodies toward the p18 of *B. garinii* (n = 12), *B. burgdorferi* s.s. (n = 5) or *B. bavariensis* (n = 14).

Table 2. Background data of the analysed serum samples, including sample sizes for the significant GLM factors and Bbsl seroprevalences (%).

	Total	**1970**	**1980**	**2000**	**2017**
Factor	**No. IgG positive (%)**	**No. IgG positive (%)**	**No. IgG positive (%)**	**No. IgG positive (%)**	**No. IgG positive (%)**
TOTAL	522/3990 (13.08)	248/991 (25.03)	166/999 (16.62)	74/1000 (7.40)	34/1000 (3.40)
Area					
Helsinki	240/1105 (21.72)	117/226 (51.77)	86/327 (26.30)	29/352 (8.24)	8/200 (4.00)
Kuopio	162/796 (20.35)	73/182 (40.11)	50/260 (19.23)	29/154 (18.83)	10/200 (5.00)
Turku	52/683 (7.61)	25/181 (13.81)	11/110 (10.00)	9/192 (4.69)	7/200 (3.50)
Tampere	25/505 (4.95)		14/152 (9.21)	6/153 (3.92)	5/200 (2.50)
Oulu	43/901 (4.77)	33/402 (8.21)	5/150 (3.33)	1/149 (0.67)	4/200 (2.00)
Sex					
Female	228/2035 (11.20)	108/447 (24.16)	73/515 (14.17)	33/551 (5.99)	14/522 (2.68)
Male	294/1955 (15.04)	140/544 (25.74)	93/484 (19.22)	41/449 (9.13)	20/478 (4.18)
Age (years):					
15-39	40/841 (4.76)	15/112 (13.39)	18/257 (17.00)	5/240 (2.08)	2/232 (0.86)
40-49	82/842 (9.74)	33/186 (17.74)	42/257 (16.34)	3/233 (1.29)	4/166 (2.41)
50-59	145/926 (15.66)	84/290 (28.97)	44/223 (19.73)	13/212 (6.13)	4/201 (1.99)
60-69	130/772 (16.84)	70/251 (27.89)	32/148 (21.62)	21/161 (13.04)	7/212 (3.30)
≥70	125/609 (20.53)	46/152 (30.26)	30/114 (26.32)	32/154 (20.78)	17/189 (8.99)

When examining two-way interactions, a significant interaction between year and age group was found (GLM: $F_{12, 3958} = 2.91$, $p = 0.001$). In 1970, all the age groups ≥50 years had higher seroprevalence than the younger age groups (27.9%–30.3% vs. 13.4%–17.7%, respectively), whereas in the three more recent surveys the oldest age group (≥70 years) peaked in seropositivity. However, a rather similar positive age-related trend was observed in the probability of being seropositive in each study year, and the probability generally decreased towards the last study year 2017 (**Figure 6**). When the 505 samples were removed from Tampere district (missing information from FMC1970), a significant interaction was observed between year and university hospital district as well (GLM: $F_{9, 3430} = 2.89$, $p = 0.002$). The probability of sample being seropositive decreased significantly in

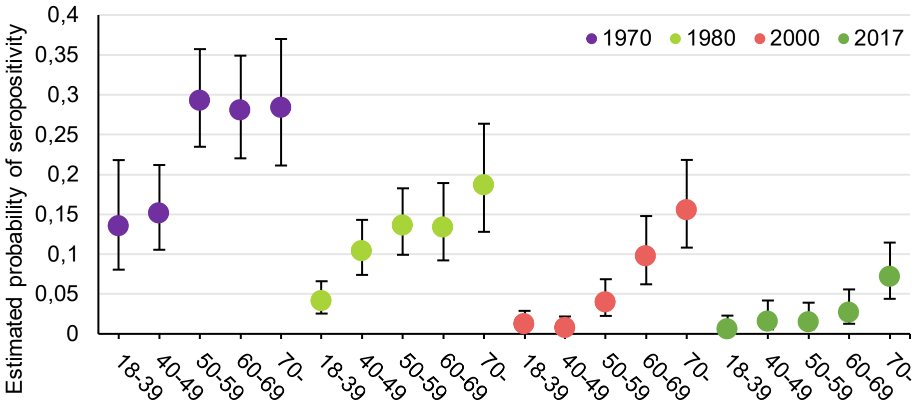

Figure 6. Interaction between year and age group on probability (least-squares means with 95 % confidence intervals) of sample being *Borrelia* seropositive. From the original publication of Study **III**.

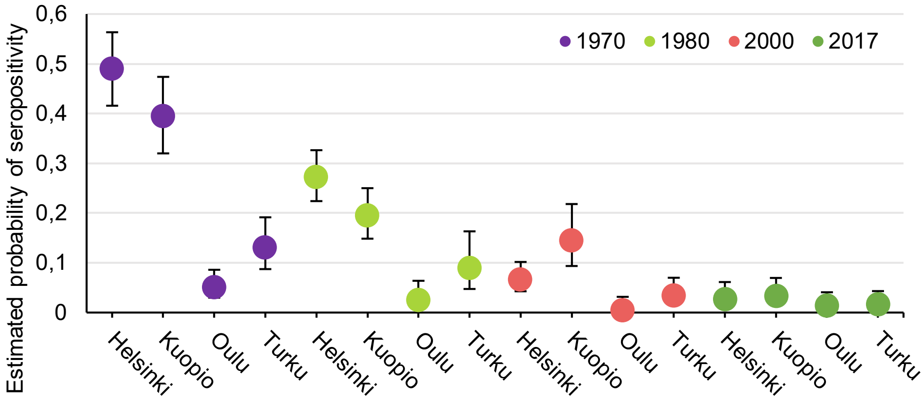

Figure 7. The interaction between year and study area (university hospital district) on probability (least-squares means with 95% confidence intervals) of sample being *Borrelia burgdorferi* sensu lato seropositive. Tampere university hospital district was excluded from the analysis due to missing data in FMC1970.

Helsinki and Kuopio districts between 1970 and 1980 ($p < 0.001$). The seroprevalence in Helsinki continued to decrease considerably between 1980 and 2000, from 26.3% (95% CI: 21.5%–31.1%) to only 8.2% (95% CI: 5.4%–11.1%), while at the same time, the decrease in seroprevalence in another high prevalence district, Kuopio, was not prominent (from 19.2% [95% CI: 14.4%–24.0%] to 18.8%;

[95% CI: 12.7%–25.0%]). Beside Helsinki district, a significant decrease was observed in Turku district between 1980 and 2000 ($p = 0.044$). Kuopio was the only district where the probability decreased between 2000 and 2017 ($p = 0.001$). No significant changes in seropositivity were detected in Oulu district during the study period. The differences in seroprevalence among the study areas levelled off in 2017 (**Figure 7**).

3.2.2 Other factors associated with Bbsl seropositivity (**III**)

University hospital district was statistically significantly associated with seropositivity (GLM: $F_{4, 3958} = 52.47$, $p < 0.001$). The probability of being Bbsl seropositive was higher among residents from southern (Helsinki, 0.164) or central and eastern Finland (Kuopio, 0.141), than from western (Turku and Tampere, 0.047 and 0.053, respectively) and northern Finland (Oulu, 0.019). As a main effect, males had a significantly higher probability (0.081) of being seropositive than females (0.054) (GLM: $F_{1, 3958} = 10.16$, $p = 0.001$). A clear increase of age-related seroprevalence was observed (GLM: $F_{4, 3958} = 22.15$, $p < 0.001$), with the oldest age-group (≥70 years) having the highest probability of being seropositive (0.159). After adjustment for year, sex, age group and district, main effects of health-related questions and other demographic factors were not found to be significantly associated with seropositivity.

When analysing the samples from FMC1970 and MF1980 only, the surveys with information on the work status of the participants available, a significant association between seropositivity and the work status was observed (GLM: $F_{5, 1913} = 2.44$, $p = 0.033$). People working in outdoors, e.g. farming, had the highest probability (0.197) of being seropositive and people working indoors, e.g. office, had the lowest probability (0.112) of being seropositive.

4 Discussion

4.1 Crowdsourcing (I)

Crowdsourcing is a scientific model where individuals from a heterogenous group are mobilized to contribute to a specific task. Although the number of studies involving crowds is increasing, citizen science is still utilized relatively rarely. In tick-related research, the most commonly used methods are field studies including cloth dragging and flagging (Kjellander et al. 2021). However, tick collection using traditional methods is both time-consuming and laborious. Mapping tick and TBP occurrence across vast geographical regions is challenging with a limited number of researchers. Through a crowdsourcing approach, in which Finnish citizens contributed to tick collection, a nationwide, geographically comprehensive collection of ticks could be established.

While crowdsourcing is effective for gathering data, the method has limitations that can affect the generalization and reliability of the results. Since tick samples were mostly collected by untrained citizens, information such as the exact collection site or date cannot be considered as fully reliable. In addition, crowdsourcing data represent human observations, and observations are therefore likely biased towards areas with higher population densities. Factors such as survey promotion and site accessibility also influence the number of observers in a given area (Cretois et al. 2021; Mair and Ruete 2016). Furthermore, volunteer citizens may have a particular interest in ticks, which could further bias the number of ticks collected in specific areas. Indeed, many shipments in the crowdsourcing study contained multiple tick samples, and some of the most active citizens sent several shipments over the collection period. One exceptionally devoted citizen sent over 700 tick samples via many shipments from May to September. Nevertheless, with nearly 7,000 shipments received from 5,000 citizens across the country, we expect that not only those especially interested in ticks participated. Regarding the collection site, the precise location from where the tick was acquired is often uncertain, since tick samples were, in most cases, detected on a human or pet animal. On a host, ticks may be transported long distances before being detected. In certain areas where only few samples were collected, e.g. in the northernmost Finland, we attempted to verify these observations by asking the citizens who reported them for more background information. For example, if they had been travelling in the past weeks, the observation was in most cases excluded from distribution analyses. For ecological research, our tick collection is also heavily biased by the proportion of different tick life stages. Most of the samples collected by citizens were adult females, probably due to the better detectability and manageability and longer feeding times of adults compared to younger life stages, and the requirement of the third blood meal of adult female ticks compared to adult male ticks, whose main interest on the host is to mate. In conclusion, human factors and uneven spatiotemporal sampling effort can cause sampling bias in the data which must be accounted for. Despite some limitations regarding crowdsourced data, our study provides valuable insights about where, when and how frequently people and companion animals are encountering ticks. Importantly, it enables nationwide mapping of *I. ricinus* and *I. persulcatus*, along with the occurrence of associated TBPs, in a way that would be challenging to achieve through traditional field studies alone.

General trust in scientific experts and the media is likely an important factor supporting public engagement in crowdsourcing studies. Based on the particularly great success of recent crowdsourcing efforts (**I**, Laaksonen 2016; Sormunen et al. 2023), Finnish people seem to have widespread willingness to help and be part of research, perhaps due to a general interest in science as well as a shared sense of curiosity and concern regarding ticks. In addition, the opportunity to know the result from species identification, as we promised in the case of *I. persulcatus* ticks, may have also served as a form of compensation. Citizen science projects can further increase public knowledge and interest towards the study subject.

4.2 Geographical distribution of ticks in Finland (I, II)

The previous nationwide distribution map of *Ixodes* ticks in Finland was drawn based on a survey from the late 1950s and was therefore outdated (Öhman 1961). In the 1950s, the northernmost observations of ticks were made from Ostrobothnia and Northern Savonia and back then, all tick observations were assumed to be *I. ricinus*. However, the presence of other *Ixodes* species could not be ruled out. The author conducted some field surveys, but the distribution map was otherwise drawn based on questionnaire responses from veterinarians and nature enthusiasts. The next nationwide research on tick distribution was organised in 2014, when citizens were asked to report their tick sightings in a web questionnaire (Laaksonen 2016). This study indicated an expansion of the tick distribution range. However, in this study, tick species were not taken into account either. Prior to our study, *I. persulcatus* had only been recorded through some sporadic observations in Finland (Alekseev et al. 2007; Jääskeläinen et al. 2006; Jääskeläinen et al. 2011), leaving its geographical range largely unknown. Inspired by the success of the questionnaire in 2014, the nationwide tick collection was conducted in the next year (**I**). Compared to a previous report published over 50 years earlier (Öhman 1961), Study **I** showed that ticks were found at higher latitudes (approximately 200–300 km further north), suggesting a northward expansion of their distribution. During this time, *I. ricinus* populations became established in new locations, especially in coastal areas of the Bothnian Bay. Furthermore, *I. persulcatus* was found to be much more common in Finland than previously assumed, now co-occurring with *I. ricinus* in most parts of Finland and even dominating in some regions.

Most of the tick samples were received from the coastlines and around the Finnish Lakeland. A substantial number of ticks were collected from the southern coast of Finland, all of which were identified as *I. ricinus*. Many of the southern ticks came from urbanized areas near cities and towns, likely due to a denser human population in these regions, thus concealing the actual tick abundance in different areas. However, a high number of collected ticks around large water areas might also indicate higher suitability for ticks or that the dry continental climate elsewhere is suboptimal for ticks. Indeed, field studies also suggest that tick abundance is higher in coastal areas in Finland compared to inland regions that are not located near large bodies of water (Kokkonen 2022; Sormunen, Andersson, et al. 2020; Sormunen, Klemola, et al. 2016). Ticks' survival depends on relative humidity, especially during off-host periods (Medlock et al. 2013), and relative humidity has been found to positively correlate with the abundance of active *I. ricinus* ticks in Finland as well (Sormunen, Klemola, et al. 2016).

The northernmost tick samples were from latitudes of 67° N, where stable tick populations are unlikely to occur due to short vegetation periods (Jaenson et al. 2016; Jaenson and Lindgren 2011; Uspensky 2016). Indeed, only sporadic tick collections were made at this latitude. Thus, it can be speculated whether these ticks came from established populations or whether they were stragglers transported by migratory birds, cervids, or pet animals. While some tick observations have been made from the northernmost municipalities in Finland in 2014 and 2021 as well by other citizen science studies (Laaksonen 2016; Sormunen, Kulha, et al. 2023), field surveys conducted over several years in northern Finland have found no local ticks, except in the Perämeri research station in the coastal area of North Ostrobothnia (Sormunen, Andersson, et al. 2020). After contacting some of the collectors, most of the reported northernmost tick samples were concluded to represent ticks that were transported via humans or dogs from more southerly areas and thus excluded from the distribution analysis. However, some samples were considered reliable enough to be included in the map to represent the tick encounters. These individual introductions of ticks far from their distributional boundaries may have been carried there by natural hosts, like birds or cervids, and do not usually lead to established populations (Hasle 2013). No established populations have yet been proven to occur north of 66° N in Finland. Nevertheless, there appears to be a general expansion of tick encounter areas toward northern regions (Sormunen, Sääksjärvi et al. 2023). Moreover, the subarctic region has experienced above-average warming in recent decades, which may lead to further spread of ticks in the near future (Post et al. 2019). In Finland, the rise in temperature has been markedly rapid since the late 1960s (Mikkonen et al. 2015), while the abundance of ticks' host animals has simultaneously increased (Helle and Kauhala 1991; Kekkonen et al. 2012; Lavsund et al. 2003). Particularly, the northwestern expansion of *I. persulcatus* from western Russia to western Finland and northeastern Sweden, where one of the northernmost populations of *I. persulcatus* currently occurs, appears to be relatively recent and rapid (Jaenson et al. 2016; Tokarevich et al. 2011; Wang et al. 2023). Moreover, the first observation of *I. persulcatus* in Norway was made just recently (Cotes-Perdomo et al. 2025). In further east, continentality limits the northern expansion of *I. persulcatus* (Stonevicius et al. 2018). Although ticks have occasionally been sighted around Oulu since the 1930s (Pakanen et al. 2020), these instances may have involved individual ticks brought by hosts rather than stable, reproducing populations, as the established distributional range of ticks in the late 1950s was located over 200 km further south (Öhman 1961). However, it is more than likely that the crowdsourcing study from the 1950s did not detect all established tick populations. Besides the observed extension in the distributional ranges of *Ixodes* ticks in Finland, other studies have also indicated local increases in tick abundance (Sormunen, Andersson, et al. 2020; Sormunen, Klemola, et al. 2016). The similar extension in tick distribution as well as the increase in tick abundance have been observed in other northern countries as well (Bugmyrin et al. 2013; Jaenson et al. 2012; Jore et al. 2011; Lindgren et al. 2000; Ogden and Lindsay 2016; Talleklint and Jaenson 1998). Climate change and the density of key hosts for adult ticks are believed to be key drivers of changes in tick populations. In the northern hemisphere, climate change causes increasing temperatures and precipitation, milder winters, and extended growing seasons, which further affect tick survival, tick developmental rates, tick questing activity, tick population density and fluctuations in host animal populations (Dobson and Randolph 2011; Gray et al. 2009; Jaenson, Jaenson, et al. 2012; Jaenson and Lindgren 2011; Lindgren et al. 2000). Moreover, as noted by Sirotkin and Korenberg (2018), changes in the ecosystems or regional microclimatic and environmental conditions caused by increasing human actions, such as deforestation, urbanization and other economic activity, can significantly impact tick abundance and contribute to their observed range expansion as well.

4.2.1 Distributional features of *I. ricinus* and *I. persulcatus* in Finland (**I**, **II**)

Ixodes ricinus and *I. persulcatus* now co-occur in western Russia (Tokarevich et al. 2011), Estonia (Katargina et al. 2015), Hungary (Hornok et al. 2020), Latvia (Capligina et al. 2020), Sweden (Jaenson et al. 2016; Omazic et al. 2023), Norway (Cotes-Perdomo et al. 2025) and Finland (**I**). The first observations of *I. persulcatus* in Finland were made about a decade before our crowdsourcing study, from Kokkola archipelago (Jääskeläinen et al. 2006, 2010). Thus, it appears that *I. persulcatus* has established itself in Finland sometime during the late 20th–early 21st century. In contrast, historical records indicate a centuries-long presence of *I. ricinus* in Finland (Latva 2017). It was expected that *I. persulcatus*, being a more recent arrival in Finland, would likely have failed to establish in areas where *I. ricinus* populations were already well established. However, *I. persulcatus* ticks have been observed to displace local *I. ricinus* populations in Russia, in areas close to the Finnish border (Bugmyrin et al. 2013). Study **I** also showed that, while *I. ricinus* is still predominant in southern Finland, *I. persulcatus* populations now dominate in some of the eastern areas as well as in western coastal areas from Ostrobothnia to southern Lapland, and central Finland is a sympatric area where both tick species coexist.

Harsh environmental conditions lead to a more uneven distribution and lower overall tick abundance of ticks (Sirotkin and Korenberg 2018), which can be seen near their distributional ranges in southern Lapland, further from the coast. The most obvious explanation for *I. persulcatus* dominance in northwestern coast and south Lapland would be its better adaptation to cold environments compared to *I. ricinus* (Korenberg et al. 2021). *Ixodes persulcatus* especially have a high ecological flexibility, facilitating their broad geographic distribution from continental climates in Asia to more variable climates in eastern and northern Europe (Sirotkin and Korenberg 2018; Wang et al. 2023). *Ixodes persulcatus* can overwinter under more severe conditions, is active at lower temperatures and can occur in areas with shorter growing season, less precipitation, lower humidity index and temperature sum than *I. ricinus* (Jaenson et al. 2016; Sirotkin and Korenberg 2018). In Finland, the climate in the southernmost part of Finland is mostly hemiboreal, while it gradually turns to boreal climate in north. In the highest latitudes of its occurrence in Finland and Sweden, *I. persulcatus* lives in areas where the length of growing season varies between 140 and 150 days, while *I. ricinus* prefers areas with a growing season exceeding 180 days (Jaenson et al. 2016). However, recent studies on the occurrence of *I. ricinus* and *I. persulcatus* in Finland have found that, although there may be some differences in the environmental factors predicting their presence, environmental factors alone do not fully explain habitat suitability or the distributional limits of ticks in Finland (Kulha et al. 2022; Uusitalo et al. 2020). Moreover, Kulha et al. (2022) found no major differences in winter conditions between sites where either *I. ricinus* or *I. persulcatus* were present in Finland in the area of their co-occurrence. They also suggested that in the area of *I. ricinus* and *I. persulcatus* co-occurrence in Finland, *I. ricinus* might actually be more resistant to desiccating conditions than *I. persulcatus,* as it inhabits sites that are more prone to drought such as urban inland areas and rocky and elevated sites, which might be explained by differences in the temporal activity patterns between the species. Since the activity period of *I. persulcatus* only lasts 3 months in Finland (Pakanen et al. 2020; Sormunen, Andersson, et al. 2020), *I. persulcatus* must survive longer periods of dormancy, when they need to conserve energy as much as possible. In contrast, the activity period of *I. ricinus* could potentially last even up to 8-10 months, which shortens the winter dormancy, potentially leading to better survival in xeric environments than *I. persulcatus*. Although cities are generally warmer and drier than the surrounding countryside, small-scale environmental variability can significantly affect the local conditions, resulting in patches of high humidity within urban areas as well. Urban green spaces are known to sustain several host species and provide suitable habitats for ticks (Klemola et al. 2019; Rizzoli et al. 2014; Sormunen et al. 2025). However, while in the area of their co-occurrence, *I. ricinus* prevails in major inland cities, *I. persulcatus* is the dominant species in major coastal cities (**Figure 5**). A reason suggested by Kulha et al. (2022) for *I. perculatus* dominance in western coastal cities may be the reverse urban heat inland effect (UHI), since the effect may reverse in high-latitude coastal cities (Suomi and Käyhkö 2012). However, higher number of inhabitants in urban areas might partly explain why tick observations were also related to urban areas. Most of the ticks were collected from humans and their companion animals and not from their natural habitats. The collection method, such as cloth dragging and collection from pets, can further affect the proportion of different tick species detected (Bugmyrin et al. 2013), reflecting differences in host contact patterns and questing behaviour. Moreover, species-specific differences in tick activity together with human activity might affect the observed differences in tick occurrence. For example, the coincidence of the second activity peak of *I. ricinus* in July with the popular holiday season in Finland might affect the higher number of *I. ricinus* observations around Lake Finland.

In 2015, *I. persulcatus* was not yet established on the southern coast of Finland. The southern distribution limit of *I. persulcatus* observed in our study was notably sharp, and some of the areas where we received the highest numbers of *I. persulcatus* samples were right at the distribution boundary **(Figure 5).** At the time, the absence of *I. persulcatus* in southern Finland was also observed by studies conducted with cloth dragging (Sormunen, Andersson, et al. 2020; Sormunen, Penttinen, Klemola, Hänninen, et al. 2016). No prominent landform feature corresponds to the observed distribution boundary, and no obvious distribution barrier for *I. persulcatus* exists. The most plausible environmental explanation for the distribution boundary would be climatic differences or more subtle environmental factors. However, the southernmost distribution limit of *I. persulcatus* in Finland is probably affected more by the distribution history of the species than by environmental factors, since *I. persulcatus* is well established in certain regions of corresponding latitudes in Russian Karelia (Bugmyrin et al. 2013; Jääskeläinen et al. 2010) and even further south in Estonia and Latvia (Capligina et al. 2020; Katargina et al. 2015). Moreover, using the same crowdsourced tick data, Kulha et al. (2022) predicted high relative habitat suitability for *I. persulcatus* in certain areas in southern Finland, where it did not yet have established populations in 2015 (**I**). The same study suggested that the recent establishment and ongoing dispersion of *I. persulcatus* in Fennoscandia is the main cause for the southernmost distribution limit of the two *Ixodes* species in Finland. Shortly after Study **I**, *I. persulcatus* ticks were detected in Helsinki (Zakham et al. 2021), but these specimens were collected from pets and therefore raise doubts as to whether they originate from a locally established population in the south. Some *I. persulcatus* samples from dogs were reported as having been collected in Helsinki in our study as well, but background research suggested they originated from elsewhere.

Regarding the expansion of *I. ricinus* and *I. persulcatus* geographical distribution, both tick species rely on host animals. In the long-distance dispersal of ticks, migrating birds are among the most important ones (Buczek et al. 2020; Hornok et al. 2020; Tardy et al. 2023). During the northward migration occurring in spring in Finland, birds could acquire *I. persulcatus* from Estonia and Latvia (Capligina et al. 2020; Katargina et al. 2015). On the other hand, *I. persulcatus* could be distributed southwards and westwards during the autumn migration. However, as *I. persulcatus* populations in Finland are no longer active during autumnal migration period, it is unlikely that migrations have any major role in distributing *I. persulcatus* to south or southwest. Moreover, although birds are known as important hosts for *I. persulcatus* as well, in a recent survey, no *I. persulcatus* were detected on migrating birds in Finland (Sormunen et al. 2022). Thus, the short activity period of *I. persulcatus*, as well as the mobility of available hosts, might have a role in limiting *I. persulcatus* distributional range in Finland.

Competition through hybridization of *I. ricinus* and *I. persulcatus* could be one of the underlying reasons for the absence or the domination of one species in certain areas, by converting a substantial portion of the arriving population of the competing species into hybrids (Todesco et al. 2016). Thus, it may be difficult for *I. persulcatus* to gain ground in locations where *I. ricinus* is already well established. For example, in southern Finland, a small number of arriving *I. persulcatus* individuals could be hybridized to local extinction, since *I. ricinus* is abundant there. It has long been thought that interbreeding between *I. ricinus* and *I. persulcatus* results in sterile offspring (Balashov et al. 1998), a notion recently supported by laboratory findings demonstrating that hybrids of the two species are sterile (Belova et al. 2023). However, suggested *I. ricinus* and *I. persulcatus* backcrosses have also been detected (Alale et al. 2024; Kovalev et al. 2016). Hybrids formed by mating between an *I. ricinus* female and an *I. persulcatus* male occur more commonly than vice versa (Kovalev et al. 2016), which might actually support the domination of established *I. persulcatus* populations in some areas. In the case of hybridization asymmetry, if the less common species is more likely to serve as the mother of hybrid progeny, the risk of extinction is higher for this species (Todesco et al. 2016). The backcrosses of *I. ricinus* and *I. persulcatus* hybrids are suggested to mate more often with *I. ricinus* (Kovalev et al. 2016). Hybridization between *I. ricinus* and *I. persulcatus* in their sympatric zones in Estonia is a more common phenomenon than previously thought, with the detected frequency of interspecific hybrids up to 11% (Kovalev et al. 2016). In a study conducted in Finland, around 5 % of the studied ticks (9/172 individuals from crowdsourced tick material, **I**) were identified as putative hybrids, with genomic admixture ranging from approximately 24% to 76%, suggesting that not all were first-generation hybrids with allele frequencies close to the Mendelian 50:50 proportion (Alale et al. 2024). Most of the hybrids analysed in their study were suggested as first-generation hybrids, though the possibility of backcrossing was indicated in one case. In Estonia, among ticks morphologically identified as *I. ricinus*, 24.6% were actually interspecific hybrids and 3.3% were *I. persulcatus*, while the accuracy of morphological species identification was over 99% for *I. persulcatus* (Kovalev et al. 2016). This underlines the possibility of misidentification when relying solely on morphological characteristics, especially in areas where both species occur.

4.3 Presence and distribution of TBPs in Finland (I, II)

More than one-fourth of studied ticks were infected with at least one pathogen. Of the total nine studied pathogen groups, Studies **I** and **II** found seven pathogen groups and twelve pathogen species altogether from Finnish ticks, many of which are capable of infecting humans and companion animals and some regarded as new emerging tick-borne pathogens. Diversity of different TBPs was higher in *I. ricinus* (seven pathogen groups) than *I. persulcatus* (five pathogen groups). A higher diversity of tick-borne pathogens in *I. ricinus* has also been observed in previous studies (Movila et al. 2014). Most of the studied pathogens were also more prevalent in *I. ricinus* than in *I. persulcatus* samples, with the exception of the two most important TBPs in Finland, Bbsl and TBEV. Higher infection rates of Bbsl and TBEV have been reported in *I. persulcatus* (Geller, Nazarova, Katargina, and

Golovljova 2013; Katargina et al. 2013) and it has been suggested that *I. persulcatus* is more efficient vector for Bbsl and TBEV than *I. ricinus* (Korenberg et al. 2001).

Species of Bbsl, *Rickettsia*, *B. miyamotoi*, and TBEV were all detected north of 65°N, whereas *Anaplasma* spp. *Neoehrlichia mikurensis* and *Babesia* spp. were detected only south of 65°N, possibly due to the lower abundance of *I. ricinus* at higher latitudes. There was no direct correlation between tick infection prevalence and latitude, since the highest prevalence of infected ticks were found in the area below 61°N and in the area between 65°N and 66°N. A decreasing trend in infection prevalence towards the higher latitudes was observed only for *Rickettsia* spp., though differences across collection areas were not significant. Local environmental conditions may have a bigger influence on pathogen diversity and prevalence than latitude alone, although temperature and the duration of the activity season are important factors determining the distributional limits for ticks and TBPs (Coipan et al. 2013; Estrada-Peña et al. 2012; Ogden et al. 2021). According to previous observations, pathogen prevalence is also expected to correlate with the density of questing ticks, especially nymphs (Ogden 2013; Randolph 2001; Tälleklint and Jaenson 1996). Moreover, tick life stage, sex, and the season of tick collection may have an influence on the observed pathogen prevalences. In our dataset, 85% of the *I. persulcatus* samples were collected by the end of May, while 85% of the *I. ricinus* samples were not collected until the end of July. Around 95% of analysed ticks in our pathogen analyses were adults and less than one third were males. The assumption that in the zone of sympatry, the pathogen prevalence in one vector species would either increase or decrease by the influence of other closely related species, was not supported. This assumption was abandoned by previous study (Korenberg et al. 2001) as well, when they concluded that in the broad zone of *I. persulcatus* and *I. ricinus* sympatry, the presence and proportion of one species do not have any significant influence on the extensity of infection in the other species. In Study **II**, the highest infection rates were observed in areas dominated by one species, in south for *I. ricinus* and in north for *I. persulcatus*, while pathogen prevalence was lower for both species in the zone of their sympatry in middle Finland, indicating that environmental factors might explain the lower prevalence in sympatric region. Moreover, when all analysed ticks were considered, southern Finland showed the highest infection rate, but infection rates did not differ between central and northern Finland. It remains uncertain whether the higher prevalence in southern Finland is related to *I. ricinus* dominance and its higher overall prevalence of various TBPs, or to environmental factors.

Almost 2% of ticks were found to be co-infected in Study **II**. Since the diversity of different pathogen groups was higher in *I. ricinus* than *I. persulcatus*, it was not surprising that *I. ricinus* were more frequently co-infected (2.4% vs. 0.8%, respectively) as well. However, these numbers did not include *B. miyamotoi* and

TBEV, which were only analysed in Study **I** and were mainly found from *I. persulcatus*. Thus, the total diversity of different pathogen infection combinations was 6 in *I. ricinus* and 3 in *I. persulcatus* (*B. miyamotoi* and TBEV included). In Study **II**, when investigating co-infections among infected adult ticks only, there were no significant differences between species or the three collection areas. Most of the co-infections were between the two most prevalent pathogen groups, Bbsl and *Rickettsia* spp. pathogens. However, in Study **I**, eight *I. persulcatus* ticks were co-infected with TBEV and Bbsl and two *I. persulcatus* ticks were co-infected with Bbsl and *B. miyamotoi*. Thus, co-infection prevalence was as high as 25% among TBEV-positive samples and 33% among *B. miyamotoi* -positive samples. Moreover, in Study **II**, A particularly high number of co-infections were observed in positive *N. mikurensis* samples (6/17), all with Bbsl, and the only genospecies identified among these co-infections was *B. afzelii*. Among nymphs, three of four positive *N. mikurensis* samples were also co-infected with *B. afzelii*. Higher prevalence in nymphs and co-occurrence between these pathogens have been observed in other studies as well, due to shared reservoir hosts, mainly small rodents (Andersson et al. 2013; Kjelland et al. 2018; Klemola et al. 2019). Co-infections may have a significant clinical significance, since co-infections of multiple pathogens may cause unpredictable or more severe diseases in humans (Diuk-Wasser et al. 2016; Swanson et al. 2006). For example, a rare fatal case of babesiosis in Finland has been reported from a co-infected man (Haapasalo et al. 2010).

4.3.1 Bbsl in Finnish ticks (**I**, **II**)

The most prevalent pathogen group detected was Bbsl (17%), the causative agent of LB, the most prevalent tick-borne disease in Finland. The observed prevalence of Bbsl in Finland corresponds with the average prevalence observed in Europe (Strnad et al. 2017), although prevalence estimates may vary greatly among years and areas. In studies conducted in Finland, tick infection rates have most often varied between 5-30% (Mäkinen et al. 2003; Sormunen, Penttinen, Klemola, Hänninen, et al. 2016), although prevalences up to around 50% in *I. ricinus* (Junttila et al. 1999; Klemola et al. 2019; Sormunen, Andersson, et al. 2020) and around 60% in *I. persulcatus* have also been reported (Pakanen et al. 2020). In our tick data, the shipment ID as a clustering factor was found to influence Bbsl prevalence, indicating that positive samples were often associated with the same collection area.

The most northern Bbsl-positive samples were detected beyond the latitude of 65°N. Bbsl have dispersed to higher latitudes along with ticks and host animals during the last decades (Simon et al. 2014). However, like with the most of the other TBPs, the prevalence of Bbsl infected ticks did not correlate directly with latitude (**II**). Beside local environmental conditions, variety and density of host animals are the primary factors determining the occurrence of Bbsl in nature. As both tick species are capable of using a wide range of different host animals and each host species has a different reservoir competence for Bbsl, the presence of different hosts affects the infection prevalences observed in ticks. Cervids, such as white-tailed deer (*Odocoileus virginianus*), are considered reservoir incompetent hosts for Bbsl, as they are generally incapable of sustaining Bbsl infections, do not transmit the pathogen to feeding ticks and the serum of white-tailed deer has also been demonstrated to kill *B. burgdorferi* s.s. bacteria (Luttrell et al. 1994; Pearson et al. 2023; Telford et al. 1988). Non-reservoir hosts can dilute the pathogen infection rates in ticks if their presence reduces the likelihood of ticks encountering reservoir hosts (Kurtenbach et al. 2006; Norman et al. 1999; Tälleklint and Jaenson 1996). However, large non-reservoir hosts are significant for Bbsl and other TBP dynamics, by amplifying tick populations and thereby allowing pathogens to persist or by enhancing pathogen reproduction due to increased larval and nymphal feedings on additional reservoir hosts. The simultaneous presence of high densities of deer and reservoir competent small mammals can create conditions that result in exceptionally high nymphal tick densities and infection prevalence (O'Neill et al. 2023). Although the crowdsourced material included samples from all over Finland, sample collections concentrated around more densely populated areas. Therefore, we did not regard tick density in our analyses. Moreover, the actual site where the infected tick was questing cannot be determined with certainty from crowdsourced material. However, studying Bbsl prevalence in crowdsourced material is meaningful from a public health perspective, as it provides insight into the overall risk of humans encountering Bbsl-infected ticks in Finland.

In Studies **I** and **II**, the Bbsl prevalence in ticks was higher in adults (17.1% and 17.3%, respectively) than in nymphs (14.3% and 13.4%, respectively), which is seen in other studies as well (Rauter and Hartung 2005; Strnad et al. 2017). Higher prevalence in adults is expected, as adults have fed more often on potentially infected host animals during their life. The youngest of tick life stages, larva, presumably hatches uninfected with Bbsl (Rollend, Fish, and Childs 2013). However, in our analyses, one *I. ricinus* larva carried *B. garinii*, which might have resulted from interrupted feeding for example.

The Bbsl prevalence for adult ticks was higher in *I. persulcatus* than in *I. ricinus*, even in the sympatric area in middle Finland (17.2 and 12.4%, respectively) (**II**). A higher prevalence of Bbsl in *I. persulcatus* than in *I. ricinus* has also been observed in previous studies conducted in sympatric regions (Alekseev et al. 1998; Geller, Nazarova, Katargina, and Golovljova 2013; Korenberg 1994; Kovalevskii and Korenberg 1995). One reason for higher observed Bbsl prevalence in *I. persulcatus* may be that *I. persulcatus* nymphs rarely feed on larger hosts that are not reservoir hosts for Bbsl, while *I. ricinus* nymphs commonly feed on larger animals as well, such as humans, acting as the most common source for humans to acquire LB (Estrada-Peña et al. 2023, 2018). The exact reasons for the different prevalences observed among tick species are unknown, but likely involve timing of their activity, differences in the habitats they occupy, the variety of host animals present in those habitats, species-specific host preferences, and fluctuations in host abundance.

In Study **I**, Bbsl prevalence did not differ significantly between adult female and male ticks. Across Europe, adult *I. ricinus* females generally show higher Bbsl prevalences than males (Strnad et al. 2017). This has been suggested to result from the longer feeding duration and larger blood meals of females, already at the nymphal stage (Dusbábek 1996; Hu and Rowley 2000). Ticks usually acquire Bbsl during their juvenile life stages when feeding on competent Bbsl reservoir hosts. Although females have an opportunity to acquire Bbsl during their third blood meal as well, especially given the long feeding duration, most of the engorged females collected in the crowdsourcing campaign had fed on Bbsl-incompetent hosts, such as humans and dogs. Therefore, the possible third blood meal of females is unlikely to increase Bbsl prevalence among females in our data.

The most prevalent Bbsl genospecies detected in Finnish ticks were *B. garinii* and *B. afzelii*, two genospecies known to commonly infect people. In Europe, *B. garinii* is the main cause of LNB, while *B. afzelii* is most often associated with skin manifestations (Jahfari et al. 2017; Strle et al. 2006). In contrast to many European countries (Strnad et al. 2017), *B. garinii* was the most prevalent genospecies in both ticks in Finland, particularly in *I. persulcatus* (62.6%). Previous studies have also suggested an association between different Bbsl genospecies and tick species (Movila et al. 2014; Rudenko et al. 2011). The reason for the higher prevalence of *B. garinii* in Finland could be related to variety of available host species and the temporal variations in their abundance. *Borrelia garinii* is known to prefer migratory birds like *Turdus* spp. as their reservoir hosts (Dubska et al. 2009; Gryczyńska and Welc-Falęciak 2016; Taragelova et al. 2008), while small rodents are known as the main hosts for *B. afzelii* (Hanincova et al. 2003). Since the seasonal activity patterns for *I. ricinus* and *I. persulcatus* differ (Gray 2008; Korenberg 2000; Sirotkin and Korenberg 2018; Sormunen, Andersson, et al. 2020; Uspensky 2016) and the activity peak of *I. persulcatus* in Finland coincides with the spring migration of *Turdus* and several other potential *B. garinii* infected bird species (Dubska et al. 2009), this overlap could influence the higher observed prevalence of *B. garinii* in *I. persulcatus* ticks. In contrast, *B. afzelii* was observed relatively more often in *I. ricinus* than in *I. persulcatus*, which is observed also in previous studies (Movila et al. 2014). Another reason for the higher proportion of *B. garinii* infected ticks observed in our study could be the relatively low number of nymphs. Field studies typically collect more juvenile life stages than crowdsourcing methods, and juvenile ticks, especially larvae, primarily feed on small mammals, which are known to be key reservoir hosts for *B. afzelii* (Hanincova et al. 2003). Indeed, *B. afzelii* was the only genospecies identified from the Bbsl-positive nymphs in Study **II**. However, a study conducted in north-western Finland found that *B. afzelii* was the predominant genospecies among both nymphal and adult stages of *I. persulcatus* (Pakanen et al. 2020). Nevertheless, these two *Borrelia* pathogens are the most prevalent genospecies among Finnish ticks, although the prevalences may change temporally and spatially due to differences in environmental conditions and host populations.

Other detected genospecies were *B. valaisiana* and *B. burgdorferi* s.s.. Whereas the evidence of human pathogenity of *B. valaisiana* is limited (Margos et al. 2017), *B. burgdorferi* s.s. is the only genospecies that causes LB in USA, with a wide variety of clinical conditions (Rudenko et al. 2011). *Borrelia valaisiana* was detected in 6.4% of the Bbsl-positive ticks, which is in accordance with the findings in the neighboring countries (Fraenkel et al. 2002; Geller, Nazarova, Katargina, and Golovljova 2013; Jenkins et al. 2012). Although this bird associated pathogen is not commonly detected in *I. persulcatus*, *B. valaisiana* can also be found in *I. persulcatus* in the sympatric areas of the two ticks (Alekseev et al. 2001; Geller, Nazarova, Katargina, and Golovljova 2013). *Borrelia valaisiana* prevalence among Bbsl-positive *I. persulcatus* ticks (2.5%) was similar to the prevalence observed in Estonia (Geller, Nazarova, Katargina, and Golovljova 2013). *Borrelia burgdorferi* s.s. was detected from 3.3% of the Bbsl-positive ticks, which, in contrast, is a rodent associated pathogen. *Borrelia burgdorferi* s.s. was not detected in *I. persulcatus*, even though it has previously been found in *I. persulcatus* in western coast around the city of Kokkola (Alekseev et al. 2007). *Borrelia burgdorferi* s.s. has previously been found in *I. ricinus* samples from Kokkola and from southern Finland (Sormunen, Andersson, et al. 2020; Sormunen, Klemola, et al. 2016), where *B. burgdorferi* s.s.-positive *I. ricinus* samples were found in our study as well.

Out of the Bbsl-positive samples (n = 590), only 394 (67%) were identified further to genospecies level. The rest of the sequence results were of poor quality, which could have resulted from impurities in the DNA samples. Many of the crowdsourced tick samples were engorged females, and the presence of a tick's blood meal may have an impact on the PCR results (Dharmarajan and Rhodes 2011). Moreover, we did not examine co-infections at species level, so double infections among different genospecies, e.g. *B. afzelii* and *B. garinii* were not considered. In Finland, coinfection rate of 26% among Bbsl infected adult *I. persulcatus* ticks have been observed (Pakanen et al. 2020). Unidentified Bbsl-positive samples might also include some new genospecies that were missed in our analyses. *Borrelia bavariensis,* for example, is a close relative to *B. garinii* (Becker et al. 2020). In addition to the genospecies identified in Study **II**, only *B. spielmanii* has previously been reported in Finnish ticks (Wilhelmsson et al. 2013).

4.3.2 Other tick-borne pathogens (TBPs) in Finnish ticks (**I**, **II**)

The most prevalent pathogen after Bbsl was *Rickettsia* spp., with a slightly higher prevalence (10.8%) than in the neighboring country, Estonia (5.1%) (Katargina et al. 2015). As with Bbsl, there seem to be great variation in *Rickettsia* prevalences among ticks across different areas (Hartelt et al. 2004; Lindblom et al. 2016; May and Strube 2014; Severinsson et al. 2010). In Finland, *I. ricinus* was found twice more often positive for *Rickettsial* DNA (13.9%) than *I. persulcatus* (6.5%). Almost all of the *Rickettsia*-positive samples among *I. ricinus* were identified as *R. helvetica* (99%, 199/201) and the prevalence of *R. helvetica* was over four times higher in *I. ricinus* than in *I. persulcatus*, even though *R. helvetica* did not have a significant difference in infection prevalence between the collection areas. *Ixodes ricinus* is regarded as the main vector of *R. helvetica*. Although *Rickettsia* species have also been detected in *I. persulcatus* ticks, their prevalence have been lower compared to *I. ricinus* (in Estonia: 1.7% vs. 6.7%, respectively) (Katargina et al. 2015). *Rickettsia* prevalence was 11.1% in adults and 5.6% in nymphs. Transovarial transmission of some *Rickettsia* species has been demonstrated (Hauck et al. 2020; Ravindran et al. 2023), but there were no infected larvae in our analyses. Study **II** reported the first detection of *Ca.* R. tarasevichae in Finland and in *I. ricinus* as well. *Ca.* R. tarasevichae has a wide distribution, from Japan to Estonia, where the first detection of this pathogen was made in 2015 from *I. persulcatus* (Katargina et al. 2015). In contrast to *R. helvetica*, *Ca.* R. tarasevichae was detected almost exclusively in *I. persulcatus* (18/19 positive samples). Interestingly, the one positive *I. ricinus* sample was from the southern coast of Finland, where *I. persulcatus* had not yet been detected. The most western limit of *Ca.* R. tarasevichae currently lies in Finland and Estonia. Three *Rickettsia*-positive samples were identified as *R. monacensis*, and it was found from both tick species. Prior northernmost finding of *R. monacensis* in Europe were from Estonia (Katargina et al. 2015) and in 2016 it was reported from Finnish archipelago (Sormunen, Klemola, et al. 2016; Sormunen, Penttinen, Klemola, Hänninen, et al. 2016). Patient cases suggest that *R. helvetica*, *Ca.* R. tarasevichae and *R. monacensis* are all capable of human infection (Jado et al. 2007; Jia et al. 2013; Påhlson et al. 2021; Parola et al. 2013; Parola, Paddock, et al. 2005). Still, no patient cases of tick-borne rickettsiosis have been reported from Finland to date.

Anaplasma spp. was the most abundant pathogen of the family Anaplasmataceae and the only species identified was *A. phagocytophilum*. Observed prevalences of *A. phagocytophilum* in Europe have varied greatly among countries, study localities and tick life stages (Dumler et al. 2005; Henningsson, Hvidsten, et al. 2015; Severinsson et al. 2010; Strle 2004; Stuen 2007). In Sweden, higher prevalences of *A. phagocytophilum* have been reported in coastal areas (Severinsson et al. 2010). The previous observed prevalence in questing *I. ricinus* in southwestern Finland was

3.5% (9.2% for adults) (Sormunen, Penttinen, Klemola, Vesterinen, et al. 2016), which was higher than the overall prevalence in Finland observed in Study **II** (0.6%). The prevalence of *Anaplasma* spp. in Study **II** was higher in *I. ricinus* than in *I. persulcatus* (1.0% vs. 0.1%, respectively), and neither of the two positive samples observed in *I. persulcatus* could be identified to species level by sequencing. In Finland, Anaplasmosis (HGA) have not yet been reported from humans. The first case report of Anaplasmosis in a domestic cat with previous tick exposure was made in 2008 from southeastern Finland (Heikkilä et al. 2010).

Another human pathogen from the family *Anaplasmataceae*, *N. mikurensis*, was detected in 2015 for the first time in Finland in the southwestern archipelago (Sormunen et al. 2018), and Study **II** detected this pathogen for the first time from Finnish mainland. The overall prevalence of *N. mikurensis* was 0.5% and it was only detected in *I. ricinus*. It seems that *I. persulcatus* is less likely to carry *N. mikurensis*, although the pathogen has been found from *I. persulcatus* also in areas where *I. ricinus* is not present (Ivanova et al. 2017; Rar et al. 2010; Rar and Golovljova 2011). In Estonia, prevalences range from 1 to 9.1%, and is not reported from *I. persulcatus* (Ivanova et al. 2017). The prevalence of *N. mikurensis* in juvenile life stages was higher than in adults (2.2% vs 0.4%, respectively). Moreover, three of the four *N. mikurensis* -positive nymphs were collected from the same location, and positive samples were therefore strongly correlated. Studies suggest that while infections with *N. mikurensis* or *A. phagocytophilum* are usually mild or asymptomatic, they may also cause more severe or even fatal infections, especially in immunocompromised patients (Grankvist et al. 2014; Henningsson, Wilhelmsson, et al. 2015; Wang et al. 2020). Since *N. mikurensis* has a tendency for co-occurrence with Bbsl, abnormal or more severe symptoms might also be expected to occur (Swanson et al. 2006). First case of neoehrlichiosis in Finland was reported in 2024 in an immunosuppressed patient, and the infection was most likely originated from southwestern archipelago and transmitted by a tick (Hohenthal et al. 2025).

Previous studies about *Babesia* spp. prevalence in Finnish ticks are scarce, although *B. divergens* is a well-known agent for bovine babesiosis (Zintl et al. 2003). Study **II** found that *Babesia* spp. is a rare pathogen in Finnish ticks (0.3%) and the prevalence in *I. ricinus* (0.5%) corresponds to results reported from neighboring countries (Karlsson and Andersson 2016; Katargina et al. 2011; Rar et al. 2011). *Babesia divergens* and *B. venatorum* were reported for the first time from the Finnish mainland and *B. venatorum* was the most prevalent species. *Babesia venatorum* has been involved in several documented cases of human babesiosis (Hunfeld, Hildebrandt, and Gray 2008; Jiang et al. 2015), although *B. divergens* is the most common cause of zoonotic babesiosis in Europe (Gray et al. 2010). Overall, cases of human babesiosis are uncommon in Europe (Hildebrandt et al. 2021). In Finland, a single case of fatal babesiosis in 2004 was caused by *B. divergens* and believed to be transmitted by a tick bite (Haapasalo et al. 2010). Moreover, the patient was co-infected with *B. divergens* and *Borrelia* sp., and reports suggest that co-infection with these pathogens may cause more severe disease with additional symptoms (Krause et al. 1996, 2002). In Study **II**, *Babesia divergens* was detected in two samples. However, *B. divergens* and *B. capreoli* are genetically very similar, and since one of the positive samples were only 99% identical to the reference sequence U16370 (Malandrin et al. 2010), we cannot be entirely sure whether this is truly *B. divergens* or *B. capreoli*. *Babesia capreoli* was reported first time in Finnish *I. ricinus* ticks from Helsinki in 2020 (Sormunen, Kulha et al. 2020). *Babesia microti* was not detected, even though it is known to commonly infect rodents in Finland (Kallio et al. 2014) and had previously been found in *I. persulcatus* tick in western coast of Finland (Alekseev et al. 2007). In United States, it is the main causative agent for human babesiosis (Gray et al. 2010). The absence of *B. microti* in our study is likely due to low prevalence in Finnish ticks. In Sweden, however, *B. microti* is the most common *Babesia* species detected in *I. ricinus* (Karlsson and Andersson 2016).

In Study **I**, *B. miyamotoi* was detected for the first time in ticks from mainland of Finland and from both species. The first detection of the pathogen in Finland was made in Åland Islands in 2008–2009 (Wilhelmsson et al. 2013). *Borrelia miyamotoi* has also been found from southwestern archipelago since 2012, where it has been detected from larvae as well (Sormunen, Klemola, et al. 2016; Sormunen, Penttinen, Klemola, Hänninen, et al. 2016). In Study **I**, *B. miyamotoi* was found in 6 out of 2038 (0.3%) ticks, which is approximately in accordance with the results of studies conducted in neighboring countries (Geller et al. 2012; Wilhelmsson et al. 2010). Even if the reported prevalences for *B. miyamotoi* have generally been low, higher prevalences have also been observed (Crowder et al. 2014; Kubiak, Szczotko, and Dmitryjuk 2021; Platonov et al. 2011).

Occurrence of TBEV, the causing agent of TBE, the second most important tick-borne disease in Finland after LB, was analysed in Study **I**. The overall prevalence in Finnish ticks was 1.6%. In general, the prevalence of TBEV in ticks is relatively low, between 0.1–5% (Pettersson et al. 2014; Süss 2003). Moreover, since the transmission cycle of TBEV is fragile, several factors, such as microclimatic conditions and host availability, affect its survival in nature (Randolph and Rogers 2000; Uusitalo et al. 2020), and thus the occurrence of TBEV is highly patchy, and annual prevalence of TBEV in ticks even in one site can vary remarkably (Bormane et al. 2004). This was also observed in Study **I**, with TBEV-positive samples aggregating in distinct clusters, and some were from the same collectors and collection sites. Interestingly, none of the ticks from the southern and southwestern coasts of Finland tested positive for TBEV, despite these regions reporting the majority of human TBE cases. This may be related to the clustered nature of TBEV distribution and its low expected prevalence in nature. In addition, TBEV can occur at low concentrations in ticks, but may replicate during blood feeding and thus become detectable in engorged ticks (Belova et al. 2012). Nevertheless, human cases are relatively rare and focal as well (Lamsal et al. 2023). Ticks can acquire TBEV by feeding on viremic hosts, like rodents or birds (Achazi et al. 2011; Kazarina et al. 2015; Waldenström et al. 2007), through transovarial and sexual transmission (Chitimia-Dobler 2024), or through co-feeding transmission, which is proven to be one of the major pathways for the transmission and maintenance of TBEV in foci (Randolph 2011; Randolph et al. 2000). Co-feeding of nymphs and larva has been associated with spring temperatures in northern Europe, as warmer springs allow larvae to become active earlier, resulting in simultaneous questing alongside nymphs (Jaenson, Hjertqvist, et al. 2012). In Study **I**, all but one of the TBEV-positive ticks were adults, probably due to the relatively small number of analysed nymphs. However, adult female ticks typically show a higher infection prevalence than nymphs (Süss et al. 1999). Moreover, a higher TBEV prevalence was observed in *I. persulcatus* (1.6%) than in *I. ricinus* (0.2%), which has also been found in previous studies, even though prevalences vary annually (Bormane et al. 2004; Capligina et al. 2020). In Finland, subtypes of Eur-TBEV and Sib-TBEV are endemic, of which Eur-TBEV is mainly transmitted by *I. ricinus*, while Sib-TBEV is often transmitted by *I. persulcatus*, although both virus subtypes have been found in both *Ixodes* ticks in Finland (Jääskeläinen et al. 2016). In addition to previously known endemic areas in Finland, several TBEV-positive ticks were received from Tampere region, where only sporadic TBE cases had been reported, suggesting a new endemic focus there. Indeed, today Tampere is considered a risk area for acquiring TBE. For several years, new foci of TBEV have appeared annually in Finland (Jääskeläinen et al. 2016; Smura et al. 2019; Tonteri et al. 2015). It is suggested that TBEV introduction into new areas likely occurs via migratory birds, followed by local spread (Geller, Nazarova, Katargina, Leivits, et al. 2013; Kazarina et al. 2015; Waldenström et al. 2007).

Neither *Bartonella* spp. nor *Francisella tularensis* were found in Study **II**, although some species of *Bartonella* have been reported from mammals and arthropod vectors, like fleas and deer keds, also in Finland (Korhonen et al. 2015; Veikkolainen et al. 2014). *Bartonella* have been reported in one *I. persulcatus* tick in Estonia (Movila et al. 2014), while the prevalence in questing *I. ricinus* ticks in Europe has been much higher (over 30% in nymphs) (Dietrich et al. 2010). However, the relevance of ticks as *Bartonella* vectors to humans remains unverified (Telford and Wormser 2010). In addition, the role of *Ixodes* ticks in the transmission of *F. tularensis* in northern Europe is still unclear, even if *Ixodes* ticks are important vectors of *F. tularensis* in North America and Central Europe (Keim, Johansson, and Wagner 2007; Maurin and Gyuranecz 2016). In Finland and Sweden, infection of

F. tularensis most likely occurs through mosquito bites (Eliasson et al. 2002; Rossow et al. 2014; Ryden et al. 2012; Thelaus et al. 2014) and, as shown by both Study **II** and the more recent investigation by Sormunen et al. (2021), *F. tularensis* does not appear to be circulating in Finnish ticks.

4.4 Decreased Bbsl seroprevalence in Finland (**III**)

A significant decreasing trend in Bbsl seroprevalence in Finnish population was observed during a 50-year period. The study period lasted from the time before the identification of Bbsl as the pathogen causing LB until the present day, when LB is a widely recognised disease and can be diagnosed using targeted methods and treated effectively with antibiotics. Bbsl seroprevalence in Finland at the turn of the 1970s was 25.0%, and since then, the seroprevalence has decreased considerably being 16.6% in 1980, 7.4% in 2000 and 3.4% in 2017.

LB incidence rates have been increasing drastically in several European countries, Finland included, and it is the most common tick-borne disease in the northern hemisphere (Marques et al. 2021; Sajanti et al. 2017). This change probably reflects the increased abundance and expanded geographic distribution of ticks, and increased awareness of LB. In contrast to our findings, some studies suggest an increase in Bbsl seroprevalence during the last decades as well (Dong et al. 2022; Hoeve-Bakker et al. 2024). Our results are not entirely exceptional however, since another notable decreasing trend in Bbsl seroprevalence in general population has been observed in Czech Republic between 1978–1989 and 2001 (Kříž et al. 2018). In addition, a study from Germany found no substantial change in seroprevalence among children and adolescents from 2003 to 2017 (Böhm et al. 2023). Nevertheless, there is a great variation in LB infection rates and Bbsl seroprevalence estimates across countries, regions and specific population groups (Burn et al. 2023; Dong et al. 2022; Hart et al. 2025), and there are only few studies on nationally representative seroprevalence estimates on general population over time. Moreover, the heterogeneity in the research setups, methods and surveillance systems imposes limitations on comparisons among different studies. Our own results underline the influence of serological methodology, since our seroprevalence estimate for the 1970s data (25%) differed somewhat from the previous estimate for the same data (20%) using different serological method (Cuellar et al. 2020).

After the recognition of Bbsl as the cause of LB in 1975, regular antibiotic treatments began in the 1980s in Europe (Stanek and Strle 2022). Even though antibodies can remain elevated for years after infection, despite successful treatment (Kalish et al. 2001), the concentration of antibodies declines after antibiotic treatment (Marangoni et al. 2006; Pietikäinen et al. 2022). In Study **III**, the concentrations of IgG antibodies in the positive samples were highest among the samples from 1970 and decreased towards the latest study years. This finding may indicate that, 50 years ago, people experienced ongoing disseminated LB more frequently, as IgG antibodies against the p18 protein are associated with late disseminated LB (Dessau et al. 2018), or that repeated exposure to Bbsl has resulted in a stronger immune response. The vast majority (73.8%) of our seropositive samples had the IgG antibody level elevated against the p18 of *B. afzelii*, although *B. garinii* is the most prevalent Bbsl genospecies in Finnish *I. ricinus* and *I. persulcatus* ticks (**II**).

The increased awareness among healthcare providers and the general population as well as the use of antibiotics as an effective treatment method could be the main reasons for the observed decrease in Bbsl seroprevalence. While the increase in reported acute LB infections might partly reflect a decrease in the number of people testing positive for past infections or developing late disseminated LB after the 1990s, the breakthrough in LB diagnostics and treatment in the 1980s and 90s does not explain the significant decrease in seroprevalence between the 1970 and 1980, a period when antibiotics were not yet in regular use. However, increasing concern about Kumlinge disease (tick-borne encephalitis, TBE), which was first detected in Kumlinge in the Åland Islands in 1959 (Wahlberg et al. 2006), and therefore increasing awareness of tick-related risks, might have a role in the decreasing trend in Bbsl seroprevalence in Finland already in the 1970s and 1980s. Another underlying cause for decreasing seroprevalence could be Finland's economic shift from the agrarian society to a more industrialised and service-based one (Eloranta and Ojala 2022). Fifty years ago, Finland was still largely relying on agriculture and forestry, and humans may have encountered ticks more often than in 2017. In addition, during the late 20th century, Finland experienced fast population migration to urban centres. Moreover, when the associations of work status and seropositivity were analysed among 1970s and 1980s participants, people working outdoors, e.g. in farming and forestry, had the highest probability of being seropositive and people working indoors had the lowest probability of being seropositive. European studies confirm that seroprevalence among risk-groups like hunters and forestry-workers can be very high compared to general population (Burn et al. 2023). Unfortunately, the influence of work-factor in 2000 and 2017 could not be studied, since work information of the participant was not available. Finally, it is possible that Borrelia prevalence among ticks may have been decreasing in some areas during the last decades, due to possible changes in host animal populations, thereby affecting the population's exposure risk to Borrelia.

4.4.1 Regional variation in Bbsl seropositivity (**III**)

When we compared seroprevalence estimates across the five university hospital districts, we observed that the seroprevalence varied by location. The probability of being Bbsl-seropositive was higher among residents from southern (Helsinki district) or central and eastern Finland (Kuopio district) than from western (Turku and Tampere districts) and northern Finland (Oulu district). As expected, due to the lower abundance of ticks in the north, residents from northern Finland had also the lowest Bbsl seroprevalence rate. However, Oulu is the only district where seroprevalence may have even increased during the last decade, from 0.67% in 2000 to 0.87% in 2011 (van Beek et al. 2018) and 2.0% in 2017. This could be related to the increasing tick abundance, especially *I. persulcatus* populations, in northern coastal areas around Kemi, Oulu and Kokkola (**I,** Pakanen et al. 2020). The low seroprevalence in western Finland (Turku district) is quite surprising, since southwest Finland has one of the highest tick densities, Bbsl prevalences among ticks and LB incidence rates in Finland (Klemola et al. 2019; Sajanti et al. 2017; Sormunen et al. 2020). On the other hand, the neighbouring district in south, Helsinki, had the highest Bbsl seroprevalence in Finland, and participants from Helsinki district had over three times higher probability of being seropositive than participants from Turku district (0.164 vs. 0.047, respectively). Observed differences might be caused by different levels of tick and LB awareness among laymen and physicians, since southwest Finland has long had one of the highest incidences of LB and TBE (Sajanti 2017; Wahlberg 2006). In addition, Finland has experienced rapid urbanization in recent decades (Eloranta and Ojala 2022), with many people having migrated from surrounding countryside to urban areas, especially to Helsinki, which may have influenced the exceptionally high seroprevalence rates seen in participants from Helsinki district in the 1970s and 1980s. Moreover, university hospital districts include participants not only from major university cities but also from surrounding areas with varying tick densities and LB incidences. Thus, Bbsl seroprevalence may vary substantially even within a university hospital district. In addition, participants may have acquired the Bbsl infection from summer cottages, or from other travels outside the university hospital district in question. Another interesting result was that the seroprevalence decreased considerably between 1980 and 2000 especially in Helsinki (from 26.3% to only 8.2%), while at the same time, there was hardly any decrease in seroprevalence in another high prevalence district, Kuopio (19.2% vs. 18.8%). Again, increasing awareness in southern Finland, including capital Helsinki, might be the underlying cause for the most notable decreasing trend in seroprevalence there.

From 1995 to 2014, the incidence of LB has increased most significantly in western, southern and southeastern Finland (Sajanti et al. 2017). At the same time, our Study **III** showed that Bbsl seroprevalence has decreased almost everywhere in

Finland from 1970 up until 2017, by which time the differences among the study areas had evened out, with seroprevalence ranging from 2% to 5% in all university hospital districts. Kuopio remains the district with the highest observed seroprevalence in Finland in 2017, even if the differences among study areas were not significant. A low number of tick-human encounters is unlikely to be the most plausible explanation for the low observed Bbsl seroprevalence in southwestern Finland, given the high prevalence of ticks and TBDs in southern cities (Klemola et al. 2019; Sormunen et al. 2025), the large number of ticks collected from southern coastal areas in 2015 (**I**) and the high incidence of LB cases (Sajanti et al. 2017). In contrast, the great public interest in the tick collection and the substantial number of ticks collected may exemplify the high awareness of the subject, not only along the southern coast but also elsewhere in Finland. From a general perspective, the Bbsl seroprevalence we observed in 2017 reflects the occurrence of vector ticks in 2015. (**Figure 4**).

4.4.2 Other demographic factors associated with Bbsl seropositivity (**III**)

In addition to the collection year and area of the sample, sex and age of the participants were significantly associated with Bbsl seropositivity. An age-dependent increase in seroprevalence was observed, likely reflecting the cumulative exposure to Bbsl. Age-related seroprevalence has also been observed in other studies, with higher seroprevalence in older age groups as well as in children (Kugeler et al. 2022; Wilking and Stark 2014). In our study, however, we only had nine adolescents from the 1970s data and therefore did not specify children as their own group, instead, the youngest age group comprised individuals under 40 years, which should be considered a limitation of our study. Reasons for age-specific seroprevalence are unknown but may relate to behavioural differences, such as outdoor activities, healthcare-seeking behaviour, or the ability to notice and avoid ticks, as well as age-related immunological differences. Even though the concentration of antibodies has been shown to decline after antibiotic treatment (Marangoni et al. 2006; Pietikäinen et al. 2022), some antibodies may remain elevated for years after acute infection, even despite successful treatment (Kalish et al. 2001). Encounters with ticks and Bbsl accumulate with age (Dehnert et al. 2012), which most likely affects the observed higher seroprevalence in older people. Moreover, 50 years ago seroprevalence was particularly high among people who were at least 50 years old, whereas in later study years the seroprevalence peaked among people who were at least 70 years old. Reduced cumulative exposure to Bbsl may be related to increasing life expectancy, improving health among aging people, and the overall decrease in seroprevalence. Since the 1990s, new LB infections have been systematically treated with antibiotics. As a result, overall seroprevalence has declined, and the peak in seropositivity is now observed among the oldest age group.

Our results also showed that men had a higher probability of being seropositive than females. Interestingly, while some European studies are in accordance with our results, showing higher seroprevalence in males than in females (van Beek et al. 2018; Cuellar et al. 2020; Hjetland et al. 2014; Johansson et al. 2017), many LB incidence studies have found females to have a higher incidence rate than males, especially among EM patients (Bennet, Stjernberg, and Berglund 2007; Fülöp and Poggensee 2008; Sajanti et al. 2017; Stanek and Strle 2022). The contradiction between seroprevalence and incidence rates in Europe may reflect gender-associated behavioural differences in healthcare seeking or genetic differences in immune response. Females may be more likely to notice the early signs of LB, such as EM, and seek healthcare services already in the early phase of infection. As a result, females may be less likely to develop the disseminated phase of LB compared to males. Biological or sociological explanations for this contradiction have not yet been identified (Bennet et al. 2007; Rebman, Soloski, and Aucott 2015).

Bbsl seropositivity was not found to be statistically associated with any of the studied health-related background information after adjusting for demographic factors. Previous study noticed that in 1970 in Finland, self-reported perception of feeling unhealthy, previous heart failure and heart valvular disease were associated with Bbsl seropositivity (Cuellar et al. 2020). One of the reasons for not finding significant correlations with any of the health-related questions in our study might be the small number of seropositive individuals within these subgroups. In 2017, over 90% of participants reported at least a moderate health, while only about 60% of the participants reported at least moderate health in 1970. The most often significantly correlated factors with health-related questions were age of the participant and the collection year. Moreover, as Bbsl seropositivity reflects past exposure rather than ongoing disease, this finding is not surprising. Nevertheless, our results are consistent with findings from Norway, where no association between Bbsl seropositivity and subjective health complaints were found (Hjetland et al. 2015).

5 Conclusions

Tick research has grown significantly in Finland in the last decade. One of the first major advances in understanding tick ecology in Finland was the mapping of the geographical distribution of two important tick species across the country (**I**). Study **I** updated the nationwide distribution map for *I. ricinus*, replacing the outdated map from the late 1950s (Öhman 1961). In addition, the nationwide distribution of *I. persulcatus* was studied for the first time, and *I. persulcatus* was found to be much more common in Finland than previously thought, even appearing to dominate in certain areas of the country. Studies **I** and **II** confirmed that both tick species affecting humans in Finland are now widely abundant in the southern half of the country and the range of the ticks has shifted northwards during the past few decades, along the coast of Bothnian Bay.

Study **II** showed that the highest prevalence of infected ticks was in the *I. ricinus*-dominated area in southern Finland. However, the highest infection rates for both species were in the areas of their dominance, either in south for *I. ricinus* or north for *I. persulcatus*. The overall prevalence and diversity of different pathogens were higher in *I. ricinus* samples and it was more often co-infected than *I. persulcatus*. However, the prevalence of the two pathogens causing the most important TBDs for humans in Finland, Bbsl and TBEV, were both higher in *I. persulcatus*. The overall prevalence of Bbsl in Finland was 16.9%, and the prevalence of TBEV was 1.6%. Moreover, Studies **I** and **II** revealed the presence of some rare and potentially dangerous pathogens occurring in Finnish ticks.

While Studies **I** and **II** showed that the distributional area of ticks in Finland has increased during the last 60 years, with Bbsl being widely distributed across the country, Study **III** showed that the seroprevalence of Bbsl has been decreasing markedly among Finnish adult people over recent decades. Our results suggest that in today's Finland people develop or sustain a detectable IgG response against Bbsl less often than 50 years ago. Effective diagnostics, prompt antibiotic treatments, increased awareness and societal and economic changes are among the possible reasons explaining the decreasing Bbsl seroprevalence trend in Finland. Further, this study emphasises how continued surveillance and preventive measures, such as awareness campaigns, remain essential for managing risks of LB and other tick-borne diseases, while at the same time it provides new insights into current concerns regarding ticks.

Together, these results provide an important foundation for future research. Due to climate change, temperatures are expected to increase in Finland in the upcoming decades (Ruosteenoja and Jylhä 2021). As a result, the distribution of ticks may continue to shift, pathogens may spread into new areas, and new vector-borne pathogens may emerge. Although current tick data provide opportunities to search for novel pathogens and microbes that were not analysed here, a new collection of ticks is needed to detect changes over the past ten years in tick distribution, species composition, and pathogen occurrence. Moreover, experimental research is required to address certain important questions, such as how co-infections influence pathogen persistence and transmission between hosts and vectors. Regarding the observed changes in Bbsl seroprevalence, further studies, such as temporal studies in different risk groups and case-control studies on seroconversion and seroreversion rates, are needed to better understand the factors behind the observed decrease in Bbsl seroprevalence in Finland.

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