Geospatial risk analysis of disease vectors and vector-borne diseases in boreal and tropical landscapes

RUUT UUSITALO

ACADEMIC DISSERTATION
To be presented for public discussion with the permission of the Faculty of Science
of the University of Helsinki, in Festsal of Svenska Social- och kommunalhögskolan
(Snellmaninkatu 12), on June 7th, 2022 at 12 o’clock.

DEPARTMENT OF GEOSCIENCES AND GEOGRAPHY A101 / HELSINKI 2022

Cover photos: Ruut Uusitalo (front), Essi Rajamäki (back)

Author:
Ruut Uusitalo
Department of Geosciences and Geography
University of Helsinki, Finland

Supervised by:
Professor Petri Pellikka
Department of Geosciences and Geography
University of Helsinki, Finland

Professor Olli Vapalahti
Department of Virology
Department of Veterinary Biosciences
University of Helsinki, Finland

Doctor Mika Siljander
Department of Geosciences and Geography
University of Helsinki, Finland

Docent Eili Huhtamo
Department of Virology
Department of Veterinary Biosciences
University of Helsinki, Finland

Pre-examined by:
Assistant Professor Henrikki Tenkanen
Department of Built Environment
Aalto University, Finland

Senior scientist René Bødker
Animal Welfare and Disease Control
University of Copenhagen, Denmark

Opponent:
Associate Professor Janey P. Messina
Oxford School of Global and Area Studies
University of Oxford, The United Kingdom

Publisher:
Department of Geosciences and Geography
Faculty of Science
PO Box 64, FI-000140 University of Helsinki
Finland

ISSN-L 1798-7911
ISSN 1798-7911 (print)
ISBN 978-951-51-8137-4 (paperback)
ISBN 978-951-51-8138-1 (pdf)
https://ethesis.helsinki.fi
Unigrafia Helsinki 2022

Uusitalo R., 2022. *Geospatial risk analysis of disease vectors and vector-borne diseases in boreal and tropical landscapes.* Department of Geosciences and Geography A101.

Abstract

Emerging vector-borne infectious diseases pose one of the most significant global threats to human health. The outbreaks and burden of vector-borne infectious diseases are estimated to rise in the face of climate warming. Many emerging infectious diseases, such as COVID-19 and Ebola virus disease, are zoonoses; diseases caused by an agent transmitted between animals and humans, but these diseases are also followed by human-to-human transmission. In this thesis, we consider arthropod-borne infectious diseases, which are also zoonoses but in which humans are most commonly infected as dead-end hosts. Mosquitoes and ticks are vectors for numerous pathogens causing infectious diseases and are globally responsible for millions of human deaths each year. Most vector-borne diseases emerge in the subtropics and tropics, but endemic diseases are present also in northern latitudes. Due to climate warming, numbers of disease cases, and disease severity and also variety are expected to increase especially in Northern Hemisphere which become more suitable for vectors to spread. To avoid costs from the loss of human lives or money, there is a strong need to assess impacts on vector species and their habitats. It is a global responsibility to focus on improving vector control strategies, and disease prevention, first, to “ensure healthy lives and promote well-being for all at all ages” (The United Nations’ Sustainable Development Goal 3), but also to understand that human health is closely connected to animal health and environment (One Health- approach). As such, it is vital to produce new information on vectors’ and vector-borne disease’ (VBD) distributions and the influential factors on their emergence, particularly, in understudied regions.

In this thesis, environmentally suitable areas for the mosquito and tick species of medical importance in boreal and tropical landscapes, and the risk areas for two endemic VBDs in Finland were identified for the first time. We utilized climate, vegetation, host and vector data known to affect emergence of these vectors and VBDs at varying spatial scales. To our knowledge, this is the first species distribution modelling (SDM) study on vector species which uses good quality host data, and there are only a handful of earlier studies which included suitability data of vectors to predict VBD occurrence. We used SDM approach with a suite of predictive modelling techniques in two different platforms to explore correlations in species-host-disease-environment relationships and to predict spatial patterns of vector distributions and VBD risk in Finland, and in Kenya. Although SDM approaches are widely used by international and national health agencies such as European Centre for Disease Prevention and Control (ECDC), Centers for Disease Control and Prevention (CDC) and World Health Organization (WHO) in their vector control strategy and disease prevention programs, it is a new study approach in Finland with no earlier research. In tropical regions, including Kenya, where the need for vector control and disease prevention is highest, rural regions, particularly, remain understudied.

Using data on mosquito collections in the Taita Hills region in Kenya, we found that *Stegomyia* (*St., Aedes*) and *Culex* (*Cx.*) genera, of which species are vectors of many significant pathogens in the tropics, are widely distributed across the region, both in villages and rural areas with rich and sparse vegetation. In Finland, we identified high-risk areas for tick-borne-encephalitis (TBE), one of the most severe endemic infectious disease in the country, based on environmental and host data, and under current and future climate. Future climate forecasts indicated a wider geographical extent of TBE risk especially in southern and western coast, and southern Lapland. We also identified environmentally suitable areas for the potential SINV vectors *Aedes* (*Ae.*) *cinereus/geminus*, *Cx. pipiens/torrentium* and *Culiseta* (*Cs.*) *morsitans* in Finland, and estimated the risk areas for SINV infections on environmental, host and produced habitat suitability data on vectors. Municipalities with an increased risk for SINV infections were characterized by high environmental suitability for *Ae. cinereus/ geminus*, high densities of black grouse, capercaillie and hazel grouse, a high proportion of mixed forest in peatlands, and a high number of lakes. The risk of transmission was predicted to be greatest in eastern and central Finland, along the western coast up to southern Lapland in latitudes between 61–64°N. Two tick species; *Ixodes (I.) ricinus* and *Ixodes (I.) persulcatus* are responsible of transmitting TBE virus (TBEV) in Finland, and we estimated their distributions utilizing historical data, and newly collected ticks, of which we also screened pathogens TBEV and *Borrelia burgdorferi* sensu lato (b.s.l.). In these ticks, we found none positive for TBEV, but ≈ 47 % of the tick pools were positive for *Borrelia* b.s.l. High suitability areas for *I. ricinus* occurred throughout southern and central Finland up to Central Ostrobothnia (64°N), excluding the narrow areas in Ostrobothnia and Pirkanmaa. For *I. persulcatus*, the regions northwards from Ostrobothnia along the northern coast up to southern Lapland (66°N), Kainuu, North Savo, North Karelia, and areas in Pirkanmaa and Päijät-Häme were estimated to be suitable areas. Based on the predictions, locations with higher air temperature, higher relative humidity, higher precipitation sum and middle infrared reflectance (MIR) levels, and higher densities of white-tailed deer, European hare and red fox were suitable for *I. ricinus*. For *I. persulcatus*, higher mean precipitation, higher densities of white-tailed deer, roe deer and mountain hare indicated higher probability of occurrence.

Together, these results have implications for improving knowledge on disease prevention, applying geographic information systems (GIS) and SDM approaches for identifying risk areas and environmental determinants, optimizing the use of limited resources for mitigation strategies, and improving public health outcomes. This data is vital for better understanding of the current and future threats, and will help to find facts which assist the authorities in decision-making on correct and effective actions. The results can be applied to other regions located in similar environmental conditions to study regions. Within this work, we also created a framework in which multidisciplinary and multi-organizational data were combined to the same database. With the produced data, we researchers can prioritize the research topics and funding to correct targets and actions in future studies.

During the ongoing and following decades, further actions and research are needed to combat new emergences of vectors and VBDs. Vector surveillance, vector distribution studies in space and time, and mapping risks of VBDs under current and future climate, are essential to gain deeper insights into the spatial nature of recent and future global threats for which we have a shared responsibility to combat.

Abstract in Finnish

Uhkaavat vektorivälitteiset tartuntataudit ovat yksi suurimmista globaaleista uhkakuvista ihmisen terveydelle. Vektorivälitteisten tartuntatautien aiheuttaman taakan odotetaan lisääntyvän voimakkaasti ilmastonmuutoksen seurauksena. Monet uhkaavat tartuntataudit, kuten COVID-19 ja ebola, ovat alkujaan eläimistä ihmisiin tarttuvia tauteja, zoonooseja, jotka kykenevät edelleen siirtymään ihmisestä toiseen. Tässä työssä käsitellään niveljalkaisvälitteisiä infektiotauteja, jotka ovat myös zoonooseja, mutta joissa ihminen on useimmiten taudinaiheuttajan leviämisen kannalta umpikuja. Hyttyset ja puutiaiset ovat välittäjiä monille taudinaiheuttajille ja ovat vastuussa miljoonien ihmisten kuolemista vuosittain. Useimmat vektorivälitteiset tartuntataudit ilmaantuvat subtrooppisilla ja trooppisilla alueilla, mutta endeemisiä tartuntatauteja on aina esiintynyt myös pohjoisilla leveysasteilla. Tartuntatautilukujen ja vakavien tartuntatautien odotetaan lisääntyvän ilmaston lämpenemisen vaikutuksesta myös pohjoisella pallonpuoliskolla, jossa alueet tulevat suotuisimmiksi monien vektorilajien leviämiselle. Jotta ihmisten ja talouden menetyksistä maksettava hinta olisi minimoitavissa, tulee meidän arvioida nykytilannetta ja tulevia ilmaston lämpenemisestä johtuvia vaikutuksia vektorilajeihin ja niiden elinympäristöihin. Meillä on globaali vastuu keskittyä tartuntatauteja välittävien lajien ohjaus- ja lieventämisstrategioiden kehittämiseen sekä tartuntatautien ehkäisyyn, ei vain jotta ”kaikenikäisille taataan terveellinen elämä ja hyvinvointi” (YK:n kestävän kehityksen tavoite 3), mutta myös ymmärtääksemme, että ihmisen terveys on läheisesti yhteydessä eläinten terveyteen ja ympäristöön (One Health- näkökulma). Siksi on tärkeää tuottaa uutta tietoa vektorilajien ja vektorivälitteisten tautien levinneisyydestä ja näiden ilmaantumiseen vaikuttavista tekijöistä erityisesti alueilla, joissa aiempi tutkimus on vähäistä.

Tässä työssä lääketieteellisesti merkittävien hyttys- ja puutiaislajien ympäristöllisesti soveltuvia alueita boreaalisella ja trooppisella alueella sekä kahden endeemisen vektorivälitteisen tartuntataudin riskialueita Suomessa arvioitiin ensimmäistä kertaa. Hyödynsimme ilmasto-, kasvillisuus-, isäntäeläin- ja vektorilajiaineistoa, joiden tiedetään vaikuttaneen kyseisten vektorilajien ja vektorivälitteisten infektiotautien ilmaantumiseen eri spatiaalisilla mittakaavoilla. Tietääksemme tämä työ on ensimmäinen vektorilajilevinneisyyteen liittyvä tutkimus, jossa hyödynnetään korkealaatuista isäntäeläinaineistoa. Lisäksi vain muutama aiempi tutkimus on sisällyttänyt vektorilajilevinneisyyden yhtenä muuttujana vektorivälitteisen taudin riskimallinnuksessa. Käytimme lajilevinneisyysmallinnusmenetelmää ja useaa ennustemallinnustekniikkaa kahdella eri mallinnusalustalla vektori-isäntä-tauti-ympäristövälisten suhteiden tutkimiseen. Vaikka kansainväliset ja kansalliset terveysjärjestöt, kuten Euroopan tautienehkäisy- ja -valvontakeskus (ECDC), Yhdysvaltain tautikeskus (CDC) sekä Maailman terveysjärjestö (WHO) käyttävät laajasti lajilevinneisyysmallinnusta vektorivalvonta- ja tartuntatautien ehkäisemisohjelmissaan, lajilevinneisyysmallinnuksen ja terveyskysymysten yhdistäminen on uusi lähestymistapa Suomessa ilman aiempaa tutkimusta. Trooppisilla alueilla, kuten Keniassa, jossa tarve vektorivalvontaan ja tautien ehkäisemiseen on suurin, erityisesti kaukaisimmat maaseutualueet pysyvät tutkimattomina.

Taita Hills- alueella Keniassa keräämäämme hyttysaineistoa hyödyntäen havaitsimme, että *Stegomyia-* (*St.*, *Aedes*) ja *Culex-* hyttyssuvut, joiden lajit ovat vektoreita monille merkittäville taudinaiheuttajille tropiikissa, ovat laajasti levittäytyneet biodiversiteetiltään monipuolisen Taita Hillsin alueelle. *Stegomyia-* ja *Culex*-hyttysten arvioitiin esiintyvän niin vuoristoisilla maaseutualueilla kuin alangon kylissä runsaan ja harvan kasvillisuuden peittämil-

lä alueilla. Tässä työssä tunnistimme myös puutiaisaivokuumetulehduksen, yhden vakavimman Suomessa esiintyvän infektiotaudin, riskialueita ympäristö- ja isäntälajiaineistoon sekä nykyisen ja tulevaisuuden ilmastoaineistoon pohjautuen. Tulevaisuuden ilmastoon pohjautuvat riskimallinnukset osoittivat maantieteellisesti laajemman puutiaisaivokuumetulehdusriskin esiintyvän erityisesti etelä- ja länsirannikolla sekä Etelä-Lapissa. Tunnistimme myös ympäristön kannalta soveltuvia alueita mahdollisille Sindbis- viruksen välittäjinä toimiville hyttyslajeille *Aedes* (*Ae.*) *cinereus*/*geminukselle*, *Culex* (*Cx.*) *pipiens/torrentiumille* sekä *Culiseta* (*Cs.*) *morsitansille*, sekä arvioimme sindbis-virusinfektion riskialueita. Korkea elinympäristön soveltuvuus *Ae. cinereus/geminus*-hyttyslajille, korkeat teeri-, metso- ja pyytiheydet, korkea sekametsien osuus sekä järvien korkea lukumäärä kunnissa olivat yhteydessä korkeaan Sindbis-viruksen aiheuttamaan infektioriskiin. Tartuntariskin ennustettiin olevan suurin Itä- ja Keski-Suomessa, sekä länsirannikolla ulottuen eteläiseen Lappiin saakka 61–64°N leveysasteille asti. Arvioimme myös kahden, muun muassa puutiaisaivokuumetulehdusta levittävän *Ixodes (I.) ricinus*- ja *I. persulcatus*- puutiaislajin levinneisyyttä Suomessa hyödyntäen historiallista aineistoa ja uutta, vuoden 2021 kesällä keräämäämme puutiaisaineistoa, josta myös seuloimme TBEV- ja *Borrelia burgdorferi* sensu lato- taudinaiheuttajia. Kerätyistä puutiaisista ei löytynyt TBE- virusta, mutta n. 47 % puutiaispooleista seulottiin *Borrelia* b.s.l.-positiivisiksi. Alueet, joissa elinympäristöjen soveltuvuus *I. ricinus* -lajille arvioitiin olevan suuri, sijaitsivat Etelä- ja Keski-Suomessa ulottuen Keski-Pohjanmaan maakuntaan saakka (64°N). Ennusteiden mukaan korkea ilmalämpötila, korkea suhteellinen ilmankosteus ja sademäärän summa, kasvillisuuden runsautta kuvaava keski-infrapunasäteily sekä korkeat valkohäntäpeura-, rusakko- ja kettutiheydet sijainneissa osoittivat korkeaa soveltuvuutta *I. ricinus*- lajille. *Ixodes persulcatukselle* sen sijaan alueet Pohjanmaalta rannikkoa pitkin Etelä-Lappiin saakka (66°N), Kainuun, Pohjois-Savon ja Pohjois-Karjalan maakunnat, sekä kapeammat kaistaleet Pirkanmaalla ja Päijät-Hämeessä arveltiin soveltuvan lajille elinympäristöiltään. Korkeampi sademäärä *I. persulcatuksen* aktiivisena aikana, sekä korkeammat valkohäntäpeura-, metsäkauris- ja metsäjänistiheydet viittasivat lajin korkeampaan esiintymistodennäköisyyteen.

Tämän työn tulokset kehittävät tietoa vektorivälitteisten tartuntatautien ehkäisyä varten, auttavat optimoimaan lieventämisstrategioihin käytettyjä rajoitettuja resursseja ja parantamaan siten kansanterveydellisiä tuloksia. Tuotettu aineisto on tärkeä, jotta ymmärrämme nykyhetken ja tulevaisuuden terveyteemme kohdistuneet uhat. Se auttaa kansanterveysviranomaisia ja asiantuntijoita päätöksenteossa kohdistamaan toimintoja ja valvontatoimenpiteitä oikein ja tehokkaasti. Työn tuloksia voidaan myös soveltaa muihin ympäristöolosuhteiltaan tutkimusalueita vastaaviin maailman alueisiin. Työssä tuotettu tieto auttaa meitä tutkijoita priorisoimaan tutkimusaiheita ja kohdistamaan rahoitusta oikeisiin tavoitteisiin ja toimiin tulevissa tutkimuksissa.

Meneillään olevan vuosikymmenen ja tulevien vuosikymmenten aikana tarvitsemme lisää tutkimusta ja konkreettisia tekoja, jotta voimme taistella uusia vektorilajeja ja voimakkaasti lisääntyviä vektorivälitteisiä infektiotauteja vastaan. Vektorilajien valvonta, niiden levinneisyyden tutkiminen tilassa ja ajassa sekä vektorivälitteisten tautien kartoitus nyky- ja tulevaisuuden ilmastossa ovat oleellisia toimia, jotta voimme saavuttaa syvempiä oivalluksia nykyhetken ja tulevaisuuden globaaleista uhkakuvista, joista meillä on yhteinen vastuu.

Acknowledgements

This dissertation would not have been possible without the guidance, knowledge and support of a huge number of people. I am very thankful for supervisors who have given me advice; Dr. Mika Siljander, Doc. Eili Huhtamo, prof. Olli Vapalahti and prof. Petri Pellikka. This project has been an amazing journey which began from geography studies, continued by learning the methodologies of microbiology and deepening the knowledge of GIS and SDM techniques. I have had chance to participate to many interesting projects, e.g. mosquito-borne virus studies in Kenya, Italy and Finland, and SARS-CoV-2 studies during the ongoing pandemic. I want to give specific thanks to Dr. Essi Korhonen, who has taught me in the laboratory, always been patient to give advice without being my official supervisor. I also thank prof. Markku Löytönen, who acted as a thesis committee member in the committee meetings. To all the staff in the Departments of Virology, Geosciences and Geography, and Veterinary Biosciences, thank you.

I am also thankful for AVIA-GIS staff and especially Guy Hendrickx (CEO), who provided advice in tick and mosquito sampling, and enabled us to use new platforms for sampling and modelling. I want to thank all co-authors for their input during the manuscript preparations, and anonymous reviewers for the constructive comments. I would like to thank my family and friends who believed in me. I am very thankful for the support provided by the DENVI doctoral school and Tiina and Antti Herlin Foundation. I would like to thank members of VZRU and ECHOLAB research groups for great atmosphere. We have spent countless hours in the field with Lauri Kareinen, Joni Uusitalo, Maija Suvanto, Essi Korhonen and Giulia Faolotto from which I have the greatest of memories. Specifically, I want to thank previously mentioned people, all supervisors, Ravi Kant, Esa Pohjolainen, Roope Nykänen, Lauri Kirjalainen, Johanna Martikainen, Mira Utriainen and Sanna Mäki from your joyful presence during my PhD project.

In Helsinki, Finland May 2022, Ruut Uusitalo

Contents

List of original publications

This thesis is based on the following publications:

I Uusitalo, R., Siljander, M., Culverwell, C. L., Mutai, N., Forbes, K. M., Vapalahti, O., & P.K.E. Pellikka (2019). Predictive mapping of mosquito distribution based on environmental and anthropogenic factors in Taita Hills, Kenya. International Journal of Applied Earth Observation and Geoinformation, 76, 84–92. https://doi.org/10.1016/j.jag.2018.11.004.

II Uusitalo, R., Siljander, M., Dub, T., Sane, J., Sormunen, J., Pellikka, P., & O. Vapalahti (2020). Modelling habitat suitability of human tick-borne encephalitis (TBE) cases in Finland. Ticks and Tick-borne Diseases, 101457. ISSN 1877-959X. https://doi.org/10.1016/j.ttbdis.2020.101457.

III Uusitalo, R., Siljander, M., Culverwell, C. L., Hendrickx, G., Lindén, A., Dub, T., Aalto, J., Sane, J., Marsboom, C., Suvanto, M. T., Vajda, A., Gregow, H., Korhonen, E. M., Huhtamo, E., Pellikka, P. K.E. & O.Vapalahti (2021). Predicting spatial patterns of Sindbis virus (SINV) infection risk in Finland using vector, host and environmental data. International Journal of Environmental Research and Public Health, 18, 7064. https://doi.org/10.3390/ ijerph18137064.

IV Uusitalo, R., Siljander, M., Lindgren, A., Sormunen, J., Aalto, J., Hendrickx, G., Kallio, E., Vajda, A., Gregow, H., Henttonen, H., Marsboom, C., Korhonen, E.M., Sironen, T., Pellikka, P.K.E., O. Vapalahti (In Review). Predicting habitat suitability of *Ixodes ricinus* and *Ixodes persulcatus* ticks in Finland. In Review in Parasites&Vectors.

The publications are referred to in the text by their roman numerals.

Author contributions to the publications

	Article I	**Article II**	**Article III**	**Article IV**
Original idea	OV, PP	OV, JS, TD	OV, JS	RU, MS, OV
Literature review	RU	RU	RU	RU
Data collection and preparation	RU, CLC	TD, JS	RU, AL, CLC, TD	RU, MS, JJS, EK, TS, GH, HH,
Data analyses and modelling	RU, MS, CLC	RU, MS	RU, MS	RU, MS
Visualization	RU	RU	RU	RU
Writing- original draft	RU, CLC, KMF, MS	RU	RU	RU
Writing- review and editing	RU, CLC, KMF, MS, OV, PP	RU, MS, TD, JS, JJS, OV, PP	RU, MS, CLC, GH, AL, TD, JA, JS, CM, MTS, AV, HG, EMK, EH, PP, OV	RU, MS, AL, GH, JJS, CM, HH, JA, HG, EK, EMK, TS, AV, PP, OV

AL : Andreas Lindén

AV : Andrea Vajda

CLC : C. Lorna Culverwell

CM : Cedric Marsboom

EH : Eili Huhtamo

EK : Eva Kallio

EMK : Essi Korhonen

GH : Guy Hendrickx

HG : Hilppa Gregow

HH : Heikki Henttonen

JA : Juha Aalto

JJS : Jani Sormunen

JS : Jussi Sane

KMF : Kristian Forbes

MS : Mika Siljander

MTS : Maija Suvanto

NCM : Noah Mutai

OV : Olli Vapalahti

PP : Petri Pellikka

TD : Timothée Dub

TS : Tarja Sironen

Abbreviations

AUC	Area under the curve
ANN	Artificial neural networks
CTA	Classification tree analysis
DEM	Digital elevation model
EVI	Enhanced vegetation index
GAM	Generalized additive model
GBM	Generalized boosting model
GIS	Geographic information systems
GLM	Generalized linear model
GNSS	Global navigation satellite systems
HSM	Habitat suitability modelling
LST	Land surface temperature
MARS	Multiple adaptive regression splines
MAXENT	Maximum entropy approach
MBD	Mosquito-borne disease
MIR	Middle infrared reflectance
MODIS	Moderate resolution imaging spectroradiometer
NDVI	Normalized difference vegetation index
RCP	Representative concentration pathway
RF	Random forest
RH	Relative humidity
SA	Spatial autocorrelation
SDM	Species distribution model
SINV	Sindbis virus
TBD	Tick-borne disease
TBE	Tick-borne encephalitis
TWI	Topographic wetness index
TSS	True skill statistics
WNV	West Nile virus
VBD	Vector-borne disease
VBP	Vector-borne pathogen
VIF	Variance inflation factor

List of Figures

1 Introduction

1.1 Motivation

During the past two years we have faced the most severe global health crisis during the twenty-first century when COVID-19 pandemic hit across the globe causing over 6,000,000 deaths (by March 2022, WHO, 2022a) and global economic and societal crises. Before the COVID-19 pandemic - with a likely bat origin - similar health crises of zoonotic origin have occurred at smaller scale, such as the outbreaks of Ebola virus disease in West Africa in 2014–2016 (WHO, 2022b), mosquito-transmitted West Nile fever in the United States in 2002 (CDC 2002; Pealer et al., 2003; O´Leary et al., 2004) and Zika virus disease outbreak in Brazil in 2015–2016 (WHO, 2022c). To avoid this kind of global disasters, we should focus on more efficient control and prevention strategies of emergencies of disease vectors and pathogens around the globe because a number of zoonotic diseases are increasing (Caminade et al., 2019).

Mosquitoes (Diptera, *Culicidae*) are vectors for numerous pathogens, which are collectively responsible for millions of human deaths each year. In the tropical regions, including Kenya, the most common and recent mosquito-borne outbreaks are malaria, dengue fever, Zika virus disease, Rift Valley fever and chikungunya, causing a substantial health and economic burden. In Northern Europe, in Finland, the most prevalent mosquito-borne diseases (MBDs) are tularemia, caused by the bacteria *Francisella tularensis*, and Sindbis virus (SINV) infection, also called as Pogosta disease (NIDR, 2022). During 2021, an outbreak of Pogosta disease emerged with the highest numbers of diagnosed cases and incidence rates (N=566, 10.3/100.000) since 2002 (NIDR, 2022). In addition to mosquitoes, ticks are capable to transmit pathogens that can cause severe, sometimes fatal, human disease. In Finland, two dominant tick species; the castor bean tick, *Ixodes ricinus*, and the taiga tick, *Ixodes persulcatus*, are responsible for the transmission of Lyme borreliosis (LB), caused by the *Borrelia* bacterium, and tick-borne encephalitis (TBE), the most prevalent and severe tick-borne diseases (TBDs) in Europe.

Recently, the abundance of the two tick species and the numbers of diagnosed TBDs have increased. During 2021, 151 human TBE cases were diagnosed which is 60 cases more than in the previous year (ECDC, 2021a ; NIDR, 2022). In Finland, TBE, LB and Pogosta disease have been defined as the major risks to public health in changing climate and thus, increased prepadness, risk assessment, training and research are called (Ministry of Social Affairs and Health, 2021). Following the global trend, numbers of vector-borne diseases (VBDs), mainly caused by mosquitoes, have also increased in African continent, including in Kenya. African governments have recently endorsed the region´s first aggressive plan for vector control (WHO, 2019).

Since 1855, when Dr John Snow made his well-known work on mapping cholera clusters in London, geographic information systems (GIS) has been developed, and used to analyze the patterns of spatial distribution and risk factors, to identify, prevent and control diseases, and to improve the impact of public health interventions (WHO, 2022d). Using spatial analyses we can also determine e.g. a site of origin of outbreaks or pandemics, such as in a recent study, in which the Huanan Seafood Wholesale Market in Wuhan was identified as the epicenter of SARS-CoV-2 emergence using geographical clustering method (Worobey et al., 2022). Using GIS also support better public health planning and decision-making, and enables timely and reliable decisions that can save lives. Vector and environment interactions have been studied through species distribution models (SDM) especially in Europe, Asia and North America but also increasingly in African continent. In Finland, however, there are no earlier SDM studies on risk assessment of disease vectors and VBDs, although it is a broad study approach elsewhere (Nykiforuk & Flaman 2009; Cromley & McLafferty 2011; Purse & Golding 2015 ; Wang 2019). In contrast, in Kenya, several SDM studies on risk assessments of vectors and VBDs were conducted during last decade (Drake & Beier 2014; Ochieng et al., 2016; Sintayehu et al., 2020; Kimuyu 2021; Boitt et al., 2021). Nevertheless, none of them were conducted in the Taita Hills, in rural southeastern Kenya, despite of emerging VBDs (Masika et al., 2020, Masika et al., unpublished results). Taita Hills, is an ecologically diverse area with little previous mosquito research, characterized by strong variability in rainfall and a rapidly growing human population, offering good breeding sites for mosquitoes. The emergence of disease vectors and pathogens anywhere in the world are of a global concern, with a good example of recent outbreaks. As such, we have a shared responsibility to fight against the new emergencies.

1.2 Objectives

The major aim of this work, was to predict the habitat suitabilities of medically important species in Kenya and in Finland, and to identify disease risk areas of the significant VBDs in Finland. Furthermore, the objective was to determine the environmental and other factors driving the spatial patterns. More specifically, this thesis seeks answers to the following questions:

- How are the two mosquito genera; *Culex* and *Stegomyia* (*Aedes*) distributed to the Taita Hills region in Kenya (**Article I**) ?
- What are the risk areas of tick-borne encephalitis (TBE) in Finland in current and future climate conditions (**Article II**) ?
- What are the habitat suitabilities for Sindbis virus (SINV) vectors, and the risk areas of SINV infections in Finland? (**Article III**)
- What are the environmentally suitable areas for the castor bean tick *Ixodes ricinus* and the taiga tick *I. persulcatus* in Finland? (**Article IV**)

This thesis is a multidisciplinary project linked to the fields of geography, GIScience, environmental studies, climatology, virology, vector and host ecology, spatial epidemiology and public health in the broader context.

1.3 Background

1.3.1 Mosquitoes and ticks of medical importance in tropical and boreal regions

In Kenya, the mosquitoes which are responsible for a majority of mosquito-borne pathogens belong to genera *Aedes*, *Anopheles*, *Culex*, and *Mansonia* (Karungu et al., 2019). As such, two notable mosquito genera are *Culex* Linnaeus and *Stegomyia* (*Aedes*) Theobald (following the classification of Reinert et al., 2009). *Culex* is a large genus of mosquitoes, with 769 species in 26 subgenera (MTI, 2022a), accounting for 21.6% of all mosquito species worldwide (Fig. 1A). Species of *Culex* have an almost worldwide distribution from the tropics to cool temperate regions, but do not extend into extreme northern latitudes (MTI, 2022a). Subgenus *Culex* (*Culex*) contains many of the significant human vector species, including those transmitting West Nile virus (WNV), Rift Valley virus (RFV) and Japanese encephalitis virus (JEN, ECDC, 2014; MTI, 2022b). *Stegomyia* (*Aedes*) is a moderately

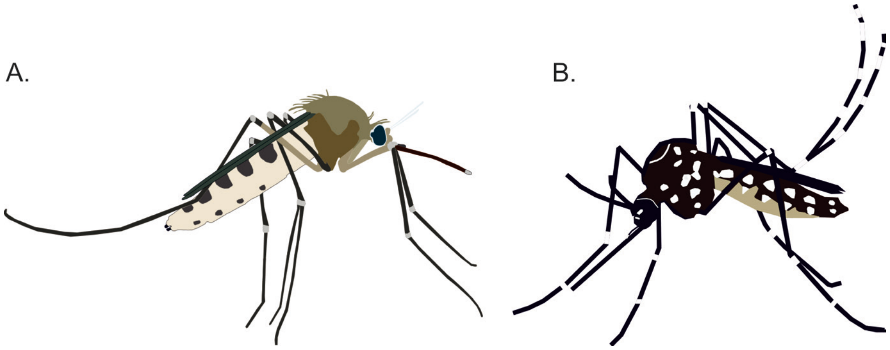

Fig. 1. (A) *Culex pipiens* on the left, and (B) *Stegomyia* (*Aedes*) *aegypti* on the right.

sized mosquito genus comprising 128 species, and distributed in the Afrotropical, Oriental and Australasian regions (Fig. 1B; MTI, 2022c). Following human dispersal, at least two species *St.* (*Ae.*) *aegypti* and *St.* (*Ae.*) *alpobicta*, are also present in Neotropical, Nearctic and Palearctic regions (Paupy et al., 2009; MTI, 2022c). Member species are competent vectors of yellow fever virus (YFV; Huang, 1986), dengue virus (DENV) serotypes 1-4, zika virus (ZIKV), and chikungunya virus (CHIKV), among others (Huang, 1990; MTI, 2022c).

In Finland, 43 mosquito species have been reported occur, of which 21 species are found to transmit one or more mosquito-borne pathogens causing human disease (Culverwell et al., 2021). These pathogens include the viruses such as Inkoo virus (INKV) (*Bunyaviridae*: Orthobunyavirus) (Brummer-Korvenkontio et al., 1973), Sindbis virus (SINV) (*Togaviridae*: Alphavirus) (Sane et al., 2012), Chatanga virus (CHATV) (*Bunyaviridae*: Orthobunyavirus) (Putkuri et al., 2014), and the bacterium *Francisella tularensis* causing tularemia (Jounio et al., 2010). *Culex pipiens*, *Cx. torrentium* Martini and *Cs. morsitans* Theobald and *Ae. cinereus* are known to be associated with SINV transmission (Francy et al., 1989; Turell et al., 1990; Lundström et al., 2001; Hubalék 2008; Turell 2012; Hesson et al., 2015). In recent studies, SINV genotype I (SINV-I) has also been detected in or isolated from *Ochlerotatus* species (Sane et al., 2012; Tingström et al., 2016; Korhonen et al., 2020) and *Aedes rossicus* Dolbeskin, Gorichaja and Mitrofanova (Lundström et al., 2019).

In addition to mosquitoes, ticks are capable of transmitting notable VBDs in Northern Europe. Finland lies in the zone where the geographical distributions of two tick species; castor bean tick *Ixodes ricinus* and the taiga tick *I. persulcatus*, overlap. To develop to the next life stage, *Ixodes* ticks need a blood-meal from suitable host, which varies depending on the life stage, from small vertebrate hosts to large-sized mammals (Fig. 2). *Ixodes ricinus* is predominant in southern Finland while *I. persulcatus* prevails typically in more northern latitudes, although *I. persulcatus* may be spreading southwards (Laaksonen et al., 2017; Zakham et al., 2021). Both tick species are capable to transmit pathogens such as *Borrelia burgdorferi* causing Lyme borreliosis (LB) (Movila et al., 2014; Michelet et al., 2014), *Borrelia miyamotoi* causing tick-borne relapsing fever (Platonov et al., 2011), genus *Rickettsia*, obligate intracellular bacteria causing spotted fever and tick-borne rickettsioses (Parola et al., 2013), *Anaplasma phagocytophilum* causing human granulocytic anaplasmosis (Rar et al., 2011; Stuen et al., 2013), and TBEV causing tick-borne encephalitis (Jääskeläinen et al., 2006; Laaksonen et al., 2018).

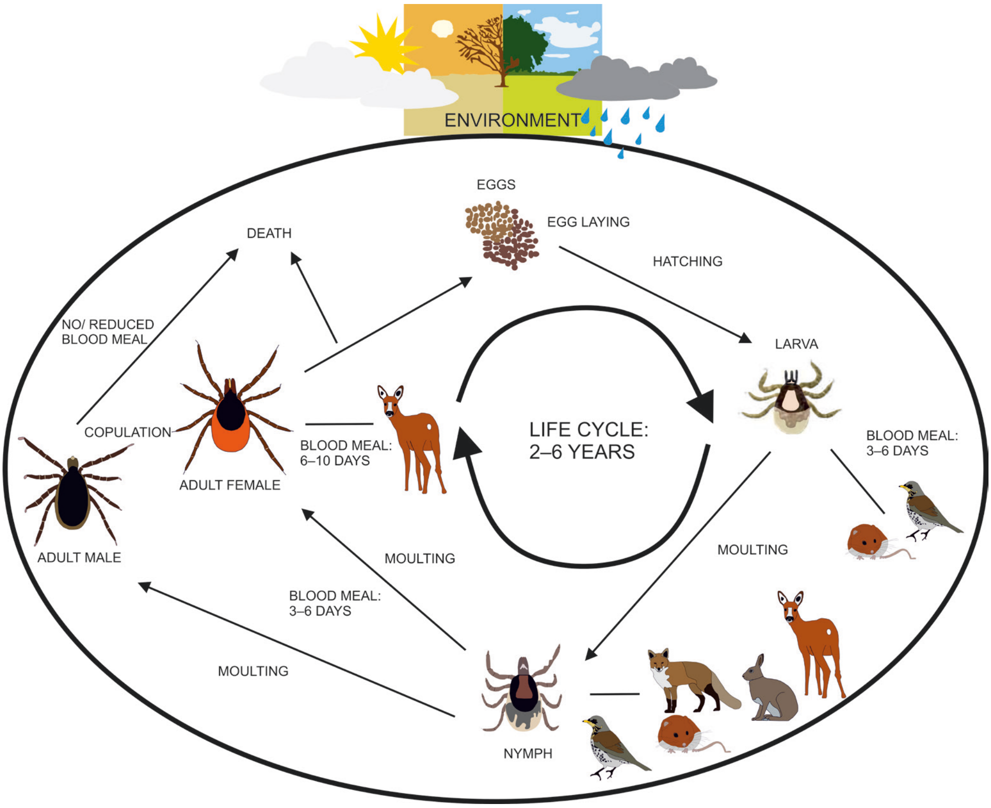

Fig. 2. The life cycle of *Ixodes* ticks.

1.3.2 Emerging mosquito- and tick-borne diseases in Finland

Pogosta disease and TBE are among the most common VBDs in Finland (NIDR, 2021). Pogosta disease is the result of SINV infection in humans, most of the cases occurring in August and September (Sane et al., 2010). The estimated seroprevalence of SINV was 5.2% between 1995–2003 (Kurkela et al., 2005; 2007). SINV infection manifests with fever, rash, headache, myalgia, arthralgia, nausea, conjunctivitis and pharyngitis (Espmark & Niklasson 1984; Turunen et al., 1998; Kurkela et al., 2005). After the acute phase, long-lasting joint pain and tendon insertions occur in 25% of infected individuals (Laine et al., 2004; Kurkela et al., 2005; 2008; Hubalék 2008). As no vaccine or specific etiologic treatment is available, clinical care is strictly symptomatic (ECDC, 2021b). SINV infections are notifiable in Australia and in some European, Asian and African countries (Go et al., 2014), but despite widespread circulation, human outbreaks associated with SINV-I, have only been documented in Northern Europe and South Africa (Jupp et al., 1986; Lundström et al., 1991; Brummer-Korvenkontio et al., 2002). In Finland, outbreaks of Pogosta disease have been strongly concentrated in eastern and central parts of the country (Kurkela et al., 2005). SINV circulates in enzootic or epidemic transmission cycles (Fig 3.).

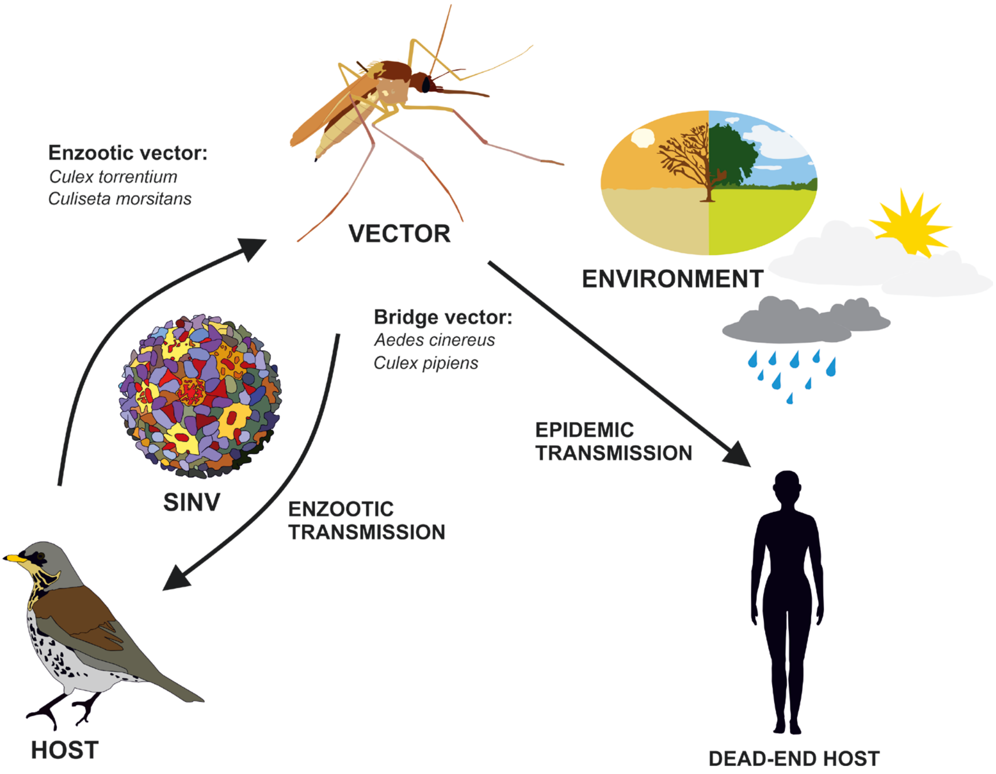

Fig. 3. The transmission cycle of SINV.

In enzootic cycles, SINV spreads between birds, which act as amplifying hosts that are able to develop enough viremia so that vector species will probably come infectious. The known bird hosts include resident grouse or migratory birds, mainly passerines, such as trushes (*Turdidae*) (Lundström et al., 2001; Brummer-Korvenkontio et al., 2002; Kurkela et al., 2008). Ornitophilic mosquitoes; *Cx. torrentium* and *Cs. morsitans*, maintain the virus in enzootic cycles (Lundström et al., 2001; Hesson et al., 2015). *Aedes cinereus* and *Cx. pipiens* are bridge vectors that transmit the virus from birds to humans (Francy et al., 1989; Turell et al., 1990; Hubálek 2008; Turell 2012). Specifically, high summer temperatures and thick snow layer in Finland during the spring (Jalava et al., 2013), and higher precipitation (Jalava et al., 2013; Uejio et al., 2012) both in Finland and South Africa, where the disease is endemic, were found to be associated with SINV transmission.

TBE, caused by the TBE virus (TBEV), typically induces a febrile disease, and in one third of cases, the initial illness may be followed by fever, meningitis, or meningoencephalitis (ECDC, 2021c). Neurological sequelae, including paresis, may occur, sometimes leading to death (1–2% of cases) (WHO, 2022e). TBE occurs focally in endemic areas across large regions of the temperate and boreal forest regions of Europe and Asia (Woolhose et al., 2001; Charrel et al., 2004; Lindqvist & Vapalahti, 2008; ECDC, 2021d). In Finland, most cases occur between June and September, and the geographical distribution of cases is mainly focused on coastal and southern Finland including the Åland Islands. However, the geographical distribution of cases has expanded during the past decade (NIDR, 2022). In 2006, TBE cases were diagnosed in 7/21 health care districts, while in 2021, diagnoses were made in 17/21 health care districts (NIDR, 2022).

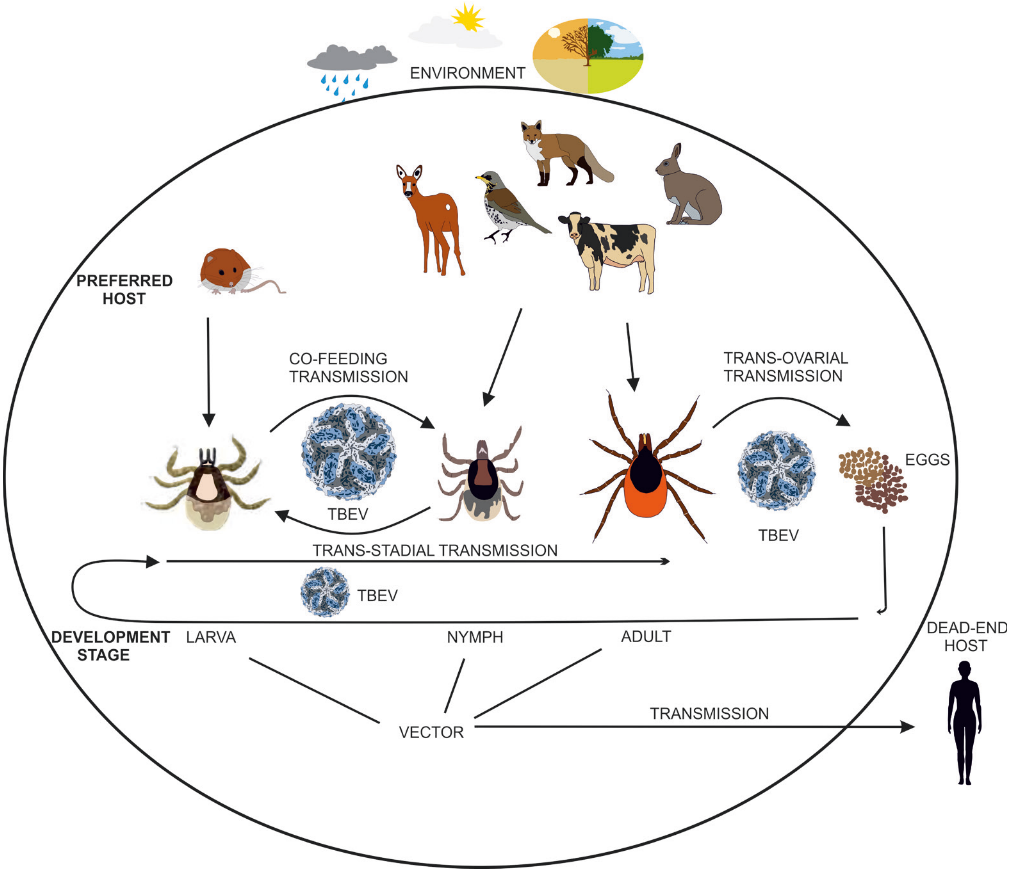

Fig. 4 The transmission cycle of TBEV.

Within the tick population, TBEV is maintained through trans-ovarial or trans-stadial transmission (Fig. 4.). In trans-ovarial transmission, an infected tick passes the virus to its offspring, and in trans-stadial transmission, the infected tick carries the virus through all four development stages (Alekseev & Chunikhin, 1990; Mischelitch et al., 2019). Furthermore, TBEV is maintained in transmission cycles, in which infected ticks pass the virus to a variety of small and large vertebrate host animals, as well as humans. Each development stage prefers for certain animal groups as their host reservoirs. Small vertebrates, such as rodents, are able to harbor the virus for a long time and transmit it to their offspring (Bakhvalova et al., 2009; Mischelitch et al., 2019). Virus transmission can also occur by co-feeding, when uninfected ticks feed simultaneously close to infected ticks (Labuda et al., 1993; Randolph et al., 1996). The natural cycles of TBEV are sensitive to various environmental and ecological factors, such as climate (Semenza & Menne 2009; Daniel et al., 2015; Brabec et al., 2017), microclimate (Randolph et al., 2001), and densities of tick hosts (Heyman et al., 2010; Brugger et al., 2017).

1.3.3 Impacts of environment and climate change on vector and VBD distributions

Arthropods are especially sensitive to changes in environmental conditions. Climatic conditions and environment influence the habitat suitability, vector activity and the rate of vector development (Reiter 2001; Hubálek 2008; Gray et al., 2009; Brady et al., 2013; ECDC, 2021e). The replication of pathogens within vectors occurs faster at warm temperatures (Reisen et al., 2007; 2014). Generally, warm temperatures and increased rainfall positively affect vector densities (Gray et al., 2009; Tian et al., 2015; Poh et al., 2019) although extreme high temperatures combined with decreased rainfall may reduce mosquito and tick populations (Apanaskevich 1991; Morin et al., 2013; Brown et al., 2014). The environmental conditions differ significantly in tropical and boreal regions and thus, vector responses to different climatic conditions vary in Finland and in Kenya. In Northern Europe, the duration of mosquito development is influenced by snow cover, as flooding after snow melt creates suitable water sources for mosquitoes to develop (Becket et al., 2010). Snow cover also influence in tick development acting as an insulator to protect nymphal ticks and larvae from freezing (Vollack et al., 2017). Relative humidity (RH), particularly long periods of low RH, affect tick activity and tick survival (Gray et al., 1998; Daniel et al., 2015). Human behaviour and human population density are factors influencing in an exposure to tick or mosquito bites, as people who spend more time outdoors are more likely to get mosquito or tick bite than others.

Global locations are influenced by the climate change in various ways depending on their geographic position. Air temperatures over equatorial eastern Africa are expected to increase between 2–5°C by the end of the 21st century (Elshamy et al., 2009; Anyah & Qiu, 2012). Also, wetter climate with more intense wet seasons and less severe droughts are estimated to occur over eastern Africa (Moise & Hudson, 2008; Shongwe et al., 2011). In Northern Europe in Finland, the annual mean temperature has already risen over 2°C since the middle of the 19th century (FMI, 2022a), and is expected to rise 3–6°C by the end of 21st century, which is faster than the global average (Ruosteenoja & Kämäräinen 2016; Ruosteenoja et al., 2016; Ruosteenoja 2021). At least following impacts on weather are estimated to occur during the ongoing century; rising temperatures especially during winter (Ruosteenoja 2013; 2021; Ruosteenoja et al., 2016), more common and longer heatwaves, longer and warmer growing season (FMI, 2011; Jylhä et al., 2012; Ruosteenoja et al., 2016), increased precipitation, more intense heavy rains (Jylhä et al., 2012; Ruosteenoja 2013), shorter snow cover period, and reduced amount of soil frost (FMI, 2011; Jylhä et al., 2012).

1.3.4 Species distribution modelling (SDM)

Across the globe, GIS analysis and SDM on vector species and VBDs are an active area of research due to their benefits for prevention and control of VBDs (Eisen & Eisen 2011; WHO, 2018). SDMs (Guisan & Thuiller, 2005), also called as ecological niche modeling (ENM) or habitat suitability modelling (HSM), is used to interpolate geographical information about where a species occurs, to predict suitable conditions for species survival, to project potential distributions of species or disease at another point in time, and to predict the impacts of environmental change on the occurrence of species or disease (Franklin et al., 2010). Niche (i.e.) habitat suitability refers to condition, when the combination of abiotic environmental variables at the site is included in the environmental condition that a species needs to survive and reproduce (Hutchinson, 1987; 1992). Here, we conduct SDM research on medically important mosquito and tick species in selected tropical and boreal regions, and on two endemic zoonosis in Finland for the first time.

2 Material and Methods

2.1 Study areas

Studies presented in this thesis were conducted in Kenya, and in Finland (Figs. 5–6). More specifically, studies focused on 1) the Taita Hills, southeastern Kenya (**Article I**), and 2) on parts of Finland or the whole country (**Articles II–IV**). Kenya (1° 00’ N, 38° 00’ E) is among the most affected tropical countries with the MBDs (Karungu et al., 2019). The Taita Hills is a range of peaks varying in altitude between 600–2200 m a.s.l. in Taita–Taveta county in southeastern Kenya (Erdogan et al., 2011). There are two dry and wet seasons in Kenya; the long rains occur between March/April–May/June, and the short rains occur between October–November/December (Kaplan et al., 1976). The Taita Hills region receives on average 1330–1910 mm of precipitation annually, which contributes to the formation of suitable mosquito breeding habitats (Erdogan et al., 2011).

Finland (64° 00’ N, 26° 00’ E) is located in Northern Europe between Sweden and Russia. Finland has so-called intermediate climate, where characteristics of both a maritime and a continental climate are combined (FMI, 2021a). The annual mean temperature varies from 5°C in southwestern Finland to -2°C in northern Lapland (FMI, 2021a). The annual amount of precipitation in Finland varies between 500–650 mm (FMI, 2021a). The average length of the growing season is 180 days in the southwestern archipelago, 140–175 days elsewhere in southern and central Finland, and 100–140 days in Lapland (FMI, 2021a). Finland lies in the zone of boreal forests which cover 75% of the land area (Turunen 2008; Ministry of Agriculture and Forestry of Finland, 2022). In addition to forest area, bogs cover 28% of the land area (Turunen 2008), and water 10% of the total area of Finland (Statistics Finland, 2021).

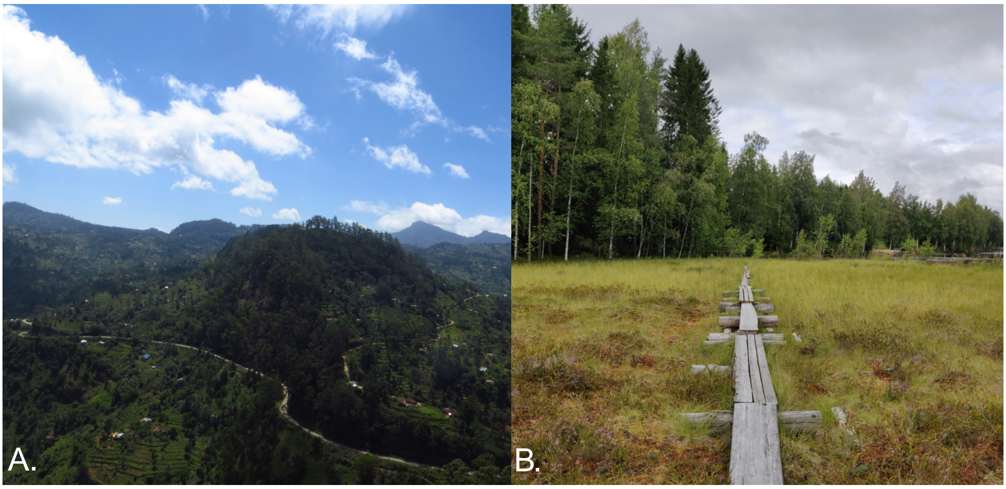

Fig. 5 Taita hills, Kenya is largely covered by afromontane cloud forests with varying altitude and precipitation (A). In Finland, bogs are important habitats for many mosquito species, and cover 28% of the land area (B).

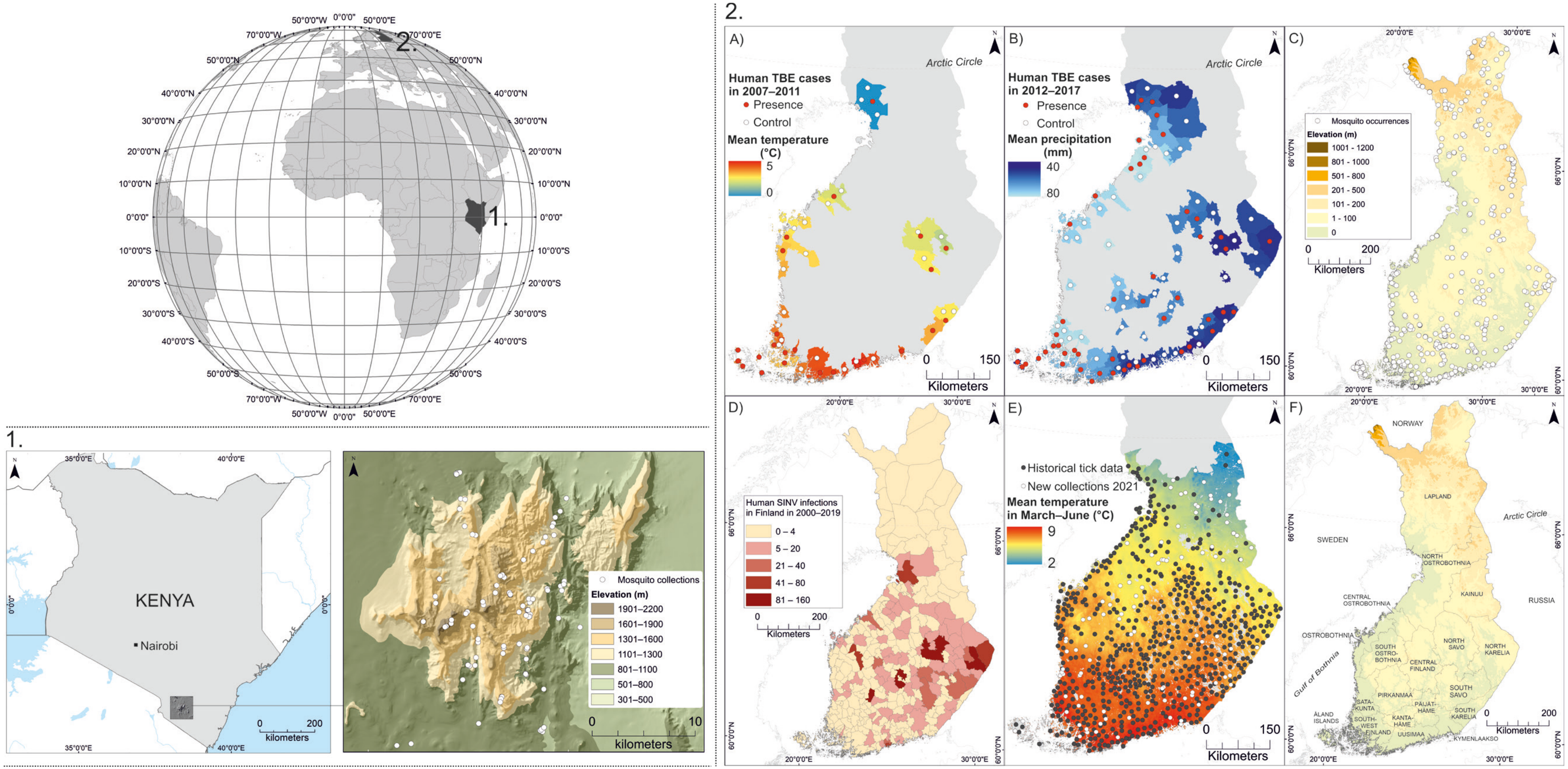

Fig. 6 The study areas of publications. Panel 1 shows mosquito collections and geographical settings in the Taita Hills, Kenya (**Article I**). Panel 2A and B indicate two study periods with TBE and control municipalities (**Article II**). Panel C and D include mosquito occurrences and human SINV infection cases used in **Article III**. Panel E shows historical tick data and d new collections in 2021. Panel F is a reference map presenting regions in Finland mentioned in this work.

2.2 Data

Data for this thesis consisted of response data including mosquito, tick and patient data, and covariates including environmental, host, distance and other data. The data properties of response variables and covariates are shown in separate tables (Tables 1–6.). Within this work and VECLIMIT consortium in Climate Change and Health- project funded by Academy of Finland, we also created a framework in which multidisciplinary and multi-organizational data presented herein were brought into a same database with same geographical units.

2.2.1 Mosquito data

Mosquito collection data were used in **Articles I** and **III**. Data for the **Article I** were collected by me at over 122 locations in the Taita Hills region in Kenya in January–March 2016. Stratified sampling scheme was applied based on the road network in which each main road from the lowlands to the highest reachable locations was used to collect mosquitoes on 100 m elevation intervals. Collection locations and sub-locations were mainly around human dwellings close to roads, but also in forest fragments and in croplands. Adults were collected using commercially available Prokopack aspirators (The John W. Hock Company, Gainesville, USA) or by using CDC Miniature Light Traps (The John W. Hock Company, Gainesville, USA). Immature life stages (larvae, pupae and eggs) were collected from stagnant water using a 1 l plastic dipper, a fine meshed aquarium net or a turkey baster. All water sources were considered, including septic tanks, discarded tires, tree cavities, leaf axils and other items filled with rain water. At each collection location, coordinates were recorded with hand-held consumer-grade GNSS (Garmin model GPSMap64s). Collections were initially sorted in a field laboratory and stored in ethanol or RNA-later to preserve the RNA and DNA for future studies. Genus-level identificatons were made in Finland using suitable identification keys (Service, 1991; Huang 2001; 2004). In **Article III**, mosquito presence data were collected in Finland in 2009 (Hesson et al., 2014), and presence/absence data between 2012–2018 (Culverwell et al., 2021).

2.2.2 Tick data

In **Article IV**, we combined historical tick data, collected by crowdsourcing by University of Turku in 2015 (Laaksonen et al., 2017), and smaller collections conducted by Universities of Jyväskylä, Turku and Helsinki between 2014–2020, with new collections collected by me and the co-authors in early summer 2021 (**Article IV**). As historical occurrence data of *I. persulcatus* didn’t cover whole Finland, we decided to make additional sampling with GIS-based sampling strategy with 100 locations targeting to collect *I. persulcatus*, specifically. Sampling strategy, in detail, is described in **Article IV**. Ticks were collected by slowly dragging 1 m x 1.5 m cotton cloth in 10 m sections, altogether 400 m dragging session in each locality. Larvae, nymphs, adult females and males were separated and placed into 15 ml Greiner falcon tubes with grass stalk. All tick samples were transported to the Department of Virology for University of Helsinki, and were stored alive in 4°C until homogenization. DNA and RNA were extracted using DNA/RNA Kits following the Kit protocols. Tick species was confirmed by molecular identification (Sormunen et al., 2016), and pathogens *Borrelia* and TBEV were screened using real-time polymerase chain reaction (PCR) assays, as previously described with few modifications (**Article IV**, Schwaiger & Cassinotti, 2003; Laaksonen et al., 2017;).

2.2.3 Patient data

For **Articles II** and **III**, patient data were obtained from the National Infectious Diseases Register (NIDR). Occurrence data of human TBE cases included serologically comfirmed TBE cases by municipality from 2007 to 2017 (**Article II**). Data were split into two different datasets (2007–2011 and 2012–2017), to identify differences in predictors and TBE risk between the two time periods. The first dataset consisted of 24 municipalities with 86 TBE cases and 24 control municipalities without TBE cases. The second dataset included 51 municipalities with 244 TBE cases and 51 control municipalities. In **Article III**, we used serologically confirmed Pogosta disease cases (n = 1825) by municipality of residence from 2000–2019. We calculated the incidences for each municipality per 1000 inhabitants between 2000–2019 and calculated the average incidence of all municipalities (0.48/1000) over a 20–year period. Municipalities with incidence rates above the average were considered presence municipalities (n = 97) and the rest were considered absence municipalities (n = 213).

Table 1. Properties of response variables; mosquito, tick and patient data.

Variable	Article	Unit	Description	Reference
Aedes (*Ae.*) genus	**I**	Presence/ absence	Occurrence data from field collections	Uusitalo et al., 2019
Culex (*Cx.*) genus	**I**	Presence/ absence	Occurrence data from field collections	Uusitalo et al., 2019
Aedes (*Ae.*) *cinereus/ geminus*	**III**	Presence/ absence	Occurrence data from field collections	Culverwell et al., 2021
Culex (*Cx.*) *pipiens/ torrentium*	**III**	Presence/ absence	Occurrence data from field collections	Culverwell et al., 2021; Hesson et al., 2014
Culiseta (*Cs.*) *morsitans*	**III**	Presence/ absence	Occurrence data from field collections	Culverwell et al., 2021
Ixodes (I.) ricinus	**IV**	Presence/ absence	Occurrence data from field collections	Laaksonen et al., 2017; Pakanen et al., 2021; Zakham et al., 2021; Uusitalo et al., 2021
Ixodes (I.) persulcatus	**IV**	Presence/ absence	Occurrence data from field collections	Laaksonen et al., 2017; Pakanen et al., 2021; Zakham et al., 2021; Uusitalo et al., 2021
TBE patient data	**II**	Presence/ absence	Laboratory-confirmed SINV infections	NIDR, 2021
Pogosta disease patient data	**III**	Presence/ absence	Laboratory-confirmed TBE cases	NIDR, 2021

2.2.4 Environmental data

Environmental data were obtained from various sources, and included interpolated data, data directly obtained from satellite imagery, or data derived from GIS layers (Table 2 and 3). Precipitation and air temperature were variables used in all four **Articles**, and were derived from different sources for Finland and for Kenya (Table 2 and 3). Land surface temperature (LST), topographic wetness index (TWI) and snow depth were used in **Articles II–IV**. A digital elevation model (DEM) was used to calculate the elevation, slope, and mean monthly solar radiation in GIS software in **Article I**.

Table 2. Environmental data properties used in the analyses.

Environmental variable	Article	Unit	Description	Data source, reference
Snow depth	**II–IV**	cm	**II:** Mean in March, April, November, December **III:** Mean per municipality in October–November, December–February, March–April in 2000–2019 **IV:** Mean in January–April 2014–2021	**II:** MODIS satellite imagery, Hall & Riggs, 2015 **III–IV:** Aalto et al., 2016
Air temperature	**I–IV**	°C	**I:** Mean in January–March **II:** Mean in April, May, June, July, August, September, October in 2007–2011, 2012–2017 **III:** Mean per municipality in July–September, October–February, March–June in 2000–2018 **IV:** Mean during the activity season of *I. ricinus* (May–September), and *I. persulcatus* (April–June) in 2014–2021	**I:** Virtanen, 2015 **II–IV:** Aalto et al., 2016
Precipitation	**I–IV**	mm	**I:** Mean in January–March **II:** Mean in April, May, June, July, August, September, October in 2007–2011, 2012–2017. **III:** Mean per municipality in July–September, October–February, March–June in 2000–2019 **IV:** Mean during the activity season of *I. ricinus* (May–September), and *I. persulcatus* (April–June) in 2014–2021	**I:** Long-term mean precipitation grids, Hutchinson 1991; Erdorgan et al., 2011 **II–IV:** Aalto et al., 2016
Relative air humidity (RH)	**I, IV**	%	**I:** Mean in January–March **IV:** Mean during the activity season of *I. ricinus* (May–September), and *I. persulcatus* (April–June) in 2014–2021	**I:** Data logger observations, Virtanen, 2015 **IV:** Aalto et al., 2016
Wind speed	**III**	m/s	Mean per municipality	50 years return interval data (1979–2015), Venäläinen et al., 2017
Elevation	**I, III–IV**	m	**I:** Mean from DEM **III:** Mean per municipality **IV:** Mean from DEM	Digital elevation model, **I:** Clark & Pellikka, 2005 **III–IV:** NLS of Finland, 2019
Topographic wetness index (TWI)	**II–IV**		Mean per municipality	Salmivaara et al., 2017

Table 3. Environmental data properties used in the analyses.

Environmental variable	Article	Unit	Description	Data source, reference
Normalized difference vegetation index (NDVI)	**I–IV**		**I:** Derived from Sentinel satellite image **II:** Derived from MODIS satellite image **III:** Mean in June 2000–2019 per municipality **IV:** Mean	**I:** Sentinel-2 A MSI satellite image, ESA, 2016 **II–III:** MODIS satellite image, Didan 2015 **IV:** Global VIIRS data, Scharlemann et al., 2008
Enhanced vegetation index (EVI)	**IV**		Mean	Global VIIRS data, Scharlemann et al., 2008
Middle infrared reflectance (MIR)	**IV**		Mean	Global VIIRS data, Scharlemann et al., 2008
Solar radiation	**I, III**	**I:** kWh/m^2 **III:** kJ/M^{-2}/d^{-1}	**I:** Mean from DEM **III:** Mean solar radiation during mosquito season May–September	**I:** Digital elevation model, Clark & Pellikka, 2005 **III:** WorldClim Global climate data, averages for 1980–2000, Fick & Hijmans, 2017
Water vapor pressure	**III**	kPa	Mean water vapor pressure during mosquito season May–September	WorldClim Global climate data, averages for 1980–2000, Fick & Hijmans, 2017
Land surface temperature (LST)	**II–IV**	°C	**II:** Mean per municipality in April, May, June, July, August, September, October in 2007–2011, 2012–2017. **III:** Mean per municipality in April–May, June–August, September–October **IV:** Mean day and night LST, 2012–2020	**II–III:** MODIS satellite imagery, Wan et al., 2015 **IV:** Global VIIRS data, Scharlemann et al., 2008
Growing season length (GSL)	**III, IV**	day	**III:** Mean per municipality **IV:** Mean	**III–IV:** Averages for 1981–2010, Pirinen et al., 2012
Precipitation during growing season	**III, IV**	mm	**III:** Mean per municipality **IV:** Mean	**III–IV:** Averages for 1981–2010, Pirinen et al., 2012
Temperature during growing season	**III, IV**	°C	**III:** Mean per municipality **IV:** Mean	**III–IV:** Averages for 1981–2010, Pirinen et al., 2012
19 bioclimatic variables	**II**	30 seconds (~1 km^2)	Current and future climate data: Mean per municipality Future climate: GCM: IPSL-CM5; RCP 4.5, RCP 8.5	WorldClim Global climate data, Current: averages for 1970–2000, Fick & Hijmans, 2017, Future: 2041–2060, 2061–2080, Hijmans et al., 2005
Slope angle	**I**	°	Derived from DEM	Digital elevation model, Clark & Pellikka, 2005

Normalized vegetation index (NDVI, **Articles I–IV**), enhanced vegetation index (EVI, **Article IV**) and middle infrared reflectance (MIR, **Article IV**) were used to measure plant greenness. Environmental data based on long-term grids included the variables relating to growing season such as growing season length (GSL), and precipitation and temperature during growing season (**Articles III, IV**). Furthermore, wind speed, water vapor pressure, monthly precipitation in Taita Hills (**Article I**), and solar radiation in **Article III**, were created based on long-term data. In **Article II**, current and future climate data included 19 bioclimatic variables derived from the WorldClim datasets (Hijmans et al., 2015; Fick & Hijmans, 2017).

2.2.5 Host data

Host data were density data created either from hunting or snow-track data (Table 4). Host data were used in **Articles II–IV**, and were selected based on earlier knowledge of their influence in the distribution of a given species or disease.

Table 4. Host density data properties used in the analyses.

Host	Article	Unit	Description	Data source, reference
European hare (*Lepus europaeus*) density	**II, IV**	individuals/ km^2	**II:** Averages per game management area (GMA) **IV**: Annual averages at a 50 km radius, further averaged over 2014–2021	**II:** Hunting data, NRIF 2020a **IV:** Snow-track data, NRIF, 2022
Mountain hare (*Lepus timidus*) density	**II, IV**	individuals/ km^2	**II:** Averages per game management area (GMA) **IV:** Annual averages at a 50 km radius, further averaged over 2014–2021	**II:** Hunting data, NRIF 2020a **IV:** Snow-track data, NRIF, 2022
Red fox (*Vulpes Vulpes*) density	**II, IV**	individuals/ km^2	**II:** Averages per game management area (GMA) **IV:** Annual averages at a 50 km radius, further averaged over 2014–2021	**II:** Hunting data, NRIF 2020a **IV:** Snow-track data, NRIF, 2022
Roe deer (*Capreolus capreolus*) density	**II, IV**	individuals/ km^2	**II:** Averages per game management area (GMA) **IV:** Annual averages at a 50 km radius, further averaged over 2014–2021	**II:** Hunting data, NRIF 2020a **IV:** Snow-track data, NRIF, 2022
White-tailed deer (*Odocoileus virginianus*) density	**II, IV**	individuals/ km^2	**II:** Averages per game management area (GMA) **IV:** Annual averages at a 50 km radius, further averaged over 2014–2021	**II:** Hunting data, NRIF 2020a **IV:** Snow-track data, NRIF, 2022
Moose (*Alces alces*) density	**II, IV**	individuals/ km^2	**II:** Averages per game management area (GMA) **IV:** Annual averages at a 50 km radius, further averaged over 2014–2021	**II:** Hunting data, NRIF 2020a **IV:** Snow-track data, NRIF, 2022
Black grouse (*Lyrurus tetrix*) density	**III**	individuals/ km^2	Annual averages at a 100 km radius, further averaged over 2000–2019	Hunting data, NRIF 2020a
Capercaillie (*Tetrao urogallus*) density	**III**	individuals/ km^2	Annual averages at a 100 km radius, further averaged over 2000–2019	Hunting data, NRIF 2020a
Hazel grouse (*Tetrastes bonasia*) density	**III**	individuals/ km^2	Annual averages at a 100 km radius, further averaged over 2000–2019	Hunting data, NRIF 2020a
Willow grouse (Lagopus lagopus) density	**III**	individuals/ km^2	Annual averages at a 100 km radius, further averaged over 2000–2019	Hunting data, NRIF 2020a

NRIF= Natural Resources Institute Finland

2.2.6 Distance-based data

Distance-based data were used in **Articles I, III** and **IV**, in which response variables were available as accurate locations, not at municipality level. Accurate locations enabled us to calculate Euclidean distances to a selected environmental determinant known to affect species distributions (Table 5). In **Article I**, Euclidean distances were calculated from an existing Taita Hills geo-database and in **Articles III** and **IV**, from landcover data.

Table 5. Properties of distance-based data used in the analyses.

Distance-based variable	Article	Unit	Description	Data source, reference
Distance to water bodies	**III, IV**	m	Euclidean distances from mosquito/ tick PA	CORINE land cover 2018, SYKE, 2018
Distance to water courses	**III, IV**	m	Euclidean distances from mosquito/ tick PA	CORINE land cover 2018, SYKE, 2018
Distance to peatbogs	**III**	m	Euclidean distances from mosquito PA	CORINE land cover 2018, SYKE, 2018
Distance to inland marshes	**III**	m	Euclidean distances from mosquito PA	CORINE land cover 2018, SYKE, 2018
Distance to coniferous forest	**III, IV**	m	Euclidean distances from mosquito/ tick PA	CORINE land cover 2018, SYKE, 2018
Distance to broadleaved forest	**III, IV**	m	Euclidean distances from mosquito/ tick PA	CORINE land cover 2018, SYKE, 2018
Distance to mixed forest	**III, IV**	m	Euclidean distances from mosquito/ tick PA	CORINE land cover 2018, SYKE, 2018
Distance to transitional woodland/ shrub	**III**	m	Euclidean distances from mosquito PA	CORINE land cover 2018, SYKE, 2018
Distance to houses	**I**	m	Euclidean distances from mosquito/ tick PA	Building data, Siljander et al., 2011
Distance to roads	**I**	m	Euclidean distances from mosquito/ tick PA	Road data, Broberg & Keskinen 2004

PA= presence-absence

2.2.7 Other data

Other than earlier presented data included anthropogenic factors such as human popularion density, summer cottage densities and number of people working in primary sector (Table 6.). As response data in **Articles II–III** were at municipality level, we calculated the proportion of selected land cover variables in municipalities. In **Article III**, we first created suitability data for the mosquito species, and used this data to estimate the spatial distribution of SINV infections.

Table 6. Properties of other than environmental, host and distance-based data in the analyses.

Other variables	Article	Unit	Description	Data source, reference
Human population density	**I–III**	persons/ km^2	**I:** Estimated from ALS buildings data and from non-stratified household survey, modified by digitizing more houses on the study area **II, III:** Density calculated from human population data	**I:** ALS buildings data, Siljander et al., 2011 **II, III:** Statistics Finland
Summer cottage density	**III**	cottages/ km^2	Density per municipality	Statistics Finland
People working in primary sector	**II**	%	Percentage per municipality	Statistics Finland
Built-up areas	**II**	%	Percentage of built-up areas per municipality	CORINE land cover 2012, SYKE 2012
Field	**II**	%	Percentage of field per municipality	CORINE land cover 2012, SYKE 2012
Forest	**II**	%	Percentage of forest per municipality	CORINE land cover 2012, SYKE 2012
Inland wetlands	**II, III**	%	Percentage of inland wetlands per municipality	CORINE land cover 2012, SYKE 2012
Lakes	**III**	%	Percentage of lakes per municipality	CORINE land cover 2018, SYKE 2018
Mixed forest in mineral soil	**III**	%	Percentage of mixed forest in mineral soil per municipality	CORINE land cover 2018, SYKE 2018
Mixed forest in peatlands	**III**	%	Percentage of mixed forest in peatlands per municipality	CORINE land cover 2018, SYKE 2018
Mixed forest in rocky soil	**III**	%	Percentage of mixed forest in rocky soil per municipality	CORINE land cover 2018, SYKE 2018
Peatbogs	**III**	%	Percentage of peatbogs per municipality	CORINE land cover 2018, SYKE 2018
Seroprevalence of SINV in human population	**III**		Seroprevalence rate per hospital districts	Seroprevalence data, Kurkela et al., 2008
Suitability for *Cx. pipiens/torrentium*	**III**	%	Habitat suitability of *Cx. pipiens/torrentium* produced by SDM	Occurrence data of *Cx. pipiens/torrentium*, Uusitalo et al., 2021
Suitability for *Ae. cinereus/geminus*	**III**	%	Habitat suitability of *Ae. cinereus/geminus* produced by SDM	Occurrence data of *Ae. cinereus/geminus*, Uusitalo et al., 2021
Suitability for *Cs. morsitans*	**III**	%	Habitat suitability of *Cs. morsitans* produced by SDM	Occurrence data of *Cs. morsitans*, Uusitalo et al., 2021

2.3 Data analysis

In this thesis, we used the biomod2 package in R (Thuiller et al., 2009), and VECMAP software (Kruijiff et al., 2011) to model the species and disease distributions. The biomod2 is a computer platform intended for ensemble forecasting of species distributions, which enables the treatment of a range of methodological uncertainties in models and the examination of species-host-disease-environment relationships. VECMAP is a service to predict potential vector-related health risks and to reduce nuisance which enhances and simplifies traditional mathematical distribution modelling, and field and laboratory work with the help of satellite navigation (Kruijiff et al., 2011). The biomod2 platform was used in all **Articles**, and the VECMAP was used in **Articles III** and **IV**. The processing workflow of SDM is presented in Fig. 7.

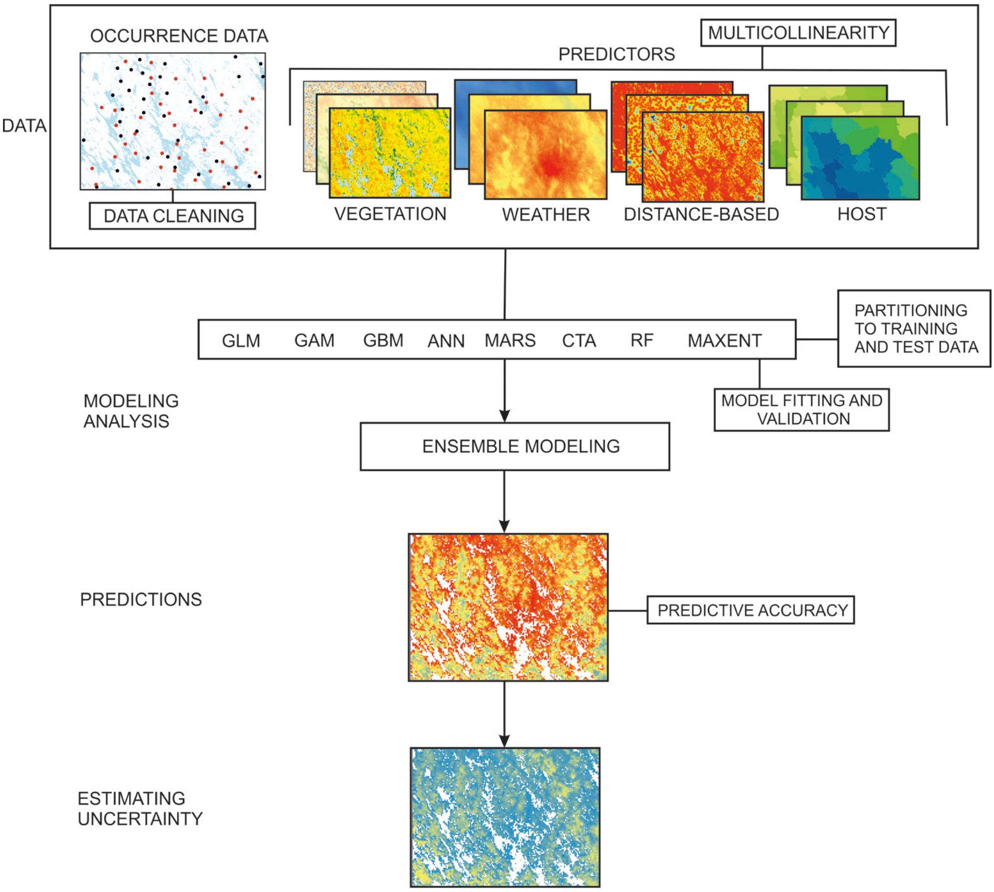

Fig. 7 The processing workflow of SDM.

The first step of data preparation was the cleaning of observation data. If the data were spatially autocorrelated (SA), we removed SA either by removing the autocorrelated occurrences manually, or with special R packages, such as with package Wallace in **Article IV**. All geospatial datasets, including environmental and other data, were processed in ESRI ArcGIS (version 10.3.1) (ESRI, Redlands, CA, USA), and were set to the same spatial extent, geographic coordinate system and resolution (Table 7). Multicollinearity of the variables was investigated with the suitable method (Table 7), and correlated variables were excluded from the final dataset.

In this thesis, we conducted empirical models which use observed data to build correlative relationships between species occurrences and environmental factors. We used several modelling algorithms including regression-based models; generalized linear models (GLM, McCullagh & Nelder, 1989) and generalized additive models (GAM, Hastie & Tibshirani, 1990), classification trees (CTAs, Breiman et al., 1984), artificial neural networks (ANNs, Ripley 1996), multivariate adaptive regression splines (MARS, Friedman 1991), ensemble decision tree methods; generalized boosted models (GBM, Ridgeway, 1999) and random forests (RF, Breiman 2001), and distance-based machine-learning approach, maximum-entropy (MAXENT, Phillips et al., 2004). In **Article I**, single-modelling methods were used to estimate the potential species distributions. As ensemble modelling has an advantage of producing more robust decision-making in the face of uncertainty in comparison with single-model forecasts (Araujo & New, 2007), we mostly used ensemble models (**Articles II–IV**). Ensembles were generated using the best-performing model algorithms ($0.7<AUC>1.0$) with statistically significant variables ($p < 0.05$). We also compared the prediction results from ensembles with the predictions from single-modelling techniques, and used consensus method of weighted mean ensemble approach (**Article III**).

Table 7. Method description of each study.

Modelling study	Spatial extent	Article	Resolution of response/ environmental data	Geographic coordinate system	Multicollinearity investigation method	Final nr. of predictors	Modelling method
SDM of *Culex*	Taita Hills	**I**	Coordinates/20 m x 20 m	UTM Zone 37S	Pearson correlation	5	GLM, GAM, RF
SDM of *Aedes*	Taita Hills	**I**	Coordinates/20 m x 20 m	UTM Zone 37S	Pearson correlation	5	GLM, GAM, RF
TBE study 2007-2011	Finland	**II**	Municipality/ 1000 m x 1000 m	EUREF FIN TM35FIN	VIF package usdm	14	Ensemble
TBE study 2012-2017	Finland	**II**	Municipality/ 1000 m x 1000 m	EUREF FIN TM35FIN	VIF package usdm	13	Ensemble
TBE study on current climate	Finland	**II**	Municipality/ 1000 m x 1000 m	EUREF FIN TM35FIN	VIF package usdm	6	Ensemble
TBE study on future climate	Finland	**II**	Municipality/ 1000 m x 1000 m	EUREF FIN TM35FIN	VIF package usdm	6	Ensemble
SINV vector	Finland	**III**	Coordinates/ 1000 m x 1000 m	EUREF FIN TM35FIN	VIF package usdm	21	Ensemble
Pogosta disease	Finland	**III**	Municipality	EUREF FIN TM35FIN	VIF package usdm	19	Ensemble/biomod2, GLM/ RF, VECMAP
SDM of *I. ricinus*	Finland	**IV**	Coordinates	EUREF FIN TM35FIN	VIF package usdm	19	Ensemble
SDM of *I. persulcatus*	Finland	**IV**	Coordinates	EUREF FIN TM35FIN	VIF package usdm	19	Ensemble

In our studies, the metrics used to assess model accuracy were the proportion of actual presences (i.e. sensitivity) and absences (i.e. specificity) accurately predicted, area under the receiver operating characteristic curve (AUC, Hanley & McNeil 1982; Pearce & Ferrier 2000), and the true skill statistic (TSS, Allouche et al., 2006). Sensitivity and specificity were calculated to quantify the omission errors (Fielding & Bell 1997). Sensitivity is calculated dividing true presences (TP) by the sum of TP and false absences (FA). Similarly, specificity is calculated dividing true absences (TA) by the sum of TA and false positives (FP). AUC is the measure of the ability of a model to distinguish between these presence and absence classes. TSS is defined as (1 – maximum (sensitivity + specificity) where sensitivity and specificity are calculated based on the probability threshold for which their sum is maximized (Allouche et al., 2006). In an ideal world, model accuracy should be evaluated with statistically independent data, which is not often possible (Fielding & Bell, 1997; Araújo et al., 2005). An alternative is to use split-sample approaches, an example of two-fold cross-validation, (Guisan & Zimmerman, 2000), where original data are divided into one portion used to calibrate the model (i.e. training data), and one portion used to validate the predictions (i.e. testing data) (Smith, 1994; Miller & Franklin, 2002). We used this cross-validation technique in all analyses, where we split the dataset into two subsets, one to calibrate the models (70%) and another to evaluate the models (30%). We estimated the importance of each variable enabling direct comparison across models, which is produced by a randomisation procedure, independent of the modelling technique (Thuiller et al., 2009). Partial dependency plots were generated to show the predictors' estimated effects on the species and disease distributions. Prediction maps were first created by using R or VECMAP, and modified in ArcGIS. Method description of each study is presented in Table 7.

3 Results

3.1 The spatial distribution of *Stegomyia* (*Aedes*) and *Culex* mosquitoes in the Taita Hills, Kenya

In **Article I**, we collected over 3,000 mosquitoes across the Taita Hills to study species distributions, circulating mosquito-borne pathogens, and to create SDMs at genus level (Fig. 6.1). The majority of mosquitoes belonged to genus *Culex* and included at least three subgenera: *Culex* (*Culex*), *Cx.* (*Culiciomyia*) and *Cx.* (*Eumelanomyia*). *Stegomyia* were the second most abundant genus in the collections. *Stegomyia aegypti* larvae were especially common in water tanks in the villages of Paranga and Kishushe in the Taita Hills north, and also in car tires in Mwatate village. Both genera were present in lowland and upland areas, including elevations up to 1900 m. We predicted the distributions of *Culex* and *Stegomyia* across Taita Hills region. From a total of eight models, GAM (AUC = 0.791) and MARS (AUC = 0.809) models produced the highest model performances for *Culex*, and GBM (AUC = 0.708) and RF models (AUC = 0.708) for *Stegomyia*. The prediction results showed that high suitabilities of *Culex* were associated with poor vegetation (NDVI ≤ 0.2), elevations between 800–2000 m, locations with moderate slope angles (0°–35°), and varying population densities of 500–6000 people/km^2 (**Article I**: Fig. 3). The suitabilities for *Stegomyia* were highest in locations with solar radiation levels ≥ 230 kWh/m^2, in air temperatures between 15–20°C, and over 23°C, and in locations with poor (NDVI ≤ -0.2) and moderate vegetation (NDVI ≥ 0.2, **Article I**: Fig. 4). Produced habitat suitability maps for *Culex* indicated that villages and forests, including elevations above 1500 m in the Taita Hills, were most suitable for *Culex* mosquitoes (80–100%, **Article I**: Fig. 5A). Areas with high suitability for *Stegomyia* were sporadically dispersed across the Taita Hills, including villages on the plateaus and locations close to roads (**Article I**: Fig. 5B).

3.2 The risk of tick-borne encephalitis (TBE) in Finland

TBE is one of the endemic VBDs in Finland with an increased number of patient cases, and requires further attention under changing climate patterns. In **Article II**, we investigated TBE risk in Finland using TBE patient case data (Fig. 6.2A–B). First, we created an ensemble mean model of best-performing single models to estimate the risk based on environmental and host data in two different datasets (**Article II**: Fig. 3). Second, we used bioclimatic drivers to estimate the risk in current and future climate conditions by using global climate models (GCM). Mean ensemble model based on environmental and host data produced an excellent predictive performance with the median TSS values of (0.988) and (0.956) in the two datasets. Based on the mean ensembles, predictor variables including proportion of built-up areas, forest, field, people working in the primary sector, human population density, mean precipitation, snow-covered land, and densities of white-tailed deer, raccoon dogs and European hare in the municipalities, were the most important drivers for TBE risk (**Article II**: Fig. 5). The results suggested moderate to high risk for TBE in the majority of coastal municipalities, municipalities in the Åland Islands, and several municipalities in southwestern, central, and eastern Finland, close to the Russian border (**Article II**: Fig. 6). We used the ensemble mean method with the bioclimatic data to explore potential changes in risk under current and projected future climate scenarios. We used medium (RCP 4.5) and high (RCP 8.5) change scenarios for 2041–2060, and 2061–2080. The risk maps of TBE under current climate conditions indicated moderate to high risk areas in the Åland Islands, in southwestern, southern and southeastern Finland, and in Ostrobothnia, North Ostrobothnia and southern Lapland (**Article II**: Fig. 8). Ensemble forecasts for 2041–2060 and 2061–2080 showed that moderate to high risk areas for TBE were wider both with medium and high change scenarios. Wider risk areas were estimated specifically for southern and western coast but also for inland municipalities in southern Lapland (**Article II**: Fig. 8).

3.3 Habitat suitabilities of SINV mosquito vectors and the risk areas for SINV infections in Finland

Article III investigated 1) habitat suitabilities of major SINV vectors *Ae. cinereus/geminus*, *Cx. pipiens/torrentium* and *Cs. morsitans* based on environmental data, and 2) the risk areas for SINV infections (i.e. Pogosta disease) based on environmental and host data, and produced habitat suitability data of mosquito vectors (Fig. 6.2C–D). The results showed that locations with high suitabilities for *Ae. cinereus/geminus* were associated with high mean LST in June–August and solar radiation during May–September, high NDVI, low wind speed, and short distances to coniferous and mixed forest. For *Cx. pipiens/torrentium*, locations with higher water vapor pressure, precipitation during March–September and LST in June–August, low wind speed and short distances to lakes were considered suitable habitats. For *Cs. morsitans* instead, longer growing season, higher precipitation in March–June and higher solar radiation in May–September, and shorter distances to coniferous and mixed forests positively influenced the species presence. Based on the predictions, the areas with moderate to high suitability for *Ae. cinereus/geminus* were located throughout Finland (30–70%), excluding the northernmost Lapland (0–30%, **Article III**: Figure 3a). Similarly, high suitabilities for *Cx. pipiens/torrentium* were found to occur throughout Finland excluding northern Lapland and the narrow areas in central and western Finland (**Article III**: Figure 3b). For *Cs. morsitans*, in contrast, high suitabilities were only estimated across southern Finland up to 64°N, along the southern and western coast, in the Åland Islands, and in sporadic areas in western and eastern Finland (**Article III**: Figure 3c).

Second, we modelled the risk of SINV infections in two platforms; the biomod2 package in R and VECMAP software. We created the weighted mean ensemble produced by the best-performing models which yielded the mean AUC of 0.98 with high sensitivity and specificity rates (**Article III**: Figure 4b). To test consistency of the study results, we used GLM and RF models in VECMAP to model the risk of SINV infections, which both resulted excellent predictive performances with AUC > 0.90. The prediction results showed that high densities of black grouse, capercaillie and hazel grouse, a high proportion of mixed forest in peatland, and a high proportion of lakes in the municipalities were associated with increased Pogosta disease risk (> 70%, **Article III**: Figure 5). Furthermore, in the municipalities with a high probability of *Ae. cinereus/geminus* occurrence, Pogosta disease risk was high (80–98%). The produced risk map suggested that municipalities with moderate to high risk (30–100%) for SINV infections were located in municipalities in eastern and central Finland, along the western coast up to southern Lapland in latitudes between 61–64°N (**Article III**: Figure 6). Contrarily, municipalities in southern- and northernmost Finland, southwestern Finland and the Åland Islands were estimated to be at a low risk (0–20%) for SINV transmission.

3.4 Habitat suitabilities of *Ixodes ricinus* and *I. persulcatus* ticks in Finland

Article IV examined the spatial distribution of *Ixodes ricinus* and *I. persulcatus* in Finland based on environmental and host data with four variable compositions with the uncertainty assessments. We used historical tick occurrence data, and new collection data from 2021 (Fig. 6.2E). The collections in early summer 2021 were designed based on the GIS-based sampling strategy, and from these samples we also screened pathogens TBEV and *Borrelia*. During May–June 2021, 25 new presences and 63 absences were found for *I. ricinus*, and only one presence and 88 new absences for *I. persulcatus*. In a total of 500 ticks were collected and analysed with no ticks positive for TBEV, and 56 (≈ 47 %) of the 120 tick pools positive for *Borrelia burgdorferi* sensu lato (**Article IV**: Additional File 1: Figure S1). The results showed that from four variable compositions, combined predictor datasets based on ensemble mean models yielded the highest predictive accuracy both for *I. ricinus* (AUC=0.91, 0.94), and for *I. persulcatus* (AUC=0.93, 0.96, **Article IV**: Table 3). The locations with higher RH, higher mean air temperature during the activity season, higher precipitation sum and middle infrared reflectance levels, and higher densities of white-tailed deer, European hare and red fox were associated with high probabilities of *I. ricinus* occurrence (**Article IV**: Fig. 5a). For *I. persulcatus*, higher mean precipitation and higher densities of white-tailed deer, roe deer and mountain hare were associated with high habitat suitabilities for *I. persulcatus* (**Article IV**: Fig. 5b). However, too high precipitation sum, higher mean air temperature during the activity season, and DLST in the locations, began to influence negatively in the suitability of *I. persulcatus*. The results suggested that areas with moderate to high suitability for *I. ricinus* were located southwards from Central Ostrobothnia, with the following exceptions; narrow areas located in southern Pirkanmaa, and southern coast of Ostrobothnia (**Article IV**: Fig. 6c). In contrast, northern parts of North Savo, North Karelia and North Ostrobothnia and Kainuu were estimated to have a low to moderate suitability for *I. ricinus*. For *I. persulcatus*, the areas with moderate to high suitabilities were located mainly northwards from Ostrobothnia up to southern Lapland including areas along the western coast and eastern Finland (**Article IV**: Fig. 7c). In southern Finland, moderate to high suitability areas for *I. persulcatus* were located across Pirkanmaa, and in narrow areas in Kanta-Häme, Päijät-Häme, South Karelia, South Savo and Uusimaa. Other areas in southern Finland, northern Kainuu and eastern North Ostrobothnia were estimated to have a low to moderate probability for *I. persulcatus* occurrence.

4 Discussion

In this work, we aimed at studying the distribution of medically important mosquito and tick species in boreal and tropical regions, and the distribution of two endemic VBDs in Finland, to explore environmental and other determinants driving the spatial patterns at regional and national scales. The thesis is closely related to predictive vector ecology and spatial epidemiology, broad study fields across the Globe, which utilize climate, vegetation and host variables known to affect distribution of a given species or a VBD, at varying spatial scale. Although SDM approach has been widely used by researchers and global health agencies, there are no earlier SDM studies on vectors or VBDs in Finland. In tropical regions, including Kenya, where the need for vector control and disease prevention is highest, SDM studies have been conducted although, rural regions, particularly, remain understudied. Here, we utilized environmental and vegetation data as predictor data, which are often considered in SDM studies. We also used good quality host data and habitat suitability data of vector species to gain a better understanding of species-host-disease-environment relationships. To our knowledge, there are no earlier SDM studies on vector species which used high-quality host data, and there are only a handful of studies which included suitability data of vectors to predict disease occurrence (Messina et al., 2019; Akhtar et al., 2019).

4.1 Geographies of vectors and VBDs

One of the key results of this thesis was the predicted occurrences of mosquito and tick vectors, and VBDs. Each vector and VBD have the environmental conditions, niches, under which they can reproduce and survive (Austin 2002) although all these factors may not be fully understood. In the Taita Hills in southeastern Kenya, *Culex* and *Stegomyia* mosquitoes were found to overlap in geographical range, but also to be common in different areas (**Article I**: Fig. 5). Predictive risk maps for *Culex* and *Stegomyia* genera indicated that highest suitabilities for *Culex* occurred in the central Taita Hills, but also in the plateau and lowland villages, strengthening previous findings of its widespread distribution in a variety of global locations but also locally, in different environments (MTI, 2022c). For *Stegomyia*, the highest suitabilities were in plateau villages and fragmented areas across the Taita Hills. This was consistent with historic records suggesting that members of *Stegomyia* genus are forest dwelling, with only some adapted to breeding close to human habitation (Powell & Tabachnick, 2013). Since our collections included several different *Stegomyia* species –with *St. aegypti* being the only species collected from around villages, and other species being restricted to the forest– the model findings were consistent with these historical reports (Powell & Tabachnick, 2013). In Finland, high-risk areas for TBEV transmission were estimated to be in the

Åland Islands, the coastal regions of southern, western, and northern Finland, and several municipalities in central and eastern Finland, based on risk maps (**Article II**: Fig. 6). In future forecasts for 2041–2060 and 2061–2080 climate, a wider geographical extent of TBE risk was introduced in the Åland Islands and southern, western and northern Finland (**Article II**: Fig. 8). Identified risk areas were consistent with previous study results, however, which were largely based on extrapolation of Central and Eastern European *I. ricinus* data (Randolph & Rogers, 2000). In this study, southern and southeastern Finland were estimated to be suitable for TBE transmission in the 2020 forecast, and risk areas were suggested to expand up to central Finland in the 2080 forecast (Randolph & Rogers, 2000). Higher TBE risk in northern regions is reasonable as temperature and precipitation increase are greater in the northernmost latitudes (Trenberth & Josey 2007; Ruosteenoja et al., 2021), which make the region more favorable for tick activity (Soucy et al., 2018; Medlock et al., 2013; Lindgren & Gustafson, 2001; Gray et al., 2009).

The habitat suitability maps of SINV vectors (**Article III**: Figure 3) suggested that suitable habitats for *Ae. cinereus/geminus* and *Cx. pipiens/torrentium* occurred throughout Finland demonstrating their widespread distribution also elsewhere in Northern Europe including Sweden, Finland´s neighboring country (Becker et al., 2010; Lundström et al., 2013). For *Cs. morsitans*, suitable habitats occurred mainly in southern Finland including sporadic areas in western and eastern Finland. *Culiseta morsitans* is a species whose distribution ranges from southern Scandinavia to Northern Africa. In Sweden, the observations of *Cs. morsitans* were documented in the same latitude where their suitability was highest in Finland (Lundström et al., 2013). The risk maps of SINV infections (**Article III**: Figure 6) suggested that moderate to high risk areas occurred in municipalities located in central, eastern, and western Finland which are populated by 2.800.000 residents (50.5 % of the total human population in Finland). Areas with the higher risk were generally consistent with previous findings about the incidence of Pogosta disease (Brummer-Korvenkontio et al., 2002; Kurkela et al., 2008; Sane et al., 2010). However, when comparing the prediction maps to the Pogosta disease incidence map 2000–2019, several differences are evident. Moderate to high risk areas extended from southern Lapland to southern Finland at latitudes between 61–66°N. These are areas in Finland characterized by abundant lakes and summer cottages where people are used to have outdoor activities, such as berry picking, altering them to mosquito bites in forests during the late summer and early fall. When comparing the prediction maps with the incidence maps, the largest differences occurred in western Finland, southern Lapland and North Ostrobothnia with either high or moderate risk in several municipalities where only few cases were documented. According to the results from predictions, locations with the highest environmental suitability for *Ae. cinereus/geminus* and *Cx. pipiens/torrentium* overlap in geographical range with the municipalities at high risk of SINV infections demonstrating their potential role in SINV transmission in Finland. Northern Lapland, in contrast, was estimated to be a low-risk area for SINV transmission. This area is characterized by low abundance of resident grouse, long winter, high snow depth and cold air temperatures compared to elsewhere in Finland, which may halt viral replication and restrict vector populations (Ciota & Keyel 2019), and influence the low probability of Pogosta disease occurrence. Southern coast, southwestern Finland, Ostrobothnia and the Åland archipelago are areas with the extreme ends of wind speed, compared with other regions in the country, which may affect the decreased exposure for mosquito bites. Although SINV vector species are present in southern coast, however, the area was estimated to be at low risk for SINV infections. A potential explanation for this may be the resident grouse population, especially capercaillie and black grouse populations, which have collapsed even 80% during the last 40 years due to fragmentation of suitable habitats caused by human activities (NRIF, 2022). As SINV circulates through a transmission cycle, all events in the cycle; vector, pathogen, host, suitable environmental conditions and human exposure to mosquito bite, should be present.

Similar to other arthropod vectors, tick species *Ixodes ricinus* and *I. persulcatus* have their own niches in which they can survive and reproduce, and which determine their geographical distributions. Based on our study results (**Article IV**: Fig. 6), moderate to high suitability areas for *I. ricinus* occurred throughout southern and central Finland up to the Central Ostrobothnia (64°N), excluding the narrow areas in Ostrobothnia and Pirkanmaa. In neighboring country in Sweden, only the areas southwards from the capital region (60°N) were predicted to be areas with abundant *I. ricinus* (Kjaer et al., 2019), although *I. ricinus* have been collected up to 66°N (Jaenson et al., 2012). Based on the recent *I. ricinus* studies from Russian Karelia, the species was absent already north from 63°N (Bugmyrin et al., 2012; Bespyatova & Bugmyrin, 2021). The narrow areas in Ostrobothnia and in Pirkanmaa which are considered sympatric areas, were estimated to have low suitability for *I. ricinus* which may, partly, be explained by the model-based uncertainty. The dominance area of *I. persulcatus* is known to be northwards from the dominance area of *I. ricinus*. The prediction results showed that northwards from Ostrobothnia along the northern coast up to southern Lapland, Kainuu, North Savo and North Karelia, the suitability of *I. persulcatus* was highest (**Article IV**: Fig. 7). Southern Finland, excluding the areas in Pirkanmaa, western Päijät-Häme, northern Kanta-Häme, and southern Uusimaa, were estimated to have a low habitat suitability for *I. persulcatus*. However, a moderate to high uncertainty in the predictions for *I. persulcatus* occurred widely across southern Finland which may indicate that there may occur suitable areas for *I. persulcatus* (**Article IV**: Fig. 9). In neighboring countries, *I. persulcatus* have only been found up to 63°N in Russian Karelia (Bugmyrin et al., 2013; Popov & Popova 2020) while in Sweden, the species was first introduced close to Finnish border ≈ 66°N in 2015 (Jaenson et al., 2016).

4.2 Climate, vegetation and host interactions on the distribution of vectors and VBDs

Consistent with previous findings, similar environmental and climatic variables were important determinants of the species or disease of interest in boreal and tropical landscapes, although suitable environmental gradients for habitat suitability of each vector are species-specific. In the Taita Hills, Kenya, *Stegomyia* favored locations with intermediate and high temperatures, supporting the argument that *Stegomyia* mosquitoes have temperature-based limits to survival (**Article I**; Brady et al., 2013). Both rich and poor vegetation were suitable for *Culex* mosquito presence, also strengthening previous findings of its occurrence in a variety of habitats (**Article I**: Fig. 3; MTI, 2022b). Residential and urban areas with poor vegetation are often recognized as important for *Culex* distributions (Reiter & LaPointe, 2007; Conley et al., 2014). A high suitability for *Culex* were found in locations with high NDVI values caused by strongly reflecting orchard trees and croplands adjacent to dwelling units in the Taita Hills. Specifically, we found that locations with high population densities positively influenced *Culex* presence (**Article I**: Fig. 3). *Stegomyia* mosquitoes preferred locations either with low or high human population densities and poor or moderate vegetation (**Article I**: Fig. 4). This finding somewhat contradicts the notion that *St. aegypti* distribution is linked to growing human population (Fatima et al., 2016), but is consistent with historic records of the variety of *Stegomyia* species indicating that most members of *Stegomyia* genus are forest dwelling, with only some adapted to breeding close to human habitation (Powell & Tabachnick, 2013).

In **Article III**, locations with high mean temperatures in June–August, rich vegetation and a long growing season positively influenced the occurrence of *Ae. cinereus/geminus* (**Article III**: Fig. A2.a). *Aedes cinereus* larvae are known to need a temperature of 12–13°C to hatch and 14–15°C to develop, the optimum temperature being 24–25°C (Mohrig 1969). Similarly, *Cx. pipiens/torrentium* favored locations with high LST (**Article III**: Fig. A2.b). For *Cs. morsitans*, higher precipitation in March–June, and moderate precipitation in July–September, and October–February, were associated with higher occurrence (**Article III**: Fig. A2.c). This finding is already evident as *Cs. morsitans* deposit their eggs during early summer in the moist substrate above the residual water level (Medlock et al., 2005; Becker et al., 2010;). For *Ae. cinereus/geminus*, instead, suitable areas were locations with short distances to coniferous and mixed forest. *Aedes cinereus* is also an acidophilic mosquito, most often found in acido-oligotrophic habitats (Becker et al., 2010). Based on the study results, *Cx. pipiens/torrentium* favored locations with barren vegetation. These species are widely distributed and able to survive in various habitats, including natural unpolluted and urban polluted habitats close to humans (Becker et al., 2010; Harbach 2012). A long growing season, and short distances to mixed or coniferous forests, were suitable conditions for *Cs. morsitans* to be present. Suitable sites for *Cs. morsitans* are known to occur in both shaded and open habitats in swampy woodlands and temporary water bodies in forests (Becker et al., 2010; Medlock & Leach 2015). The results indicated that increased Pogosta disease risk in municipalities was associated with a high proportion of mixed forest in peatlands, peatbogs, inland wetlands and lakes (**Article III**: Figure 5). These findings that the natural foci of SINV infections mainly occur in wetland ecosystems of diverse biomes, including lowland forested wetlands and humid forests composed of deciduous and coniferous trees, are consistent with previous studies from other European locations (Ernek et al., 1973; Lundström et al., 2001). The results showed that the risk of SINV infections was high in municipalities with a high probability of *Ae. cinereus/geminus* to occur (**Article III**: Figure 5). A recent study by Lundström et al. (2019) suggests that the increased prevalence of SINV-I, especially in *Ae. cinereus* and *Cx. pipiens/torrentium*, is a major cause of recent SINV outbreaks in Northern Europe. Our prediction results also suggested that the habitat suitability for *Cs. morsitans* negatively influenced the risk of SINV infections. This observation somewhat contradicts the notion that the presence of *Cs. morsitans* is linked to SINV transmission elsewhere in Northern Europe (Francy et al., 1989; Lundström et al., 2019). The role of *Cs. morsitans* in SINV transmission has not yet been studied in Finland, but would benefit from more mosquito collection data to boost predictions of presence. In **Article II**, the results showed that the distribution of TBE is affected by mean precipitation from April to July

(**Article II**: Fig. 5A). Both *Ixodes ricinus* and *I. persulcatus* are vulnerable to desiccation and consequently require high RH (> 80%) in their microhabitats to be able to quest and survive (Gray, 1998). The increased bursts of humidity provided by more rainfall help in maintaining adequately humid shelters for ticks on the ground floor and reduce moisture loss during questing, improving tick survival and lengthening questing periods. Precipitation in April were previously found to correlate with TBE incidence (Czupryna et al., 2016). Dry periods at the beginning of the tick season were found to lead to tick mortality and reduced late-season populations for *I. ricinus* (Perret et al., 2000; Berger et al., 2014). Based on risk maps for TBE, a proportion of snow-covered land affect the risk of TBE (**Article II**: Fig. 5B). Snow cover may positively affect tick activity and survival because it acts as an insulating blanket over ground litter and tends to further insulate ticks from the frigid winter air temperatures (Lundkvist et al., 2011; Dautel et al., 2016; Vollack et al., 2017). The proportion of field and forest area in municipalities had indirect effects on TBE transmission (**Article II**: Fig. 5). Forests are typical habitats for many important tick host animals, such as deer and hares, and higher amounts of forests, therefore, typically increase host animal and consequently, tick abundance. On the other hand, increasing proportion of field area often means that a more fragmented habitat mosaic is formed, wherein the amount of boundary areas between different habitats increases. These increasing edge effects allow for greater biodiversity and often higher animal densities (Tack et al., 2012; Czupryna et al., 2016; Nadolny & Gaff, 2018). High human population density and a high proportion of built-up areas are associated with the large number of population and naturally increase TBE risk (**Article II**: Fig. 5). People who are working in the primary sector spend relatively more time outdoors than other sectors and consequently have a higher risk for getting tick bites (Randolph et al., 2008). The results also showed that white-tailed deer, European hare, and raccoon dog density were associated with higher TBE risk (**Article II**: Fig. 5). Medium-sized and large animals such as deer, hares and raccoon dogs are potential hosts for *I. ricinus* nymphs and adults, and *I. persulcatus* adults (Gray et al., 2016; Klemola et al., 2019). The population sizes of white-tailed deer and raccoon dogs have significantly increased in Finland recently (NRIF, 2022), and may possibly be connected with higher *I. persulcatus* and *I. ricinus* density. White-tailed deer density and hare density have earlier been confirmed to correlate with *I. ricinus* abundance and consequently, TBE distribution (Brugger et al., 2017; Jaenson et al., 2018). In the future forecasts for TBE, mean temperature of the warmest month and wettest quarter and temperature seasonality were the most influential bioclimatic factors on TBE risk (**Article II**: Fig. 7). High spring and summer temperatures and mild winter temperatures are drivers of new tick establishment and higher TBE risk at high-latitudes in Northern Europe (Randolph & Rogers, 2000; Gray et al., 2009).

In **Article III**, we found that high densities of hazel grouse, capercaillie and black grouse positively influenced the occurrence of SINV infections, with very similar response functions, indicating the role of resident grouse in the epidemiology of SINV in humans (**Article III**: Figure 5). On the contrary, we found that high willow grouse density was not associated with high Pogosta disease risk as with other resident grouse. Historically the distribution of willow grouse extended from southern Finland to Lapland, but as a result of population decline, the majority of the remaining willow grouse population is nowadays restricted to Lapland (NRIF, 2019). Outbreaks of Pogosta disease have previously been reported to follow a 7-year cycle in Finland (Brummer-Korvenkontio et al., 2002), and were thought to be influenced by the resident grouse populations that also show 6–7-year cycles (Ernek et al., 1973). Based on the Pogosta disease cases during recent decades, distinct epidemic cycles are no longer observed, and the capercaillie population, particularly, has not shown 6–7-year cycles anymore (NRIF, 2020b). The Finnish grouse populations were at a record low in 2009, and subsequently reached similar low values during the summers of 2016–2017. However, since 2018, the grouse population has shown signs of recovery across Finland excluding southern parts, which remains in decline due to habitat fragmentation (NRIF, 2019).

Environmental, host and climatic variables were important determinants for *I. ricinus* and *I. persulcatus* occurrence which were in line with previous studies (**Article IV**: Fig. 4). Results showed that climatic factors such as higher RH, higher mean air temperature and precipitation sum were associated with higher occurrence of *I. ricinus* (**Article IV**: Fig. 5a). Higher air temperatures (Kjaer et al., 2019; Gethmann et al., 2020; Rochat et al., 2021) and precipitation, especially in spring (Jore et al., 2014) were found to positively influence in *I. ricinus* presence. Based on the study results, higher densities of red fox, white-tailed deer and European hare were associated with higher habitat suitabilities for *I. ricinus* which is in accordance with earlier findings (Tälleklint & Jaenson, 1997; Handeland et al., 2013; Hofmeester et al., 2017; Jaenson et al., 2018; Mysterud et al., 2021). Although generally red foxes have been found to be suitable hosts for ticks in Europe (Cadenas et al., 2007; Wodecka et al., 2016), they were not considered suitable hosts in the recent study from Norway (Mysterud et al., 2021). Consistent with previous research (Kjaer et al., 2019), our study showed that high MIR rates positively influenced with *I. ricinus* occurrence. Similar to *I. ricinus*, the suitabilities for *I. persulcatus* were higher in the locations with higher mean precipitation and air temperature during the activity season (**Article IV**: Fig. 5b). However, when precipitation, mean air temperature and DLST increased at a particular point, the suitability for *I. persulcatus* began to decrease. This finding may demonstrate the characteristics of *I. persulcatus* to prosper in slightly drier and colder habitats than *I. ricinus* (Sirotkin & Korenberg, 2018). However, the expansion of *I. persulcatus* have been found to correlate with the increase of mean annual air temperatures that determine compatible temperature conditions for *I. persulcatus* establishment at new territories (Tokarevich et al., 2011; Bugmyrin et al., 2019). As warmer winters and hotter summers are estimated to change the dynamics and pattern of seasonal tick activity (Gray 2009), it will be seen if *I. persulcatus* adapts to warmer and wetter habitat conditions. Some adaptation has already occurred with a recent introduction of the species in southern parts of Finland (Zakham et al., 2021). For *I. persulcatus*, higher densities of white-tailed deer, roe deer and mountain hare were associated with higher habitat suitabilities which is in line with previous findings (Kim et al., 2011; Jaenson et al., 2016; Pakanen et al., 2020). Notable is that during the last few years white-tailed deer and roe deer populations have rapidly increased in southern Finland, especially in the southwest (NRIF, 2022), which may have a potential effect, not only on the increased abundances of *I. ricinus* but also, on the spread of *I. persulcatus* southwards.

4.3 Uncertainties

In SDM studies, in general, there are often underlying data-related and methodological challenges which affect the study results (Goodchild, 1994; Barry & Elith, 2006). The highest quality of response and predictor data available are used, but there are always data- and model-related limitations, and these issues are discussed herein. A common challenge in SDM is the lack of suitable predictors most often due to lack of spatial data nor the lack of knowledge on influential factors (Dormann et al., 2007). However, we highlight that conversations between experts from various fields are needed to understand the broader context of influential determinants for a given species or disease. Sample size and extent, sampling design and data resolution are important data issues affecting the performance of SDMs by addressing whether species data is unbiased and representative; well covering all the environmental gradients within the study area (Franklin et al., 2010). Sample size has been found to be negatively associated with model performance which was also identified in our work (Cumming 2000; Hirzel & Guisan, 2002; Wisz et al., 2008; Franklin et al., 2010). In **Articles I–III**, a relatively low number of occurrence data for *Stegomyia*, TBE disease cases, and *Cs. morsitans* may have affected the representativeness of the species and disease data and influenced the model performances and the prediction results. Due to the narrow geographical range of TBE cases in **Article II**, it was not possible to predict TBE risk throughout Finland but on selected presence and control municipalities with ratio of 1:1, as suggested (**Article II**, Fielding & Bell, 1997; Wisz et al., 2008; Barbet-Massin et al., 2012). Sampling design in **Article I**, based on 100 m elevation interval along the roads, affected the *Stegomyia* predictions with a visible influence of road network in the predictions. The choice of modelling technique is also critical to produce the highest predictive accuracy with low uncertainties. In **Article I**, we used GAM and RF models to model the distributions of *Culex* and *Stegomyia*, and we note that use of ensemble, instead, might have produced higher predictive accuracy for both genera. In general, ensemble modelling has been found to produce more robust decision-making in the face of uncertainty in comparison with single-model predictions (Araujo & New, 2007, **Article III**). The lack of very high-resolution environmental data (e.g. the resolutions of 2–5 m) is a general problem in SDM. In **Article I**, we utilized the environmental data at 20 m. Although this is already reasonably good resolution, it may have produced some bias to the study results, as mosquitoes are also breeding e.g. in tree holes and water tanks in different microclimates. However, we have to note that by increasing the resolution of environmental data does not always improve the SDMs (Pradervand et al., 2014). Data from human TBE cases and SINV infections were only available at municipality level and produced results at same resolution (**Article II**–**III**). As explanatory data were mainly available at higher resolution (1000 m × 1000 m) and data were calculated to correspond the resolution of response variable, some information was lost. Disease data are often aggregated and dependent on the chosen set of aggregate-level mapping units e.g. due to privacy policy. This phenomenon, also called as the modifiable areal unit problem (MAUP), may lead to misleading conclusions (Gehlke & Biehl, 1934). Also, in **Article II**, excluding the Åland Islands, hunting data were performed in game management area (GMA) level, which is larger than municipality boundaries and thus, were not real density data per municipality.

There are also some uncertainties concerning the data of species of concern (**Article I**, **III–IV**). In **Article I**, we only used mosquito data collected during three months in 2016. Species composition and abundance vary throughout a year depending on a variation of climate-specific patterns. Also, we note that the genus-level pooling of the species will mask species distribution determinants (**Article I**). We cannot rule out some effects of other potential sample biases (e.g. time of the day and traps involved) which may have affected the mosquito and tick spectrum captured (**Articles I, III–IV**). Random selection of absences from the historical data of other species may not reflect true absence of the species but could be due to having visited sites when one or more life stages was not active or to be collected or by using collection methods which excluded some species (**Articles I, III–IV)**. However, despite of the limitations we decided to use true absences instead of pseudo-absences, as recommended (Wisz & Guisan, 2009). In **Article IV**, we utilized crowdsourcing-based tick data as historical data and thus, there may be some uncertainties related to e.g. accuracy of collection sites (Laaksonen et al., 2017). There may also exist differences in species-specific factors between *Cx. pipiens* and *Cx. torrentium* and between *Ae. cinereus* and *Ae. geminus*, which were pooled in **Article III**.

Although use of host density data are useful when predicting species distributions, host densities may be directly and indirectly affected by climate being difficult to separate factors into causal and confounding (Scharlemann et al., 2008; Jaenson et al., 2012). Furthermore, there are other influential factors affecting the spatial patterns of species and disease which were not included in this project due to lack of the data. In **Article I**, landscape fragmentation indicators such as distance from forest patch, patch size, distance from patch edge and the landscape metric of PPU (patches per unit) could have added value to the suite of predictors as they have resulted significant statistical relations with mosquito distributions (Reiter & LaPointe, 2007; Richman et al., 2018). **Article II**, would have benefited from data on vaccination coverage because an effective TBE vaccination in risk localities after a few cases may make the risk in the nature appear low or even nonexistent. Furthermore, studies would have benefited the density data on small vertebrate hosts such as rodents (**Articles II and IV**) or migratory birds (e.g., passerines) (**Article III**) but these data were not available for studies at larger spatial scales. In addition, all articles would have benefited from micro-climate data. Micro-climate data (spatial resolution < 50 m) better represents thermal and moisture conditions than coarse-scale gridded climate data (≥ 1 km2) (Lembrechts et al., 2019), but due to computationally intensive production it was not yet feasible to apply in SDMs at larger scale. In addition to the microclimate, North-Atlantic Oscillation (NAO) index and wind climate (Laurila et al., 2021) which capture the wide spectrum of conditions related to precipitation (water and snow), winds and temperature could have added value, specifically, in **Articles I–III**.

Data quality is an important aspect of the input data. Usually species and disease data are heavily spatially autocorrelated (SA) and requires reduction of SA before modelling analysis. In **Article I**, environmental, anthropogenic and distance variables were spatially autocorrelated to some extent, which may have affected e.g. the precision of coefficients (Diniz-Filho et al., 2003). In **Article IV**, particularly, efforts were made to reduce SA from the tick observation data but despite this, we note the results may still be influenced by SA to some extent. In **Article II**, game animal density data were not real density data but hunting data, and this may have caused bias in the study results although hunting data correlates with animal densities (Cattadori et al., 2003; Jore et al., 2014; Jaenson et al., 2018). In

Articles II and **III**, we used patient case data which are always affected by disease awareness among physicians, especially when diagnosing SINV infection with serological evidence. Patient data (NIDR, 2021) were documented by municipality of residence and may not reflect actual municipality where patients were infected. Because patient data were documented based on the date of sample collection rather than the onset of symptoms, it may indicate a time lag to serological diagnosis. Furthermore, using presence-absence data instead of mosquito abundance data in all articles, loses information on the relative suitability of habitats when all presences are treated as equal, regardless of the abundance of the individuals that the habitat supports (Pearce & Boyce 2005). We also note that vector data collected and aggregated for this study are not suitable for abundance modelling in which seasonal data from several years are needed. Overall limitation of SDMs are that correlation does not imply causation, and the assumption that the species are in equilibrium with contemporary environmental conditions, not spreading, being indicative of environmental tolerances, and that SDMs cannot account for dispersal or interspecific interactions (Leathwick, 1998; Franklin et al., 2010; Drew et al., 2011). The predicted distributions for *I. persulcatus* should be considered with wary, as there are findings which may indicate that the species is still spreading (**Article IV**).

4.4 Implications and future prospects

As a significant part of emerging infectious disease outbreaks occur in Africa (Chan, 2010), our study is partly conducted at the very center of potential emergence of disease vectors and zoonotic pathogens. Mosquito species; *Cx. pipiens*, *St.* (*Ae.*) *aegypti*, *Ae. cinereus*, *Cs. morsitans* and *Cx. torrentium*, and tick species; *I. ricinus* and *I. persulcatus*, are well-known vectors of significant human pathogens in boreal and tropical landscapes. Predictive modelling of these vectors, together with spatial risk analyses of important VBDs; Pogosta disease and TBE, assist both public health authorities and scientific community.

Vector surveillance and studies on predicting their current and future distribution serve public health outcomes in several ways. The data generated here, help to find significant facts to assist the authorities and experts in decision-making to determine area-specific recommendations on vector control strategies and disease prevention. The results have implications for improving knowledge on disease prevention, by applying GIS and SDM approaches to identify risk areas and environmental determinants, and for optimizing the use of limited resources for mitigation strategies. The results can also be applied to other regions located in similar environmental conditions to study regions. Produced data is vital for better understanding of the current situation of vector and VBD distributions, and future threats to plan the correct and effective actions and control measures.

In this thesis, use of different platforms for SDM, sampling design and field collections gave new improvements. The use of biomod2 package in R and VECMAP software, showed that robust model outputs may be achieved both by using programming language and GIS mapping software. Sampling design was planned in **Article I** based on elevation interval, but in **Article IV**, we used ArcGIS and VECMAP to create GIS-based sampling design based on relative shares of suitable land cover classes within selected distance from roads. This new sampling approach improved the study design by maximizing a range of environmental values within a study area and ensuring accessibility to collection locations. Mosquito collection data in **Article**

I, were manually filled in collection sheets and coordinates were saved using a hand-held consumer-grade GNSS (Garmin model GPS-Map64s). A great amount of work and time was reduced when VECMAP mobile app was used in tick collections for **Article IV**.

Our results help to prioritize the research topics and funding to correct targets and actions in future. Produced data may be used in other studies with related study topics. The habitat suitability data on tick and mosquito species (**Articles I, III–IV**) may be used in studies modelling spatial patterns of disease they transmit. Prediction data of tick vectors *I. ricinus* and *I. persulcatus* were produced (**Article IV**) which can be utilized as predictor data for modelling the risk of TBPs in Finland, or in Nordic countries in future. Human TBE cases are increasing and there is a high need for further research (NIDR, 2022; Ministry of Social Affairs and Health, 2021). **Article II** was an insight into TBE distribution modelling, and our goal in future studies is to combine larger and more detailed datasets of human TBE cases from Scandinavia and create predictions across Northern Europe under current and future climate conditions. The habitat suitability data on SINV vector species may be used in future spatial modelling studies, which may be useful, especially, after SINV infection outbreak occurred in Finland in 2021. In near future, our aims are to identify space-time clustering and risk areas of SINV infections during the 2021 outbreak and to model the spatial distribution of SINV infections cases by using environmental, host and other influential determinants. Within this work, we also created a framework in which multidisciplinary and multi-organizational data were brought into a same database with same geographical units.

We note that the genus-level pooling of the species (**Article I**) mask species distribution determinants, and thus species-level data with species-level identification and screening for arboviruses will be targeted in future work in Kenya with larger and more detailed datasets. During the ongoing and following year, we aim to collect mosquitoes in 50 locations with varying land cover classes, and from houses with different building designs across Taita Hills during each dry and wet season. During the mosquito collections in 2016 (**Article I**), we found that a higher number of mosquitoes were found in houses with modern than with traditional design, and we noted that more research and actions are needed for the justification (Uusitalo, MSc Thesis 2017). To model the seasonal abundance of *St.* (*Ae.*) *aegypti*, to screen the circulating mosquito-borne viruses, and to provide practical solutions for locals to fight against MBDs, our plans are to continue research on the area. After all the collected mosquito and tick species data from Finland and Kenya (Culverwell et al., 2021; Korhonen, unpublished results; tick collections from VECLIMIT consortium; Finnish Mosquito Projects) are aggregated and screened for the pathogens, the data enables more accurate SDM of vectors but also of pathogens they carry. In Finland, we continue studying vectors, VBDs, and their distributions in Climate Change and Health- project within VECLIMIT consortium funded by Academy of Finland until the end of 2023.

The lack of high-resolution data on species, diseases, hosts and environment is a major challenge in SDMs. New crossnational databases on the distribution of vectors and VBPs, such as VectorNet coordinated by ECDC, enables researchers to use the species and pathogen data for SDM in real time across Europe (ECDC, 2022). In Finland, fine scale disease data are hard to receive due to its sensitive nature and due to strict data policies. Data request and application processes are complicated, time consuming and costly. To balance between privacy policy and spatiotemporal studies of emerging epidemics, solutions in governmental level should be done to achieve real time research serving public health outcomes (Siljander et al., 2022). To improve resolution of environmental and climatic factors, local field measurements such as fine environmental mapping or in-situ measurements should be taking in to account (Pradervand et al., 2014; Lembrechts et al., 2018). For example, the potential solution for the lack of microclimate data could be the use of unmanned aerial vehicles (UAVs) to map the sampling areas in real time at smaller scale studies, and to produce very high-resolution environmental data of even 3 cm (Anderson & Gaston, 2013; Fornace et al., 2014).

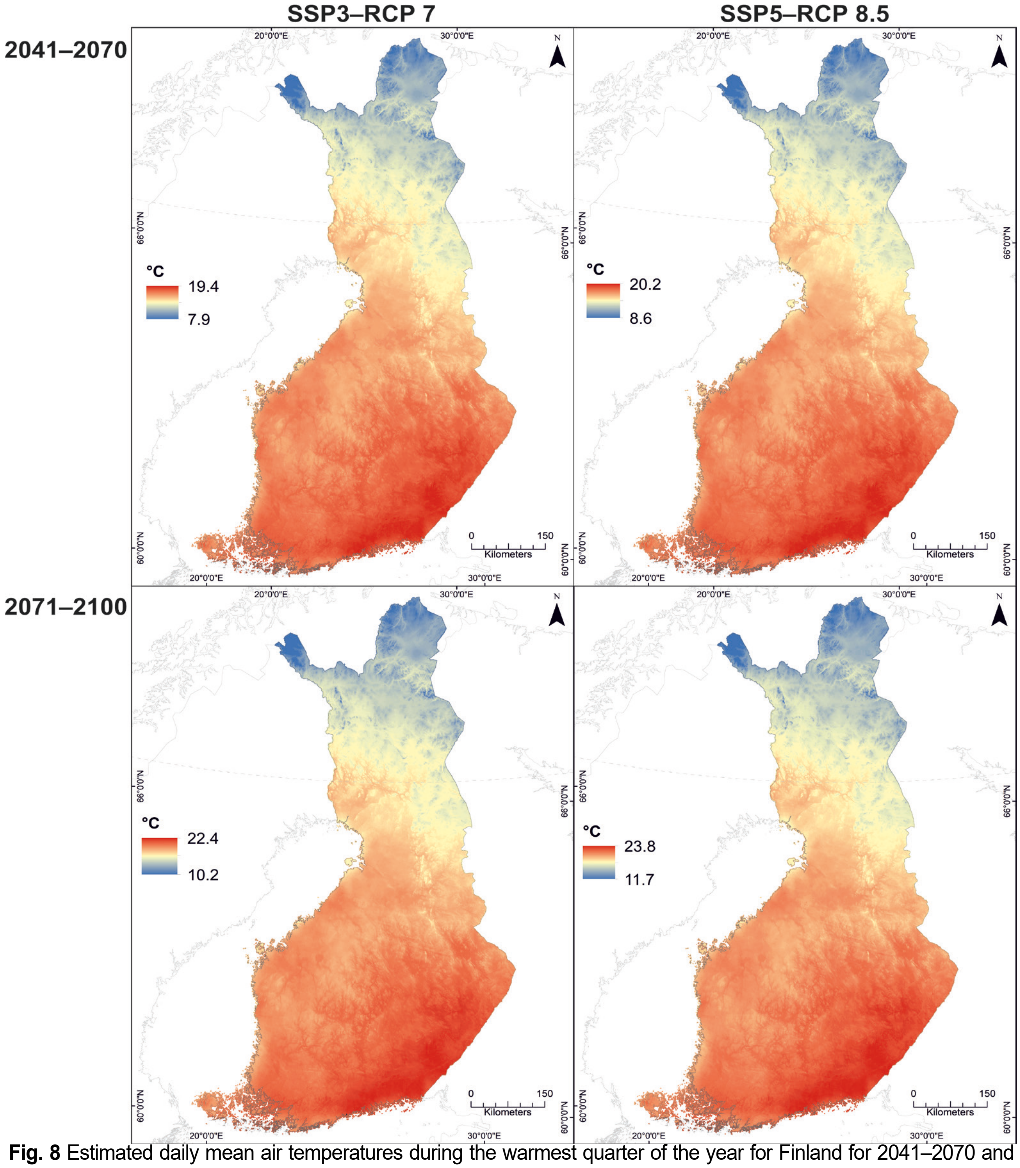

Fig. 8 Estimated daily mean air temperatures during the warmest quarter of the year for Finland for 2041–2070 and 2071–2100 by using IPSL-CM6A-LR global climate model (GCM) with SSP3–RCP7 and SSP5–RCP 8.5 scenarios (Karger et al., 2017). The warmest quarter of the year is the season when vector species are active and pathogen replication is most efficient.

Due to climate change, increases in air temperatures are expected in Northern Hemisphere during the ongoing century (Fig. 8.). Rising temperatures and higher precipitation bring favorable conditions for new invasive species and pathogens to spread in space. For example, *Ae. aegypti* and *Ae. albopictus* are invasive species which, in Europe, continue spreading northwards (Cunze et al., 2016; Kraemer et al., 2019). In Finland, the distribution of the taiga tick *I. persulcatus* may be shifting southwards (Laaksonen et al., 2017; Zakham et al., 2021).

Due to climate change and its impacts on weather patterns, new vector-borne pathogens may emerge and be transmitted from animals to humans if potential vector species and hosts are present. For example, WNV, causing fatal neurological disease (WHO, 2022f), may be a potential threat for the public health also in Finland in future. A recent study showed that *Cx. pipiens* and *Cx. torrentium*, species distributed across Finland (Culverwell et al., 2021), are able to transmit WNV through its saliva especially when daily mean temperature is 24°C during 14 consecutive days at minimum (Jansen et al., unpublished results). As daily mean temperatures are expected to rise for this temperature threshold when transmission rates in mosquitoes were most efficient by the end of 21st century (Jansen et al., unpublished results), there is a potential risk for new circulating VBD in the country. Due to increased threat for public health caused by arthropods, there is a higher demand for training and research on VBDs (Ministry of Social Affairs and Health, 2021) to produce information which supports public health planning.

5 Concluding remarks

Most emerging infectious disease outbreaks occur in the Tropics, although some outbreaks emerge in Nordic countries, with varying severity. The distribution of vectors and VBDs through GIS and SDM techniques are understudied in Finland despite their widespread use elsewhere in the world. Thus, our study is conducted both at the center of potential emergence of disease vectors and zoonotic pathogens, but also in Northern Europe in Finland, in the understudied region. This fact together with the current concern of an increased risk of vector-borne pathogens and a spread of invasive species due to changing weather patterns, adds need and requirements for increased research and concrete actions. In this thesis, environmentally suitable areas for the mosquito and tick species of medical importance in boreal and tropical landscapes, and the risk areas for two endemic VBDs in Finland were identified at first time.

With our prediction results in **Article I**, we note that both *Culex* and *Stegomyia* genera, of which species are both vectors of important VBVs in the Tropics, are present across the Taita Hills in the villages and rural areas being able to survive both with sparse and rich vegetation. In **Article II**, high-risk areas for TBE in Finland were identified based on influential environmental and host drivers, and under current and future climate. Especially field, forest, precipitation and host variables including white-tailed deer, European hare and raccoon dog density were found correlated with the occurrence of TBE. Based on future forecasts for 2041–2060 and 2061–2080 climate, a wider geographical extent of TBE risk was introduced in southern and western coast, and southern Lapland. In **Article III**, environmentally suitable areas were identified for the potential SINV vectors *Ae. cinereus/geminus*, *Cx. pipiens/torrentium* and *Cs. morsitans* in Finland, and risk areas for SINV infections were indicated based on vector, host and environmental data. Municipalities with an increased risk of Pogosta disease were characterized by high environmental suitability for *Ae. cinereus/geminus*; high densities of black grouse, capercaillie and hazel grouse; a high proportion of mixed forest in peatlands; and a high number of lakes. The risk of transmission was predicted to be greatest in eastern and central Finland, and in several municipalities in western Finland, excluding the coastal areas. In **Article IV**, we estimated the distributions of *Ixodes ricinus* and *I. persulcatus* across Finland by using historical data, and newly collected data, of which we also screened pathogens TBEV and *Borrelia*. A total of 500 ticks were analysed for the pathogens; with no ticks positive for TBEV and ≈ 47 % of tick pools positive for *Borrelia burgdorferi* s.l. High suitability areas for *I. ricinus* occurred throughout southern and central Finland up to the Central Ostrobothnia, excluding the narrow areas in Ostrobothnia and Pirkanmaa. For *I. persulcatus*, the regions northwards from Ostrobothnia along the northern coast up to southern Lapland, Kainuu, North Savo, North Karelia, and areas in Pirkanmaa and Päijät-Häme were estimated to be suitable areas. Based on the predictions, locations with higher air temperature, higher RH, higher precipitation sum and MIR, and higher densities of white-tailed deer, European hare and red fox were suitable for *I. ricinus*. For *I. persulcatus*, higher mean precipitation, higher densities of white-tailed deer, roe deer and mountain hare indicated higher probability of occurrence.

Together, these results have implications for improving knowledge on disease prevention, applying GIS and SDM approaches for identifying risk areas and environmental determinants, optimizing the use of limited resources for mitigation strategies and improving public health outcomes. The data generated in this project will help to find significant facts to assist the authorities and experts in decision-making on vector control strategies and disease prevention. Produced data help us to prioritize the research topics and funding to correct targets and actions in the following studies. The results can be applied to other regions located in similar environmental conditions to study regions. During and after the ongoing COVID-19 pandemic, it is even more vital to understand the benefits of spatial epidemic analyses to be better prepared for future disease outbreaks and new emergences of vector species, and to guide public health authorities and policymakers in implementing the correct and effective actions and control measures.

References

Aalto, J., Pirinen, P., & Jylhä, K. (2016). New gridded daily climatology of Finland: Permutation-based uncertainty estimates and temporal trends in climate. Journal of Geophysical Research: Atmospheres, 121(8), 3807-3823. https://doi.org/10.1002/2015JD024651.

Akhtar, M., Kraemer, M. U. G., & Gardner, L. M. (2019). A dynamic neural network model for predicting risk of Zika in real time. BMC Medicine, 17(1), 171. https://doi.org/10.1186/s12916-019-1389-3.

Alekseev, A. N., & Chunikhin, S. P. (1990). [The exchange of the tick-borne encephalitis virus between ixodid ticks feeding jointly on animals with a subthreshold level of viremia]. Med Parazitol (Mosk)(2), 48-50.

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43(6), 1223-1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Anderson, K., & Gaston, K. J. (2013). Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Frontiers in Ecology and the Environment, 11(3), 138-146. https://doi.org/10.1890/120150.

Anyah, R. O., & Qiu, W. (2012). Characteristic 20th and 21st century precipitation and temperature patterns and changes over the Greater Horn of Africa. International Journal of Climatology, 32, 347-363.

Apanaskevich, D.A., & Oliver, J.H. Jr. (1991). Life cycles and natural history of ticks. D.E. Sonenshine (Ed.), Biology of Ticks, 1, Oxford University

Press, New York.

Araújo, M., & New, M. (2007). Ensemble forecasting of species distributions. Trends Ecol Evol 22: 42-47. Trends in Ecology & Evolution, 22, 42-47. https://doi.org/10.1016/j.tree.2006.09.010.

Araújo, M. B., & Pearson, R. G. (2005). Equilibrium of species' distributions with climate. Ecography, 28(5), 693-695. https://doi.org/10.1111/j.2005.0906-7590.04253.x.

Austin, M. (2002). Spatial prediction of species distribution: An interface between ecological theory and statistical modelling. Ecological Modelling, 157. https://doi.org/10.1016/S0304-3800(02)00205-3.

Bakhvalova, V. N., Potapova, O. F., Panov, V. V., & Morozova, O. V. (2009). Vertical transmission of tick-borne encephalitis virus between generations of adapted reservoir small rodents. Virus Research, 140(1), 172-178. https://doi.org/10.1016/j.virusres.2008.12.001.

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution, 3(2), 327-338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Becker, N., Petrić, D., Zgomba, M., Boase, C., Madon, M., Dahl, C. H., & Kaiser, A. (2010). Mosquitoes and Their Control. https://doi.org/10.1007/978-3-540-92874-4.

Bespyatova, L. A., & Bugmyrin, S. V. (2021). On the Distribution of the Castor Bean Tick *Ixodes ricinus* (Acarina, *Ixodidae*) in the Republic of Karelia, Russia. Entomological Review, https://doi.org/10.1134/s0013873821040084.

Berger, K. A., Ginsberg, H. S., Dugas, K. D., Hamel, L. H., & Mather, T. N. (2014). Adverse moisture events predict seasonal abundance of Lyme disease vector ticks (*Ixodes scapularis*). Parasites & Vectors, 7(1), 181. https://doi.org/10.1186/1756-3305-7-181.

Brabec, M., Daniel, M., Malý, M., Danielová, V., Kott, I., & Beneš, Č. (2017). Analysis of meteorological effects on the incidence of tick-borne encephalitis in the Czech Republic over a thirty-year period. Virology: Research and Reviews, 1. https://doi.org/10.15761/VRR.1000103.

Brady, O. J., Johansson, M. A., Guerra, C. A., Bhatt, S., Golding, N., Pigott, D. M., Delatte, H., Grech, M. G., Leisnham, P. T., Maciel-de-Freitas, R., Styer, L. M., Smith, D. L., Scott, T. W., Gething, P. W., & Hay, S. I. (2013). Modelling adult *Aedes aegypti* and *Aedes albopictus* survival at different temperatures in laboratory and field settings. Parasites & Vectors, 6(1), 351. https://doi.org/10.1186/1756-3305-6-351.

Breiman, L., Friedman, J.H., Olshen, R.A., & Stone, C.J. (1984). Classification and regression trees. Chapman and Hall. New York, NY, US.

Breiman, L. (2001). Random Forests. Machine Learning, 45(1), 5-32. https://doi.org/10.1023/A:1010933404324.

Brummer-Korvenkontio, M., Saikku, P., Korhonen, P., Ulmanen, I., Reunala, T., & Karvonen, J. (1973). Arboviruses in Finland. IV. Isolation and characterization of Inkoo virus, a Finnish representative of the California group. Am J Trop Med Hyg, 22(3), 404-413.

Boitt, M., & Suleiman, M., (2021). Mapping of Freshwater Snails' Habitat—A Source of Transmitting Bilharzia in Mwea Sub-County, Kenya. Journal of Geoscience and Environment Protection, 9, 130-150. https://doi.org/10.4236/gep.2021.910010

Broberg, A., & Keskinen, A. (2022). Geodatabase over Taita Hills, Kenya.

Brown, L., Medlock, J., & Murray, V. (2014). Impact of drought on vector-borne diseases – how does one manage the risk? Public Health, 128(1), 29-37. https://doi.org/https://doi.org/10.1016/j.puhe.2013.09.006.

Brugger, K., Walter, M., Chitimia-Dobler, L., Dobler, G., & Rubel, F. (2017). Seasonal cycles of the TBE and Lyme borreliosis vector *Ixodes ricinus* modelled with time-lagged and interval-averaged predictors. Experimental & Applied Acarology, 73(3-4), 439-450. https://doi.org/10.1007/s10493-017-0197-8.

Brummer-Korvenkontio, M., Vapalahti, O., Kuusisto, P., Saikku, P., Manni, T., Koskela, P., Nygrén, T., Brummer-Korvenkontio, H., & Vaheri, A. (2002). Epidemiology of Sindbis virus infections in Finland 1981-96: possible factors explaining a peculiar disease pattern. Epidemiology and infection, 129, 335-345.

Bugmyrin, S., Bespyatova, L., Korotkov, Y., Burenkova, L., Belova, O., Romanova, L., Kozlovskaya, L., Karganova, G., & Ieshko, E. (2012). Distribution of *Ixodes ricinus* and *I. persulcatus* ticks in southern Karelia (Russia). Ticks and Tick-borne Diseases, 4. https://doi.org/10.1016/j.ttbdis.2012.07.004.

Bugmyrin, S. V., Bespyatova, L. A., & Korotkov, Y. S. (2019). Long-term dynamics of *Ixodes persulcatus* (Acari: *Ixodidae*) abundance in the north–west of its range (Karelia, Russia). Experimental and Applied Acarology, 77(2), 229-240. https://doi.org/10.1007/s10493-019-00342-y.

Bugmyrin, S. V., Bespyatova, L. A., Korotkov, Y. S., Burenkova, L. A., Belova, O. A., Romanova, L., Kozlovskaya, L. I., Karganova, G. G., & Ieshko, E. P. (2013). Distribution of *Ixodes ricinus* and *I. persulcatus* ticks in southern Karelia (Russia). Ticks Tick Borne Dis, 4(1-2), 57-62. https://doi.org/10.1016/j.ttbdis.2012.07.004.

Cadenas, F. M., Rais, O., Humair, P.-F., Douet, V., Moret, J., & Gern, L. (2007). Identification of Host Bloodmeal Source and *Borrelia burgdorferi*

feri Sensu Lato in Field-Collected *Ixodes* rici nus Ticks in Chaumont (Switzerland). Journal of Medical Entomology, 44(6), 1109-1117. https://doi.org/10.1093/jmedent/44.6.1109.

Caminade, C., McIntyre, K. M., & Jones, A. E. (2019). Impact of recent and future climate change on vector-borne diseases. Annals of the New York Academy of Sciences, 1436(1), 157-173. https://doi.org/10.1111/nyas.13950.

Cattadori, I., Haydon, D., Thirgood, S., & Hudson, P. (2003). Are indirect measures of abundance a useful index of population density? The case of red grouse harvesting. Oikos, 100. https://doi.org/10.1034/j.1600-0706.2003.12072.x.

Cayol, C., Koskela, E., Mappes, T., Siukkola, A., & Kallio, E. R. (2017). Temporal dynamics of the tick *Ixodes ricinus* in northern Europe: epidemiological implications. Parasites & Vectors, 10(1), 166. https://doi.org/10.1186/s13071-017-2112-x.

CDC. (2002). Centers for Disease Control and Prevention. Provisional surveillance summary of the West Nile virus epidemic--United States, January-November 2002. MMWR Morb Mortal Wkly Rep. 2002 Dec 20;51(50):1129-33. PMID: 12537287.

Chan, E. H., Brewer, T. F., Madoff, L. C., Pollack, M. P., Sonricker, A. L., Keller, M., Freifeld, C. C., Blench, M., Mawudeku, A., & Brownstein, J. S. (2010). Global capacity for emerging infectious disease detection. Proceedings of the National Academy of Sciences, 107(50), 21701-21706. https://doi.org/doi:10.1073/pnas.1006219107.

Charrel, R. N., Attoui, H., Butenko, A. M., Clegg, J. C., Deubel, V., Frolova, T. V., Gould, E. A., Gritsun, T. S., Heinz, F. X., Labuda, M., Lashkevich, V. A., Loktev, V., Lundkvist, A., Lvov, D. V., Mandl, C. W., Niedrig, M., Papa, A., Petrov, V. S., Plyusnin, A., Randolph, S., Süss, J., Zlobin, V. I., & de Lamballerie, X. (2004). Tick-borne virus diseases of human interest in Europe. Clinical Microbiology and Infection, 10(12), 1040-1055. https://doi.org/https://doi.org/10.1111/j.1469-0691.2004.01022.x.

Ciota, A. T., & Keyel, A. C. (2019). The Role of Temperature in Transmission of Zoonotic Arboviruses. Viruses, 11(11), 1013. https://doi.org/10.3390/v11111013.

Clark B.J.F., & Pellikka P.K.E. (2005). The development of a land use change detection methodology for mapping the Taita Hills, South-East Kenya. Proceedings of the 31st International Symposium of Remote Sensing of the Environment, 20–24 June 2005, *St.* Petersburg, Russia. CD-Rom publication.

Conley, A. K., Fuller, D. O., Haddad, N., Hassan, A. N., Gad, A. M., & Beier, J. C. (2014). Modeling the distribution of the West Nile and Rift Valley Fever vector *Culex pipiens* in arid and semi-arid regions of the Middle East and North Africa. Parasites & Vectors, 7, 289-289. https://doi.org/10.1186/1756-3305-7-289.

Cromley, E. K., & McLafferty, S. L. (2011). GIS and Public Health, Second Edition. Guilford Publications. https://books.google.fi/books?id=LeaEPg9vCrsC.

Culverwell, C. L., Uusitalo, R. J., Korhonen, E. M., Vapalahti, O. P., Huhtamo, E., & Harbach, R. E. (2021). The mosquitoes of Finland: updated distributions and bionomics. Medical and Veterinary Entomology, 35(1), 1-29. https://doi.org/https://doi.org/10.1111/mve.12475.

Cumming, G. S. (2000). Using between-model comparisons to fine-tune linear models of species ranges. Journal of Biogeography, 27(2), 441-455. https://doi.org/10.1046/j.1365-2699.2000.00408.x.

Cunze, S., Kochmann, J., Koch, L. K., & Klimpel, S. (2016). *Aedes albopictus* and Its Environmental Limits in Europe. PLoS One, 11(9), e0162116. https://doi.org/10.1371/journal.pone.0162116.

Czupryna, P., Moniuszko, A., Pancewicz, S., Zajkowska, O., Garkowski, A., Grygorczuk, S., Kondrusik, M., & Zajkowska, J. (2016). Influence of climatic, demographic and socioeconomic factors on tick-borne encephalitis incidence in 6 counties of Podlaskie region in 1994-2014. Przegl Epidemiol, 70(1), 21-25, 111-114.

Daniel, M., Malý, M., Danielová, V., Kříž, B., & Nuttall, P. (2015). Abiotic predictors and annual seasonal dynamics of *Ixodes ricinus*, the major disease vector of Central Europe. Parasit Vectors, 8, 478. https://doi.org/10.1186/s13071-015-1092-y.

Dautel, H., Kämmer, D., & Kahl, O. (2016). 24. How an extreme weather spell in winter can influence vector tick abundance and tick-borne disease incidence. In (pp. 335-349). https://doi.org/10.3920/978-90-8686-838-4_24.

Didan, K. (2015). MOD13A3 MODIS/Terra vegetation Indices Monthly L3 Global 1km SIN Grid V006. NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/MODIS/MOD13A3.006.

Diniz-Filho, J. A., Bini, L., & Hawkins, B. (2003). Spatial autocorrelation and red herrings in geographical ecology. GLOBAL ECOLOGY AND BIOGEOGRAPHY, 12, 53-64. https://doi.org/10.1046/j.1466-822X.2003.00322.x.

Dormann, C., McPherson, J., Araújo, M., Bivand, R., Bolliger, J., Carl, G., Davies, R., Hirzel, A., Jetz, W., Kissling, W., Kühn, I., Ohlemüller, R., Peres-Neto, P., Reineking, B., Schröder, B., Schurr, F., & Wilson, R. (2007). Methods to Account for Spatial Autocorrelation in the Analysis of Species Distributional Data: A Review. Ecography, 30, 609-628. https://doi.org/10.1111/j.2007.0906-7590.05171.x.

Drake, J. M., & Beier, J. C. (2014). Ecological niche and potential distribution of *Anopheles arabiensis* in Africa in 2050. Malaria Journal, 13(1), 213. https://doi.org/10.1186/1475-2875-13-213.

Drew, C. A., Wiersma, Y. F., & Huettmann, F. (2011). Predictive species and habitat modeling in landscape ecology: concepts and applications.

ECDC. (2014). European Centre for Disease Prevention and Control. Technical report. Guidelines for the surveillance of native mosquitoes in Europe. https://www.ecdc.europa.eu/sites/default/files/media/en/publications/Publications/surveillance-of%20native-mosquitoes%20-guidelines.pdf.

ECDC. (2021a). European Centre for Disease Prevention and Control. Technical report. Epidemiological situation of tick-borne encephalitis in the European Union and European Free Trade Association countries. https://www.ecdc.europa.eu/sites/default/files/media/en/publications/Publications/TBE-in-EU-EFTA.pdf.

ECDC. (2021b). European Centre for Disease Prevention and Control. Facts about Sindbis fever. https://www.ecdc.europa.eu/en/sindbis-fever/facts.

ECDC. (2021c). European Centre for Disease Prevention and Control. Factsheet about tick-borne encephalitis (TBE). https://www.ecdc.europa.eu/en/tick-borne-encephalitis/facts/factsheet.

ECDC. (2021d). European Centre for Disease Prevention and Control. Tick-borne encephalitis. https://www.ecdc.europa.eu/en/tick-borne-encephalitis.

ECDC. (2021e). European Centre for Disease Prevention and Control. Vector-borne diseases. https://www.ecdc.europa.eu/en/climate-change/climate-change-europe/vector-borne-diseases.

ECDC. (2022). European Centre for Disease Prevention and Control. European network for medical and veterinary entomology (VectorNet). https://www.ecdc.europa.eu/en/about-us/partnerships-and-networks/disease-and-laboratory-networks/vector-net.

Eisen, L., & Eisen, R. (2011). Using Geographic Information Systems and Decision Support Systems for the Prediction, Prevention, and Control of Vector-Borne Diseases. Annual review of entomology, 56, 41-61. https://doi.org/10.1146/annurev-ento-120709-144847.

Elshamy, M., Seierstad, I., & Sorteberg, A. (2008). Impacts of climate change on Blue Nile flows using bias-corrected GCM scenarios. Hydrology and Earth System Sciences Discussions, 5. https://doi.org/10.5194/hessd-5-1407-2008.

Erdogan, E., Pellikka, P., & Clark, B. (2011). Modelling the impact of land-cover change on potential soil loss in the Taita Hills, Kenya, between 1987 and 2003 using remote-sensing and geospatial data. International Journal of Remote Sensing, 32, 5919-5945. https://doi.org/10.1080/01431161.2010.499379.

Ernek E., Kozuch O., Gresikova M., Nosek J., & Sekeyova M. (1973). Isolation of Sindbis virus from the reed warbler (*Acrocephalus scirpaceus*) in Slovakia. Acta Virologica, 17, 359–361.

ESA. (2016). European Satellite Agency. Copernicus Sentinel data, 2016. Sentinel-2A MSI Level-1C. https://sentinel.esa.int/web/sentinel/user-guides/sentinel-2-msi/product-types/level-1c.

Espmark, A., & Niklasson, B. (1984). Ockelbo Disease in Sweden: Epidemiological, Clinical, and Virological Data from the 1982 Outbreak. The American Journal of Tropical Medicine and Hygiene, 33(6), 1203-1211. https://doi.org/10.4269/ajtmh.1984.33.1203.

Fatima, S., Atif, S., Rasheed, S. B., Zaidi, F., & Hussain, E. (2016). Species Distribution Modeling of *Aedes aegypti* in two dengue-endemic regions of Pakistan. Tropical medicine & international health: TM & IH, 21. https://doi.org/10.1111/tmi.12664.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37(12), 4302-4315. https://doi.org/10.1002/joc.5086.

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation, 24(1), 38-49. https://doi.org/10.1017/S0376892997000088.

FMI. (2011). Finnish Meteorological Institute. ACCLIM II-hankkeen lyhyt loppuraportti 2011. Ilmatieteen laitos, Helsinki. http://ilmatieteenlaitos.fi/c/document_library/get_file?uuid=f72ce783-0bae-4468-b67e-8e280bec1452&groupId=30106.

FMI. (2022a). Finnish Meteorological Intitute. Climateguide.fi. Finland´s changing climate. https://ilmasto-opas.fi/en/ilmastonmuutos/suomen-muuttuva-ilmasto/-/artikkeli/8c965cac-6707-4a60-bef9-712f038320be/suomen-muuttuva-ilmasto.htm.

FMI. (2021a). Finnish Meteorological Institute. Seasons in Finland. https://en.ilmatieteenlaitos.fi/seasons-in-finland.

Fornace, K. M., Drakeley, C. J., William, T., Espino, F., & Cox, J. (2014). Mapping infectious disease landscapes: unmanned aerial vehicles and epidemiology. Trends Parasitol, 30(11), 514-519. https://doi.org/10.1016/j.pt.2014.09.001.

Francy, D. B., Jaenson, T. G., Lundström, J. O., Schildt, E. B., Espmark, A., Henriksson, B., & Niklasson, B. (1989). Ecologic studies of mosquitoes and birds as hosts of Ockelbo virus in Sweden and isolation of Inkoo and Batai viruses from mosquitoes. Am J Trop Med Hyg, 41(3), 355-363.

Franklin, J. (2010). Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press. https://doi.org/DOI: 10.1017/CBO9780511810602.

Friedman, J.H. (1991). "Multivariate Adaptive Regression Splines." Ann. Stati*St.* 19 (1), 1 - 67. https://doi.org/10.1214/aos/1176347963.

Gethmann, J., Hoffmann, B., Kasbohm, E., Süss, J., Habedank, B., Conraths, F. J., Beer, M., & Klaus, C. (2020). Research paper on abiotic factors and their influence on *Ixodes ricinus* activity—observations over a two-year period at several tick collection sites in Germany. Parasitology Research, 119(5), 1455-1466. https://doi.org/10.1007/s00436-020-06666-8.

Go, Y. Y., Balasuriya, U. B. R., & Lee, C.-K. (2014). Zoonotic encephalitides caused by arboviruses: transmission and epidemiology of alphaviruses and flaviviruses. Clinical and experimental vaccine research, 3(1), 58-77. https://doi.org/10.7774/cevr.2014.3.1.58.

Gray, J. S. (1998). Review The ecology of ticks transmitting Lyme borreliosis. Experimental & Applied Acarology, 22(5), 249-258. https://doi.org/10.1023/A:1006070416135.

Gray, J. S., Dautel, H., Estrada-Peña, A., Kahl, O., & Lindgren, E. (2009). Effects of Climate Change on Ticks and Tick-Borne Diseases in Europe. Interdisciplinary Perspectives on Infectious Diseases, 2009, 593232. https://doi.org/10.1155/2009/593232.

Gray, J. S., Kahl, O., Lane, R. S., Levin, M. L., & Tsao, J. I. (2016). Diapause in ticks of the medically important *Ixodes ricinus* species complex. Ticks and Tick-borne Diseases, 7(5), 992-1003. https://doi.org/https://doi.org/10.1016/j.ttbdis.2016.05.006.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. Ecological Modelling, 135(2). 147-186. https://doi.org/https://doi.org/10.1016/S0304-3800(00)00354-9.

Hall, D. K. & Riggs, G. A. (2015). MODIS/Terra Snow Cover Monthly L3 Global 0.05Deg CMG, Version 6. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. https://doi.org/10.5067/MODIS/MOD10CM.006.

Handeland, K., Qviller, L., Vikøren, T., Viljugrein, H., Lillehaug, A., & Davidson, R. K. (2013). *Ixodes ricinus* infestation in free-ranging cervids in Norway—A study based upon ear examinations of hunted animals. Veterinary Parasitology, 195(1), 142-149. https://doi.org/10.1016/j.vetpar.2013.02.012.

Hanley, J. A., & McNeil, B. J. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology, 143(1), 29-36. https://doi.org/10.1148/radiology.143.1.7063747.

Harbach, R. (2012). *Culex pipiens*: Species Versus Species Complex – Taxonomic History and Perspective. Journal of the American Mosquito Control Association, 28, 10-23. https://doi.org/10.2987/8756-971X-28.4.10.

Hastie, T. J., & Tibshirani, R. J. (2017). Generalized Additive Models. https://doi.org/10.1201/9780203753781.

Hesson, J., Rettich, F., Merdic, e. b. u. h., Vignjević, G., Östman, Ö., Schäfer, M., Schaffner, F., Foussadier, R., Besnard, G., Medlock, J., Scholte, E. J., & Lundström, J. (2014). The arbovirus vector *Culex torrentium* is more prevalent than *Culex pipiens* in northern and central Europe. Medical and Veterinary Entomology, 28, 179–186. https://doi.org/10.1111/mve.12024.

Hesson, J. C., Verner-Carlsson, J., Larsson, A., Ahmed, R., Lundkvist, Å., & Lundström, J. O. (2015). *Culex torrentium* Mosquito Role as Major Enzootic Vector Defined by Rate of Sindbis Virus Infection, Sweden, 2009. Emerging infectious diseases, 21(5), 875-878. https://doi.org/10.3201/eid2105.141577.

Heyman, P., Cochez, C., Hofhuis, A., Giessen, J., Sprong, H., Porter, S., Losson, B., Saegerman, C., Donoso Mantke, O., Niedrig, M., & Papa, A. (2010). A clear and present danger: Tick-borne diseases in Europe. Expert review of anti-infective therapy, 8, 33-50. https://doi.org/10.1586/eri.09.118.

Hijmans, Robert, J., Cameron, Susan, E., Parra, J., Juan, L., Jones, Peter, G., Jarvis, & Andy. (2005). Very high- resolution interpolated climate surfaces for global land areas. In (pp. 14).

Hijmans, R.J., et al. (2015) Dismo: Species Distribution Modeling. R Package Version 1.0-12.http://CRAN.R-project.org/package=dismo.

Hirzel, A., & Guisan, A. (2002). Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling, 157, 331-341. https://doi.org/10.1016/S0304-3800(02)00203-X.

Hofmeester, T. R., Sprong, H., Jansen, P. A., Prins, H. H. T., & van Wieren, S. E. (2017). Deer presence rather than abundance determines the population density of the sheep tick, *Ixodes ricinus*, in Dutch forests. Parasit Vectors, 10(1), 433. https://doi.org/10.1186/s13071-017-2370-7.

Huang, Y.-M. (1979). Medical Entomology Studies - XI. The Subgenus *Stegomyia* of *Aedes* in the Oriental Region with Keys to the Species (Diptera: *Culicidae*).

Huang, Y. M. (1986). *Aedes* (*Stegomyia*) bromeliae (Diptera: *Culicidae*), the yellow fever virus vector in East Africa. J Med Entomol, 23(2), 196-200. https://doi.org/10.1093/jmedent/23.2.196.

Huang, YM. (1990). The subgenus *Stegomyia* of *Aedes* in the Afrotropical region, I. The Africanus group of species (Diptera: *Culicidae*). Contributions of the American Entomological Institute. 26,1-90.

Huang, Y.-M. (2001). A pictorial key for the identification of the subfamilies of *Culicidae*, genera of *Culicinae*, and subgenera of *Aedes* of the Afrotropical

Region (Diptera: *Culicidae*). Proc. Entomol. Soc. Wash., 103. pp. 1-53.

Huang, Y.-M. (2004). The subgenus *Stegomyia* of *Aedes* in the Afrotropical Region with keys to the species (Diptera: *Culicidae*). Zootaxa, 700 (1), pp. 1-120.

Hubálek, Z. (2008). Mosquito-borne viruses in Europe. Parasitology Research, 103 Suppl 1, S29-43. https://doi.org/10.1007/s00436-008-1064-7.

Hutchinson, M. F. (1991). The application of thin plate splines to continent wide data assimilation, Data Assimilation Systems. BMRC Research Report NO. 27, 104-113.

Jääskeläinen, A. E., Tikkakoski, T., Uzcátegui, N. Y., Alekseev, A. N., Vaheri, A., & Vapalahti, O. (2006). Siberian subtype tickborne encephalitis virus, Finland. Emerg Infect Dis, 12(10), 1568-1571. https://doi.org/10.3201/eid1210.060320.

Jaenson, T. G. T., Jaenson, D. G. E., Eisen, L., Petersson, E., & Lindgren, E. (2012). Changes in the geographical distribution and abundance of the tick *Ixodes ricinus* during the past 30 years in Sweden. Parasites & Vectors, 5, 8-8. https://doi.org/10.1186/1756-3305-5-8.

Jaenson, T. G. T., Petersson, E. H., Jaenson, D. G. E., Kindberg, J., Pettersson, J. H. O., Hjertqvist, M., Medlock, J. M., & Bengtsson, H. (2018). The importance of wildlife in the ecology and epidemiology of the TBE virus in Sweden: incidence of human TBE correlates with abundance of deer and hares. Parasites & Vectors, 11(1), 477. https://doi.org/10.1186/s13071-018-3057-4.

Jaenson, T. G. T., Värv, K., Fröjdman, I., Jääskeläinen, A., Rundgren, K., Versteirt, V., Estrada-Peña, A., Medlock, J. M., & Golovljova, I. (2016). First evidence of established populations of the taiga tick *Ixodes persulcatus* (Acari: *Ixodidae*) in Sweden. Parasites & Vectors, 9(1), 377. https://doi.org/10.1186/s13071-016-1658-3

Jalava, K., Sane, J., Ollgren, J., Ruuhela, R., Rätti, O., Kurkela, S., Helle, P., Hartonen, S., Pirinen, P., Vapalahti, O., & Kuusi, M. (2012). Climatic, ecological and socioeconomic factors as predictors of Sindbis virus infections in Finland. Epidemiology and infection, 141, 1-10. https://doi.org/10.1017/S095026881200249X.

Jounio, U., Renko, M., & Uhari, M. (2010). An Outbreak of Holarctica-Type Tularemia in Pediatric Patients. The Pediatric Infectious Disease Journal, 29(2), 160-162. https://doi.org/10.1097/INF.0b013e3181b9a6b4.

Jore, S., Vanwambeke, S. O., Viljugrein, H., Isaksen, K., Kristoffersen, A. B., Woldehiwet, Z., Johansen, B., Brun, E., Brun-Hansen, H., Westermann, S., Larsen, I.-L., Ytrehus, B., & Hofshagen, M. (2014). Climate and environmental change drives *Ixodes ricinus* geographical expansion at the northern range margin. Parasites & Vectors, 7(1), 11. https://doi.org/10.1186/1756-3305-7-11.

Jore, S., Viljugrein, H., Hofshagen, M., Brun-Hansen, H., Kristoffersen, A. B., Nygård, K., Brun, E., Ottesen, P., Sævik, B. K., & Ytrehus, B. (2011). Multi-source analysis reveals latitudinal and altitudinal shifts in range of *Ixodes ricinus* at its northern distribution limit. Parasites & Vectors, 4(1), 84. https://doi.org/10.1186/1756-3305-4-84.

Jupp, P. G., Blackburn, N. K., Thompson, D. L., & Meenehan, G. M. (1986). Sindbis and West Nile virus infections in the Witwatersrand-Pretoria region. S Afr Med J, 70(4), 218-220.

Jylhä, K., Ruosteenoja, K., Räisänen, J., & Fronzek, S. (2012). Ilmasto. Julkaisussa: Ruuhela, R. (toim.) 2012. Miten väistämättömään ilmastonmuutokseen voidaan varautua? - yhteenveto suomalaisesta sopeutumistutkimuksesta eri toimialoilla. Maa- ja metsätalousministeriö, Helsinki. MMM:n julkaisuja 2011(6). 16–23. http://www.mmm.fi/attachments/mmm/julkaisut/julkaisusarja/2012/67Wke725j/MMM_julkaisu_2012_6.pdf.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. Scientific Data, 4(1), 170122. https://doi.org/10.1038/sdata.2017.122.

Karungu, S., Atoni, E., Ogalo, J., Mwaliko, C., Agwanda, B., Yuan, Z., & Hu, X. (2019). Mosquitoes of Etiological Concern in Kenya and Possible Control Strategies. Insects, 10(6), 173. https://doi.org/10.3390/insects10060173.

Kim, H. C., Han, S. H., Chong, S. T., Klein, T. A., Choi, C.-Y., Nam, H.-Y., Chae, H.-Y., Lee, H., Ko, S., Kang, J.-G., & Chae, J.-S. (2011). Ticks collected from selected mammalian hosts surveyed in the Republic of Korea during 2008-2009. The Korean journal of parasitology, 49(3), 331-335. https://doi.org/10.3347/kjp.2011.49.3.331.

Kimuyu, J. S. (2021). Comparative spatial–temporal analysis and predictive modeling of climate change-induced malaria vectors' invasion in new hotspots in Kenya. SN Applied Sciences, 3(8), 741. https://doi.org/10.1007/s42452-021-04722-1.

Kjær, L. J., Soleng, A., Edgar, K. S., Lindstedt, H. E. H., Paulsen, K. M., Andreassen, Å. K., Korslund, L., Kjelland, V., Slettan, A., Stuen, S., Kjellander, P., Christensson, M., Teräväinen, M., Baum, A., Klitgaard, K., & Bødker, R. (2019). Predicting and mapping human risk of exposure to *Ixodes ricinus* nymphs using climatic and environmental data, Denmark, Norway and Sweden, 2016. Eurosurveillance, 24(9), 1800101. https:// doi.org/10.2807/1560-7917.ES.2019.24.9.1800101.

Klemola, T., Sormunen, J. J., Mojzer, J., Mäkelä, S., & Vesterinen, E. J. (2019). High tick abundance and diversity of tick-borne pathogens in a Finnish city. Urban Ecosystems, 22(5), 817-826. https://doi.org/10.1007/s11252-019-00854-w.

Korhonen, E. M., Suvanto, M. T., Uusitalo, R., Faolotto, G., Smura, T., Sane, J., Vapalahti, O., & Huhtamo, E. (2020). Sindbis Virus Strains of Divergent Origin Isolated from Humans and Mosquitoes During a Recent Outbreak in Finland. Vector borne and zoonotic diseases (Larchmont, N.Y.), 20(11), 843-849. https://doi.org/10.1089/vbz.2019.2562.

Kraemer, M. U. G., Reiner, R. C., Brady, O. J., Messina, J. P., Gilbert, M., Pigott, D. M., Yi, D., Johnson, K., Earl, L., Marczak, L. B., Shirude, S., Davis Weaver, N., Bisanzio, D., Perkins, T. A., Lai, S., Lu, X., Jones, P., Coelho, G. E., Carvalho, R. G., Van Bortel, W., Marsboom, C., Hendrickx, G., Schaffner, F., Moore, C. G., Nax, H. H., Bengtsson, L., Wetter, E., Tatem, A. J., Brownstein, J. S., Smith, D. L., Lambrechts, L., Cauchemez, S., Linard, C., Faria, N. R., Pybus, O. G., Scott, T. W., Liu, Q., Yu, H., Wint, G. R. W., Hay, S. I., & Golding, N. (2019). Past and future spread of the arbovirus vectors *Aedes aegypti* and *Aedes albopictus*. Nature Microbiology, 4(5), 854-863. https://doi.org/10.1038/s41564-019-0376-y.

Kruijff, M., Hendrickx, G., Wint, W., & Ginati, A. (2011). Mapping habitats for vectors of infectious disease: VECMAP.

Kurkela, S., Manni, T., Myllynen, J., Vaheri, A., & Vapalahti, O. (2005). Clinical and laboratory manifestations of Sindbis virus infection: prospective study, Finland, 2002-2003. J Infect Dis, 191(11), 1820-1829. https://doi.org/10.1086/430007.

Kurkela, S., Rätti, O., Huhtamo, E., Uzcátegui, N. Y., Nuorti, J. P., Laakkonen, J., Manni, T., Helle, P., Vaheri, A., & Vapalahti, O. (2008). Sindbis virus infection in resident birds, migratory birds, and humans, Finland. Emerging infectious diseases, 14(1), 41-47. https://doi.org/10.3201/eid1401.070510.

Laaksonen, M., Klemola, T., Feuth, E., Sormunen, J. J., Puisto, A., Mäkelä, S., Penttinen, R., Ruohomäki, K., Hänninen, J., Sääksjärvi, I. E., Vuorinen, I., Sprong, H., Hytönen, J., & Vesterinen, E. J. (2018). Tick-borne pathogens in Finland: comparison of *Ixodes ricinus* and *I. persulcatus* in sympatric and parapatric areas. Parasites & Vectors, 11(1), 556. https://doi.org/10.1186/s13071-018-3131-y.

Laaksonen, M., Sajanti, E., Sormunen, J. J., Penttinen, R., Hanninen, J., Ruohomaki, K., Saaksjarvi, I., Vesterinen, E. J., Vuorinen, I., Hytonen, J., & Klemola, T. (2017). Crowdsourcing-based nationwide tick collection reveals the distribution of *Ixodes ricinus* and *I. persulcatus* and associated pathogens in Finland. Emerg Microbes Infect, 6(5), e31. https://doi.org/10.1038/emi.2017.17.

Labuda, M., Jones, L. D., Williams, T., & Nuttall, P. A. (1993). Enhancement of tick-borne encephalitis virus transmission by tick salivary gland extracts. Medical and Veterinary Entomology, 7(2), 193-196. https://doi.org/10.1111/j.1365-2915.1993.tb00674.x.

Laine, M., Luukkainen, R., & Toivanen, A. (2005). Sindbis viruses and other alphaviruses as cause of human arthritic disease. Journal of internal medicine, 256, 457-471. https://doi.org/10.1111/j.1365-2796.2004.01413.x.

Laurila, T.K., Gregow, H., Corner, J.S., & Sinclair, V. (2021). Characteristics of extratropical cyclones and precursors to windstorms in northern Europe. Weather and Climate Dynami*Cs*. 2(4),1111-1130. https://doi.org/10.5194/wcd-2-1111-2021.

Leathwick, J. R. (1998). Are New Zealand's Nothofagus species in equilibrium with their environment? Journal of Vegetation Science, 9(5), 719-732. https://doi.org/10.2307/3237290.

Lembrechts, J. J., Nijs, I., & Lenoir, J. (2019). Incorporating microclimate into species distribution models. Ecography, 42(7), 1267-1279. https://doi.org/10.1111/ecog.03947.

Lindgren, E., & Gustafson, R. (2001). Tick-borne encephalitis in Sweden and climate change. Lancet, 358(9275), 16-18. https://doi.org/10.1016/s0140-6736(00)05250-8.

Lindquist, L., & Vapalahti, O. (2008). Tick-borne encephalitis. The Lancet, 371(9627), 1861-1871. https://doi.org/10.1016/S0140-6736(08)60800-4.

Lundkvist, Å., Wallensten, A., Vene, S., & Hjertqvist, M. (2011). Tick-borne encephalitis increasing in Sweden, 2011. Euro surveillance: bulletin européen sur les maladies transmissibles = European communicable disease bulletin, 16. https://doi.org/10.2807/ese.16.39.19981-en.

Lundström, J., Schäfer, M., Hesson, J., Blomgren, E., Lindström, A., Wahlqvist, P., Halling, A., Hagelin, A., Ahlm, C., Evander, M., Broman, T., Forsman, M., & Persson Vinnersten, T. (2013). The geographic distribution of mosquito species in Sweden. Journal of the European Mosquito Control Association, 31, 35.

Lundström, J. O., Hesson, J. C., Schäfer, M. L., Östman, Ö., Semmler, T., Bekaert, M., Weidmann, M., Lundkvist, Å., & Pfeffer, M. (2019). Sindbis virus polyarthritis outbreak signalled by virus prevalence in the mosquito vectors. PLOS Neglected Tropical Diseases, 13(8), e0007702. https://doi.org/10.1371/journal.pntd.0007702.

Lundström, J. O., Lindström, K. M., Olsen, B., Dufva, R., & Krakower, D. S. (2001). Prevalence of sindbis virus neutralizing antibodies among Swedish passerines indicates that thrushes are the main amplifying hosts. J Med Entomol, 38(2), 289-297. https://doi.org/10.1603/0022-2585-38.2.289.

Lundström, J. O., Vene, S., Espmark, A., Engvall, M., & Niklasson, B. (1991). Geographical and temporal distribution of Ockelbo disease in Sweden. Epidemiol Infect, 106(3), 567-574. https://doi.org/10.1017/s0950268800067637.

Masika, M. M., Korhonen, E. M., Smura, T., Uusitalo, R., Vapalahti, K., Mwaengo, D., Jääskeläinen, A. J., Anzala, O., Vapalahti, O., & Huhtamo, E. (2020). Detection of dengue virus type 2 of Indian origin in acute febrile patients in rural Kenya. PLoS Negl Trop Dis, 14(3), e0008099. https://doi.org/10.1371/journal.pntd.0008099.

McCullagh, P., & Nelder, J.A. (1989). Generalized Linear Models. 2nd Edition, Chapman and Hall, London.http://dx.doi.org/10.1007/978-1-4899-3242-6.

Medlock, J. M., Hansford, K. M., Bormane, A., Derdakova, M., Estrada-Peña, A., George, J.-C., Golovljova, I., Jaenson, T. G. T., Jensen, J.-K., Jensen, P. M., Kazimirova, M., Oteo, J. A., Papa, A., Pfister, K., Plantard, O., Randolph, S. E., Rizzoli, A., Santos-Silva, M. M., Sprong, H., Vial, L., Hendrickx, G., Zeller, H., & Van Bortel, W. (2013). Driving forces for changes in geographical distribution of *Ixodes ricinus* ticks in Europe. Parasites & Vectors, 6(1), 1. https://doi.org/10.1186/1756-3305-6-1.

Medlock, J. M., & Leach, S. A. (2015). Effect of climate change on vector-borne disease risk in the UK. Lancet Infect Dis, 15(6), 721-730. https://doi.org/10.1016/s1473-3099(15)70091-5.

Medlock, J. M., Snow, K. R., & Leach, S. (2005). Potential transmission of West Nile virus in the British Isles: an ecological review of candidate mosquito bridge vectors. Med Vet Entomol, 19(1), 2-21. https://doi.org/10.1111/j.0269-283X.2005.00547.x.

Messina, J. P., Brady, O. J., Golding, N., Kraemer, M. U. G., Wint, G. R. W., Ray, S. E., Pigott, D. M., Shearer, F. M., Johnson, K., Earl, L., Marczak, L. B., Shirude, S., Davis Weaver, N., Gilbert, M., Velayudhan, R., Jones, P., Jaenisch, T., Scott, T. W., Reiner, R. C., & Hay, S. I. (2019). The current and future global distribution and population at risk of dengue. Nature Microbiology, 4(9), 1508-1515. https://doi.org/10.1038/s41564-019-0476-8.

Michelet, L., Delannoy, S., Devillers, E., Umhang, G., Aspan, A., Juremalm, M., Chirico, J., van der Wal, F. J., Sprong, H., Boye Pihl, T. P., Klitgaard, K., Bodker, R., Fach, P., & Moutailler, S. (2014). High-throughput screening of tick-borne pathogens in Europe. Front Cell Infect Microbiol, 4, 103. https://doi.org/10.3389/fcimb.2014.00103.

Michelitsch, A., Wernike, K., Klaus, C., Dobler, G., & Beer, M. (2019). Exploring the Reservoir Hosts of Tick-Borne Encephalitis Virus. Viruses, 11(7), 669. https://doi.org/10.3390/v11070669.

Miller, J., & Franklin, J. (2002). Modeling the distribution of four vegetation alliances using generalized linear models and classification trees with spatial dependence. Ecological Modelling, 157(2), 227-247. https://doi.org/10.1016/S0304-3800(02)00196-5.

Ministry of Agriculture and Forestry of Finland. (2022). Forest resources in Finland. https://mmm.fi/en/forests/forestry/forest-resources.

Ministry of Social Affairs and Health. (2021). Raportteja ja muistioita 2021(16). Uusien vektorivälitteisten tautien mahdollinen saapuminen Suomeen ilmastonmuutoksen ja ihmisten liikkuvuuden kylkiäisinä. http://urn.fi/URN:ISBN:978-952-00-5402-1.

Mohrig, W. (1969). Die Culiciden Deutschlands. Untersuchungen zur Taxonomie, Biologie und Ökologie der einheimischen Stechmücken. Parasitologische Schriftenreihe, 18, 1-260.

Moise, A. F., & Hudson, D. A. (2008). Probabilistic predictions of climate change for Australia and southern Africa using the reliability ensemble average of IPCC CMIP3 model simulations. Journal of Geophysical Research (Atmospheres), 113, D15113. https://doi.org/10.1029/2007jd009250.

Movila, A., Dubinina, H. V., Sitnicova, N., Bespyatova, L., Uspenskaia, I., Efremova, G., Toderas, I., & Alekseev, A. N. (2014). Comparison of tick-borne microorganism communities in *Ixodes* spp. of the *Ixodes ricinus* species complex at distinct geographical regions. Experimental and Applied Acarology, 63(1), 65-76. https://doi.org/10.1007/s10493-013-9761-z.

MTI. (2022a). Mosquito Taxonomic Inventory. *Culex* classification. https://mosquito-taxonomic-inventory.myspecies.info/ltemgt*Culex*ltemgt-classification.

MTI. (2022b). Mosquito Taxonomic Inventory. Subgenus *Culex* Linnaeus.
https://mosquito-taxonomic-inventory.myspecies.info/Subgenus-*Culex*.

MTI. (2022c). Mosquito Taxonomic Inventory. Genus *Stegomyia* Theobald, 1901. https://mosquito-taxonomic-inventory.myspecies.info/genus-*Stegomyia*-theobald-1901.

Mysterud, A., Hügli, C., & Viljugrein, H. (2021). Tick infestation on medium–large-sized mammalian hosts: are all equally suitable to *Ixodes ricinus* adults? Parasites & Vectors, 14(1), 254. https://doi.org/10.1186/s13071-021-04775-6.

Nadolny, R., & Gaff, H. (2018). Modelling the effects of habitat and hosts on tick invasions. Letters in Biomathematics, 5, 2-29. https://doi.org/10.1080/23737867.2017.1412811.

NIDR. (2022). Finnish National Infectious Diseases Register. Finnish National Institute of Health and Welfare.https://thl.fi/fi/web/infektiotaudit-ja-rokotukset/seurantajarjestelmat-ja-rekisterit/tartuntatautirekisteri.

NLS of Finland. (2019). National Land Survey of Finland. Elevation model 2019, 10 m x 10 m. CSC - IT Center for Science Ltd. http://urn.fi/urn:nbn:fi:csc-kata00001000000000000622

NRIF. (2019). National Resources Institute Finland. LUKE: Metsäkanalintujen kannat edelleen kasvussa. https://riista.fi/luke-metsakanalintujen-kannat-edelleen-kasvussa/?doing_wp_cron=1646923235.8417429924011230468750.

NRIF. (2020a). National Resources Institute Finland. Hunting data. https://www.riistakolmiot.fi/riistakolmio/.

NRIF. (2020b). National Resources Institute Finland. METSO (Tetrao urogallus).https://www.riistakolmiot.fi/animal/metso-tetrao-urogallus/

NRIF. (2021). National Resources Institute Finland. Snow-track data. https://www.riistakolmiot.fi/riistakolmio/.

NRIF. (2022). National Resources Institute Finland. Luke: Metsäkauriiden ja valkohäntäpeurojen määrät ruokintapaikoilla suuria, myös kuokkavieraita paljon. https://riista.fi/luke-metsakauriiden-ja-valkohantapeurojen-maarat-ruokintapaikoilla-suuria-myos-kuokkavieraita-paljon/.

Nykiforuk, C. I. J., & Flaman, L. M. (2011). Geographic Information Systems (GIS) for Health Promotion and Public Health: A Review. Health Promotion Practice, 12(1), 63-73. https://doi.org/10.1177/1524839909334624.

O'Leary, D. R., Marfin, A. A., Montgomery, S. P., Kipp, A. M., Lehman, J. A., Biggerstaff, B. J., Elko, V. L., Collins, P. D., Jones, J. E., & Campbell, G. L. (2004). The epidemic of West Nile virus in the United States, 2002. Vector borne and zoonotic diseases (Larchmont, N.Y.), 4(1), 61-70. https://doi.org/10.1089/153036604773083004.

Ochieng, A. O., Nanyingi, M., Kipruto, E., Ondiba, I. M., Amimo, F. A., Oludhe, C., Olago, D. O., Nyamongo, I. K., & Estambale, B. B. (2016). Ecological niche modelling of Rift Valley fever virus vectors in Baringo, Kenya. Infect Ecol Epidemiol, 6, 32322. https://doi.org/10.3402/iee.v6.32322.

Pakanen, V. M., Sormunen, J. J., Sippola, E., Blomqvist, D., & Kallio, E. R. (2020). Questing abundance of adult taiga ticks *Ixodes persulcatus* and their *Borrelia* prevalence at the north-western part of their distribution. Parasit Vectors, 13(1), 384. https://doi.org/10.1186/s13071-020-04259-z.

Parola, P., Paddock, C. D., Socolovschi, C., Labruna, M. B., Mediannikov, O., Kernif, T., Abdad, M. Y., Stenos, J., Bitam, I., Fournier, P. E., & Raoult, D. (2013). Update on tick-borne rickettsioses around the world: a geographic approach. Clin Microbiol Rev, 26(4), 657-702. https://doi.org/10.1128/cmr.00032-13.

Paupy, C., Delatte, H., Bagny Beilhe, L., Corbel, V., & Fontenille, D. (2009). *Aedes albopictus*, an arbovirus vector: From the darkness to the light. Microbes and infection / Institut Pasteur, 11, 1177-1185. https://doi.org/10.1016/j.micinf.2009.05.005.

Pealer, L. N., Marfin, A. A., Petersen, L. R., Lanciotti, R. S., Page, P. L., Stramer, S. L., Stobierski, M. G., Signs, K., Newman, B., Kapoor, H., Goodman, J. L., & Chamberland, M. E. (2003). Transmission of West Nile Virus through Blood Transfusion in the United States in 2002. New England Journal of Medicine, 349(13), 1236-1245. https://doi.org/10.1056/NEJMoa030969.

Pearce, J. L., & Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling, 133, 225-245.

Pearce, J., & Boyce, M. (2005). Modeling distribution and abundance with presence-only data. Journal of Applied Ecology, 43, 405-412. https://doi.org/10.1111/j.1365-2664.2005.01112.x.

Perret, J.-L., Guigoz, E., Rais, O., & Gern, L. (2000). Influence of saturation deficit and temperature on *Ixodes ricinus* tick questing activity in a Lyme borreliosis-endmic area (Switzerland). Parasitology Research, 86, 554-557. https://doi.org/10.1007/s004360000209.

Phillips, S., Dudík, M., & Schapire, R. (2004). A Maximum Entropy Approach to Species Distribution Modeling (Vol. 21). https://doi.org/10.1145/1015330.1015412

Pirinen, P., Simola, H., Aalto, J., Kaukoranta, J. P., Karlsson, P., & Ruuhela, R. (2012). Tilastoja Suomen ilmastosta 1981–2010. Climatological statistics of Finland 1981–2010. Finnish Meteorological Institute Reports, 2012.

Platonov, A. E., Karan, L. S., Kolyasnikova, N. M., Makhneva, N. A., Toporkova, M. G., Maleev, V. V., Fish, D., & Krause, P. J. (2011). Humans infected with relapsing fever spirochete *Borrelia miyamotoi*, Russia. Emerg Infect Dis, 17(10), 1816-1823. https://doi.org/10.3201/eid1710.101474.

Poh, K. C., Chaves, L. F., Reyna-Nava, M., Roberts, C. M., Fredregill, C., Bueno, R., Debboun, M., & Hamer, G. L. (2019). The influence of weather and weather variability on mosquito abundance and infection with West Nile virus in Harris County, Texas, USA. Science of The Total Environment, 675, 260-272. https://doi.org/10.1016/j.scitotenv.2019.04.109.

Popov, I. O., & Popova, E. N. (2020). Identification of Climate Conditions Restricting the Distribution of the Taiga Tick *Ixodes Persulcatus* on the Territory of Russia and in Neighboring Countries. Doklady Earth Sciences, 493(1), 562-564. https://doi.org/10.1134/S1028334X20070144.

Powell, J. R., & Tabachnick, W. J. (2013). History of domestication and spread of *Aedes aegypti*--a review. Memorias do Instituto Oswaldo Cruz, 108 Suppl 1(Suppl 1), 11-17. https://doi.org/

10.1590/0074-0276130395.

Pradervand, J.-N., Anne, D., Pellissier, L., Guisan, A., & Randin, C. (2014). Very high resolution environmental predictors in species distribution models: Moving beyond topography? Progress in Physical Geography, 38, 79-96. https://doi.org/10.1177/0309133313512667.

Putkuri, N., Kurkela, S., Levanov, L., Huhtamo, E., Vaheri, A., Sironen, T., & Vapalahti, O. (2014). Isolation and characterization of a California encephalitis serogroup orthobunyavirus from Finnish mosquitoes. Infection, genetics and evolution: journal of molecular epidemiology and evolutionary genetics in infectious diseases, 22. https://doi.org/10.1016/j.meegid.2014.01.023.

Randolph, S. (2001). The Shifting Landscape of Tick-borne Zoonoses: Tick-borne Encephalitis and Lyme borreliosis in Europe. Philosophical transactions of the Royal Society of London. Series B, Biological sciences, 356, 1045-1056. https://doi.org/10.1098/rstb.2001.0893.

Randolph, S., & Sumilo, D. (2007). Tick-borne encephalitis in Europe: Dynamics of changing risk. In (pp. 187-206).

Randolph, S. E., Asokliene, L., Avsic-Zupanc, T., Bormane, A., Burri, C., Gern, L., Golovljova, I., Hubalek, Z., Knap, N., Kondrusik, M., Kupca, A., Pejcoch, M., Vasilenko, V., & Žygutiene, M. (2008). Variable spikes in tick-borne encephalitis incidence in 2006 independent of variable tick abundance but related to weather. Parasites & Vectors, 1(1), 44. https://doi.org/10.1186/1756-3305-1-44.

Randolph, S. E., Gern, L., & Nuttall, P. A. (1996). Co-feeding ticks: Epidemiological significance for tick-borne pathogen transmission. Parasitol Today, 12(12), 472-479. https://doi.org/10.1016/s0169-4758(96)10072-7.

Randolph, S. E., & Rogers, D. J. (2000). Fragile transmission cycles of tick-borne encephalitis virus may be disrupted by predicted climate change. Proceedings. Biological sciences, 267(1454), 1741-1744. https://doi.org/10.1098/rspb.2000.1204

Rar, V., & Golovljova, I. (2011). Anaplasma, Ehrlichia, and “*Candidatus Neoehrlichia*” bacteria: pathogenicity, biodiversity, and molecular genetic characteristics, a review. Infect Genet Evol, 11(8), 1842-1861. https://doi.org/10.1016/j.meegid.2011.09.019.

Reinert, J. F., Harbach, R. E., & Kitching, I. J. (2009). Phylogeny and classification of tribe *Aedini* (Diptera: *Culicidae*). Zoological Journal of the Linnean Society, 157(4), 700-794. https://doi.org/10.1111/j.1096-3642.2009.00570.x.

Reisen, W., Fang, Y., & Martinez, M. (2007). Vector competence of *Culiseta incidens* and *Culex thriambus* for West Nile virus. Journal of the American Mosquito Control Association, 22, 662-665. https://doi.org/10.2987/8756-971X(2006)22[662:VCOCIA]2.0.CO;2.

Reisen, W. K., Fang, Y., & Martinez, V. M. (2014). Effects of Temperature on the Transmission of West Nile Virus by *Culex tarsalis* (Diptera: *Culicidae*). Journal of Medical Entomology, 43(2), 309-317. https://doi.org/10.1093/jmedent/43.2.309.

Reiter, M. E., & LaPointe, D. A. (2007). Landscape factors influencing the spatial distribution and abundance of mosquito vector *Culex quinquefasciatus* (Diptera: *Culicidae*) in a mixed residential-agricultural community in Hawai’i. J Med Entomol, 44(5), 861-868. https://doi.org/10.1603/0022-2585(2007)44[861:lfitsd]2.0.co;2.

Reiter, P. (2001). Climate Change and Mosquito-Borne Disease. Environmental Health Perspectives, 109, 141-161. https://doi.org/10.2307/3434853.

Richman, R., Diallo, D., Diallo, M., Sall, A. A., Faye, O., Diagne, C. T., Dia, I., Weaver, S. C., Hanley, K. A., & Buenemann, M. (2018). Ecological niche modeling of *Aedes* mosquito vectors of chikungunya virus in southeastern Senegal. Parasites & Vectors, 11(1), 255. https://doi.org/10.1186/s13071-018-2832-6.

Ridgeway, G. (1999). “The state of boosting,” Computing Science and Statistics, 31, 172-181.

Ripley, B.D. (1996). Pattern Recognition and Neural Networks. Cambridge University Press, Cambridge.https://doi.org/10.1017/CBO9780511812651

Rochat, E., Vuilleumier, S., Aeby, S., Greub, G., & Joost, S. (2020). Nested Species Distribution Models of Chlamydiales in *Ixodes ricinus* (Tick) Hosts in Switzerland. Appl Environ Microbiol, 87(1). https://doi.org/10.1128/aem.01237-20.

Ruosteenoja, K., Räisänen, J., Venäläinen, A., Kämäräinen, M., & Pirinen, P. (2016). Terminen kasvukausi lämpenevässä ilmastossa. Terra, 128(1): 3-15. http://en.ilmatieteenlaitos.fi/documents/31422/83635880/Ruosteenoja+Terminen+kasvukausi+l%C3%A4mpenev%C3%A4ss%C3%A4%20ilmastossa+2016/5cd98a30-cab8-421d-970b-432ceb67fefd.

Ruosteenoja, K. (2013). Maailmanlaajuisiin ilmastomalleihin perustuvia lämpötila- ja sademääräskenaarioita. Sektoritutkimusohjelman ilmastoskenaariot (SETUKLIM) 1. osahanke. Finnish Meteorological Institute. 15 p. http://ilmatieteenlaitos.fi/c/document_library/get_file?uuid=c4c5bf12-655e-467a-9ee0-f06d8145aaa6&groupId=30106.

Ruosteenoja, K. (2021). Applicability of CMIP6 models for building climate projections for northern Europe. Raportteja - Rapporter - Reports 2021 (7). https://helda.helsinki.fi/bitstream/handle/10138/334477/Raportteja_Ruosteeno ja_2021_7.pdf?sequence=1&isAllowed=y.

Salmivaara, A. (2017). Topographical Wetness Index for Finland, 16m, 2016. CSC - IT Center for Science Ltd. http://urn.fi/urn:nbn:fi:csc-kata20170511114638598124

Sane, J., Guedes, S., Kurkela, S., Lyytikäinen, O., & Vapalahti, O. (2010). Epidemiological analysis of mosquito-borne Pogosta disease in Finland, 2009. Eurosurveillance, 15(2), 19462. https://doi.org/10.2807/ese.15.02.19462-en.

Sane, J., Kurkela, S., Putkuri, N., Huhtamo, E., Vaheri, A., & Vapalahti, O. (2012). Complete coding sequence and molecular epidemiological analysis of Sindbis virus isolates from mosquitoes and humans, Finland. The Journal of general virology, 93, 1984-1990. https://doi.org/10.1099/vir.0.042853-0.

Scharlemann, J. P. W., Johnson, P. J., Smith, A. A., Macdonald, D. W., & Randolph, S. E. (2008). Trends in ixodid tick abundance and distribution in Great Britain. Medical and Veterinary Entomology, 22(3), 238-247. https://doi.org/10.1111/j.1365-2915.2008.00734.x.

Schwaiger, M., & Cassinotti, P. (2003). Development of a quantitative real-time RT-PCR assay with internal control for the laboratory detection of tick-borne encephalitis virus (TBEV) RNA. J Clin Virol, 27(2), 136-145. https://doi.org/10.1016/s1386-6532(02)00168-3.

Semenza, J. C., & Menne, B. (2009). Climate change and infectious diseases in Europe. Lancet Infect Dis, 9(6), 365-375. https://doi.org/10.1016/s1473-3099(09)70104-5.

Service, M. (1991). Mosquito Ecology: Field Sampling Methods. (2nd edition), Elsevier. p. 988.

Shongwe, M., Van Oldenborgh, G. J., Hurk, B., De Boer, B., Coelho, S., & Aalst, M. (2009). Projected changes in mean and extreme precipitation in Africa under global warming. Part 1: Southern Africa. Journal of Climate, 100807022647046. https://doi.org/10.1175/2008JCLI2317.1.

Siljander, M., Clark, B. J. F., & Pellikka, P. K. E. (2011). A predictive modelling technique for human population distribution and abundance estimation using remote-sensing and geospatial data in a rural mountainous area in Kenya. International Journal of Remote Sensing, 32(21), 5997-6023. https://doi.org/10.1080/01431161.2010.499383.

Siljander, M., Uusitalo, R., Pellikka, P., Isosomppi, S., & Vapalahti, O. (2022). Spatiotemporal clustering patterns and sociodemographic determinants of COVID-19 (SARS-CoV-2) infections in Helsinki, Finland. Spatial and Spatio-temporal Epidemiology, 41, 100493. https://doi.org/10.1016/j.sste.2022.100493.

Sintayehu, D. W., Tassie, N., & De Boer, W. F. (2020). Present and future climatic suitability for dengue fever in Africa. Infection Ecology & Epidemiology, 10(1), 1782042. https://doi.org/10.1080/20008686.2020.1782042.

Sirotkin, M. B., & Korenberg, E. I. (2018). Influence of Abiotic Factors on Different Developmental Stages of the Taiga Tick *Ixodes persulcatus* and the Sheep Tick *Ixodes ricinus*. Entomological Review, 98(4), 496-513. https://doi.org/10.1134/S0013873818040115.

Smith, P. (1994). Autocorrelation in logistic regression modeling of species' distributions. Global Ecol. Biogeography Lett., 4, 47-61.

Sormunen, J. J., Penttinen, R., Klemola, T., Hänninen, J., Vuorinen, I., Laaksonen, M., Sääksjärvi, I. E., Ruohomäki, K., & Vesterinen, E. J. (2016). Tick-borne bacterial pathogens in southwestern Finland. Parasites & Vectors, 9(1), 168. https://doi.org/10.1186/s13071-016-1449-x.

Soucy, J.-P. R., Slatculescu, A. M., Nyiraneza, C., Ogden, N. H., Leighton, P. A., Kerr, J. T., & Kulkarni, M. A. (2018). High-Resolution Ecological Niche Modeling of *Ixodes scapularis* Ticks Based on Passive Surveillance Data at the Northern Frontier of Lyme Disease Emergence in North America. Vector borne and zoonotic diseases (Larchmont, N.Y.), 18(5), 235-242. https://doi.org/10.1089/vbz.2017.2234.

Statistics Finland. (2021). Environment and Nature. https://www.stat.fi/tup/suoluk/suoluk_alue_en.html.

Stuen, S., Granquist, E. G., & Silaghi, C. (2013). *Anaplasma phagocytophilum*--a widespread multi-host pathogen with highly adaptive strategies. Frontiers in cellular and infection microbiology, 3, 31-31. https://doi.org/10.3389/fcimb.2013.00031

SYKE. (2018). Finnish Environment Institute. Corine maanpeite 2018. https://ckan.ymparisto.fi/dataset/corine-maanpeite-2018.

SYKE. (2012). Finnish Environment Institute. Corine maanpeite 2012. https://ckan.ymparisto.fi/dataset/corine-maanpeite-2012.

Tack, W., Madder, M., Baeten, L., De Frenne, P., & Verheyen, K. (2012). The abundance of *Ixodes ricinus* ticks depends on tree species composition and shrub cover. Parasitology, 139(10), 1273-1281. https://doi.org/10.1017/S0031182012000625.

Tälleklint, L., & Jaenson, T. G. (1997). Infestation of mammals by *Ixodes ricinus* ticks (Acari: *Ixodidae*) in south-central Sweden. Exp Appl Acarol, 21(12), 755-771. https://doi.org/10.1023/a:1018473122070.

Thuiller, W., Lafourcade, B., Engler, R., & Araújo, M. B. (2009). BIOMOD – a platform for ensemble forecasting of species distributions. Ecography, 32(3), 369-373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Tian, H., Bi, P., Cazelles, B., Zhou, S., Huang, S., Jing, Y., Pei, Y., Wu, X., Fu, S.-H., Tong, S.-L., Wang, H.-Y., & Xu, B. (2015). How environmental conditions impact mosquito ecology and Japanese encephalitis: An eco-epidemiological approach. Environment International, 79. https://doi.org/10.1016/j.envint.2015.03.002.

Tingström, O., Wesula Lwande, O., Näslund, J., Spyckerelle, I., Engdahl, C., Von Schoenberg, P., Ahlm, C., Evander, M., & Bucht, G. (2016). Detection of Sindbis and Inkoo Virus RNA in Genetically Typed Mosquito Larvae Sampled in Northern Sweden. Vector borne and zoonotic diseases (Larchmont, N.Y.), 16(7), 461-467. https://doi.org/10.1089/vbz.2016.1940.

Tokarevich, N. K., Tronin, A. A., Blinova, O. V., Buzinov, R. V., Boltenkov, V. P., Yurasova, E. D., & Nurse, J. (2011). The impact of climate change on the expansion of *Ixodes persulcatus* habitat and the incidence of tick-borne encephalitis in the north of European Russia. Glob Health Action, 4, 8448. https://doi.org/10.3402/gha.v4i0.8448.

Trenberth, K. E., & Josey, S. (2007). Observations: surface and atmospheric climate change. In, Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M. and Miller, H.L. (eds.) Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK. Cambridge University Press, pp. 235-336.

Turell, M. (2012). Members of the *Culex pipiens* Complex as Vectors of Viruses. Journal of the American Mosquito Control Association, 28, 123-126. https://doi.org/10.2987/8756-971X-28.4.123.

Turell, M. J., Lundström, J. O., & Niklasson, B. (1990). Transmission of Ockelbo virus by *Aedes cinereus*, *Ae. communis*, and *Ae. excrucians* (Diptera: *Culicidae*) collected in an enzootic area in central Sweden. J Med Entomol, 27(3), 266-268. https://doi.org/10.1093/jmedent/27.3.266.

Turunen, J. (2008). Development of Finnish peatland area and carbon storage 1950–2000. Boreal Environment Research, 13, 319-334.

Turunen, M., Kuusisto, P., Uggeldahl, P. E., & Toivanen, A. (1998). Pogosta disease: clinical observations during an outbreak in the province of North Karelia, Finland. Br J Rheumatol, 37(11), 1177-1180. https://doi.org/10.1093/rheumatology/37.11.1177.

Uejio, C. K., Kemp, A., & Comrie, A. C. (2012). Climatic controls on West Nile virus and Sindbis virus transmission and outbreaks in South Africa. Vector borne and zoonotic diseases (Larchmont, N.Y.), 12(2), 117-125. https://doi.org/10.1089/vbz.2011.0655.

Uusitalo, R. (2017). Master's Thesis: Modeling the spatial distribution of *Culex* and *Stegomyia* mosquitoes collected in the Taita Hills, Kenya in 2016, with notes on other genera. University of Helsinki: Finland. https://helda.helsinki.fi/bitstream/handle/10138/229127/progradu_ruutjuu.pdf?sequence=3&isAllowed=y.

Uusitalo, R., Siljander, M., Culverwell, C. L., Hendrickx, G., Lindén, A., Dub, T., Aalto, J., Sane, J., Marsboom, C., Suvanto, M. T., Vajda, A., Gregow, H., Korhonen, E. M., Huhtamo, E., Pellikka, P., & Vapalahti, O. (2021). Predicting Spatial Patterns of Sindbis Virus (SINV) Infection Risk in Finland Using Vector, Host and Environmental Data. Int J Environ Res Public Health, 18(13). https://doi.org/10.3390/ijerph18137064.

Venäläinen, A., Laapas, M., Pirinen, P., Horttanainen, M., Hyvönen, R., Lehtonen, I., Junila, P., Hou, M., & Peltola, H. (2017). Estimation of the high-spatial-resolution variability in extreme wind speeds for forestry applications. Earth System Dynamics, 8, 529-545. https://doi.org/10.5194/esd-8-529-2017.

Vollack, K., Sodoudi, S., Névir, P., Müller, K., & Richter, D. (2017). Influence of meteorological parameters during the preceding fall and winter on the questing activity of nymphal *Ixodes ricinus* ticks. International Journal of Biometeorology, 61(10), 1787-1795. https://doi.org/10.1007/s00484-017-1362-9.

Wan, Z., Hook, S., Hulley, G., 2015. MOD11C3 MODIS/Terra Land Surface Temperature/Emissivity Monthly L3 Global 0.05Deg CMG V006. NASA EOSDIS Land Processes DAAC. Accessed 2022-03-10 from https://doi.org/10.5067/MODIS/MOD11C3.006.

Wang, F. (2020). Why public health needs GIS: a methodological overview. Annals of GIS, 26(1), 1-12. https://doi.org/10.1080/19475683.2019.1702099.

WHO. (2018). World Health Organization. Report of an international consultation: methodology for risk mapping of the international spread of vector-borne diseases via air travel: Geneva, Switzerland, 5-6 July 2018.

WHO Africa. (2019). World Health Organization Africa. African health ministers agree to an all-fronts push to control the rise in vector-borne diseases. https://www.afro.who.int/news/african-health-ministers-agree-all-fronts-push-control-rise-vector-borne-diseases.

WHO. (2022a). World Health Organization. WHO Coronavirus (COVID-19) Dashboard With Vaccination Data.https://covid19.who.int/.

WHO. (2022b). World Health Organization. Ebola virus disease. https://www.who.int/health-topics/ebola/#tab=tab_1.

WHO. (2022c). World Health Organization. Zika virus disease. https://www.who.int/emergencies/situations/zika-virus-outbreak.

WHO. (2022d). World Health Organization. GIS Centre for Health. https://www.who.int/data/GIS.

WHO. (2022e). World Health Organization. Tick-borne encephalitis. https://www.who.int/health-topics/tick-borne-encephalitis#tab=tab_2

WHO. (2022f). World Health Organization. West Nile virus. https://www.who.int/news-room/fact-sheets/detail/west-nile-virus.

Wisz, M. S., Hijmans, R., Li, J., Peterson, A., Graham, C., Guisan, A., Elith, J., Dudík, M., Ferrier, S., Huettmann, F., Leathwick, J., Lehmann, A., Lohmann, L., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., & Zimmermann, N. (2008). Effects of sample size on the performance of species distribution models. Diversity and Distributions, 14, 763-773.

Wisz, M. S., & Guisan, A. (2009). Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC Ecology, 9(1), 8. https://doi.org/10.1186/1472-6785-9-8.

Wodecka, B., & Skotarczak, B. (2016). Identification of host blood-meal sources and *Borrelia* in field-collected *Ixodes ricinus* ticks in north-western Poland. Ann Agric Environ Med, 23(1), 59-63. https://doi.org/10.5604/12321966.1196853.

Woolhouse, M. E. J., Dye, C., Woolhouse, M. E. J., & Dye, C. (2001). Preface. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 356(1411), 981-982. https://doi.org/10.1098/rstb.2001.0899.

Worobey, M., Levy, J.I., Malpica Serrano, L.M., Crits-Christoph, A., Pekar, J.E., Goldstein, S.A., Rasmussen, A.L., Kraemer, M.U.G., Newman, C., Koopmans, M.P.G., Suchard, M.A., Wertheim, J.O., Lemey, P., Robertson, D.L., Garry, R.F., Holmes, E.C., Rambaut, A. & K.G. Andersen. (2022). The Huanan market was the epicenter of SARS-CoV-2 emergence. Zenodo. https://doi.org/10.5281/zenodo.6299600.

Virtanen, E. (2015). Fine-resolution climate grids for species studies in data-poor regions. Unpublished MSc thesis, University of Helsinki, Finland.

Zakham, F., Jaaskelainen, A. J., Castren, J., Sormunen, J. J., Uusitalo, R., Smura, T., Von Troil, G., Kuivanen, S., Sironen, T., & Vapalahti, O. (2021). Molecular detection and phylogenetic analysis of *Borrelia miyamotoi* strains from ticks collected in the capital region of Finland. Ticks Tick Borne Dis, 12(2), 101608. https://doi.org/10.1016/j.ttbdis.2020.101608.