Dissertationes Forestales 278

Forest health monitoring in transition: Evaluating insect-induced disturbances in forested landscapes at varying spatial scales

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Academic dissertation

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Title of dissertation: Forest health monitoring in transition: Evaluating insect-induced disturbances in forested landscapes at varying spatial scales

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Dissertationes Forestales 278

https://doi.org/10.14214/df.278

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ISSN 1795-7389 (online)
ISBN 978-951-651-646-5 (pdf)

ISSN 2323-9220 (print)
ISBN 978-951-651-647-2 (paperback)

Publishers:
Finnish Society of Forest Science
Faculty of Agriculture and Forestry of the University of Helsinki
School of Forest Sciences of the University of Eastern Finland

Editorial Office:
The Finnish Society of Forest Science
Viikinkaari 6, FI-00790 Helsinki, Finland
http://www.dissertationesforestales.fi

Kantola T. (2019). Forest health monitoring in transition: Evaluating insect-induced disturbances in forested landscapes at varying spatial scales. Dissertationes Forestales 278. 146 p. https://doi.org/10.14214/df.278

ABSTRACT

Climate change is amplifying forest disturbances, especially those by insect pests. In addition to native species, biological invasions by alien insects are threatening forest health, ecosystem sustainability, and economic return. Uncertainties related to insect pest infestations are increasing along the risk of high impacts. There is a high demand of accurate, efficient, and cost-effective methods for forest health monitoring to prevent, control, and mitigate the various negative impacts, as well as to support decision-making.

Current needs for information for efficient forest management are complex and extensive. The required quality cannot be met with traditional forest inventory methods. Forest information should be up-to date and available across a range of spatial and temporal scales. Rapid development of methods for general forest inventory also support development of forest health monitoring and management. The continuously developing field of remote sensing and geographical information systems provide new means for various forest monitoring tasks. However, disturbance monitoring, especially by insect pests, gives an extra challenge and increased uncertainties compared to other forest monitoring tasks. With new approaches, however, valuable information on disturbances can be derived for evaluation of insect-induced forest disturbance at reasonable high accuracy and reduced amount of needed fieldwork.

This dissertation aims towards improved forest health monitoring, particularly disturbances by defoliating insect pests. Insect-induced disturbances from single tree level to larger areas in Fennoscandia and eastern USA were evaluated in five sub-studies. The sixth and final sub-study comprises continental scale species distribution models in North America and East Asia. In these sub-studies, different remote sensing sensors and approaches, and ecological niche modeling for species potential distributions were employed in disturbance evaluation. Study species include native insect pests and an invasive alien species. In context of recent research and the included sub-studies, issues specific to insect disturbance monitoring are discussed. Pattern, frequency, scale, and intensity of insect infestations vary depending on the insect pest and forested landscapes in question affecting disturbance detection and impact evaluation. Sensors, platform, and/or modeling methods have to be chosen accordingly. Environmental features, such as topography, and level of landscape fragmentation give restrictions to the method selection, as well as to the appropriate spatial resolution. Importance of varying information is also affected by the scale and resolution of investigation. Timing of data acquisition is crucial. Early detection and timely management operations are often the only way to control or mitigate insect outbreaks. Moreover, amount and accuracy of auxiliary information, including forest inventory data, and disturbance history, differ between countries and continents. Forest policies and practices differ depending on the region affecting further selection of usable data sets and methods.

Information on potential ranges of insect pests and, to some extent, on future impacts of infestations can be obtained employing spatial modeling techniques, such as ecological niche modeling. These models are more frequently used at the regional and continental levels, however, smaller scale can be applied. Various modeling approaches can also be applied in risk assessment, providing information for decision-making and forest health management operations. Models can be coupled with other techniques, including remote sensing. The feasibility of modeling is emphasized when predicting and projecting future events, especially those connected to the climate change related changes in insect population dynamics or adaptation to various forest management operations.

Forest health monitoring should be included into forest monitoring systems, including accurate and timely disturbance detection, monitoring of infestations, and impact evaluation. Higher and lower spatial resolution remote sensing should be combined over varying spatial ranges and modeling techniques incorporated for flexible and cost-efficient monitoring over a gradient of different forest ecosystems, climatic conditions, and forest inventory and management practices. Open access remote sensing archives with high temporal resolution could facilitate continuous monitoring of wide forest areas. Developing satellite technology may respond to these needs. Plenty of valuable research on forest health monitoring exist. However, considerably more research is still needed before comprehensive monitoring systems can be adopted at the operational level. Development of remote sensing and modeling techniques, as well as improving computational power and databases facilitate continuous improvement of forest health management practices.

Keywords: Ecological niche modeling, Forest disturbances, Forest health monitoring, Insect pests, Invasive species, Remote sensing

PREFACE

My journey towards completing this dissertation has been long and colorful with many twists. The stepping-stones during the journey have been washed with tears and colored with laughter and joy. It has not been the easiest of the journeys, or the most straightforward, but surely worth of it, every single day. These years have been rich in so many ways. They have included work and living in Finland and Texas, various forest insect pests and forest environments, collaboration with a range of different people, teaching, and thesis supervision, travelling, fieldwork, etc. I have been blessed with so many great people beside me during this part of my life. I have also gain new friendships along the route, in Finland and abroad.

I want to express my most sincere gratitude to my supervisors Adjunct prof. Päivi Lyytikäinen-Saaremaa and Prof. Markus Holopainen. This exiting part of my life started on the hallways of the Department of Forest Sciences. I met Päivi after a long while and we started a friendly chat. She suddenly dropped a straight question if I would like to start a dissertation under her supervision on monitoring insect pest disturbances. That just felt right; I didn't even need time for consideration. Since then, a beautiful and complex world of insect pests on the forest environments have opened in front of me. Markus already had a big role during my master's studies. He trusted me a lot in teaching. He enabled, e.g., several unforgettable summers in Hyytiälä field station as an assistant and later as a responsible teacher. My supervisors have provided me good working conditions facilitating independent work, development of my own ideas, and given me plenty of responsibilities from the start. They have been compassionate and understanding through the rough patches and encouraging during the whole journey. Further, it has always been so much fun to brainstorm and plan for the future!

I spent over four years at the Knowledge Engineering Laboratory, in Texas A&M University. I am extremely grateful to Prof. Robert N. Coulson for enabling these experiences and kindly supervising me throughout these years and beyond. In addition to providing me an opportunity to learn about insect outbreaks in the landscape context, he also gave me an opportunity to see the world outside the much-loved forests inviting me later to work in the project on the amazing monarch butterfly. I can also attribute my immensely improved English skills to these time periods in Texas and to Prof. Coulson's untiring work in correcting my 'Finnglish'. The welcoming work environment at the lab felt like a home away from home, of which my colleagues, including Dr. James Tracy and Sheryl Strauch, were highly responsible. There was always time for laughing and talking in between the hard work. The KEL lab will always have a special place in my heart.

In addition to the aforementioned researchers, I feel gratitude towards the other coauthors of Prof. Lars Eklundh, Prof. Hannu Hyyppä, Prof. Juha Hyyppä, Dr. Anna Maria Jönsson, Dr. Ville Kankare, Dr. Per-Ola Olsson, Dr. Hannu Saarenmaa, Douglas Streett, Mervi Talvitie, Dr. Maria Tchakerian, Dr. Antonio Trabucco, Associate prof. Mikko Vastaranta, and Dr. Michael Wulder. Thank you for enabling the diverse and broad content of the thesis. I have been a member of the delightful Forest Health research group since it was founded. Sharing work and other aspects of life has been enjoyable with the other members of the group, including Minna Blomqvist, Elina Peuhu, Maiju Kosunen, and Mikko Pelto-Arvo. Coworkers at the Department of Forest Sciences have provided me a great working environment. I have shared numerous great professional conversations over the years, as well

as plenty of joys and sorrows with these kindhearted people, especially with Dr. Ilkka Korpela.

My research extended into three different continents, and the included field inventories took me to various forested landscapes form North Karelia of eastern Finland to North Carolina of eastern USA. I wish to thank Antero Pasanen, Jari Tahvanainen, and Taisto Saarelainen from the Tornator Ltd. for enabling fieldwork in Ilomantsi and Outokumpu, and Rusty Rhea at the Forest Service, Asheville, NC, USA for showing us around the Linville River Gorge area.

I would also like to thank the pre-examiners, Prof. Olle Anderbrant and Associate prof. Tuuli Toivonen for your work and insightful comments on my dissertation. I wish to sincerely thank Docent Tarmo Virtanen (PhD) for agreeing to spent your valuable time and serve as my opponent.

I am grateful to my parents Aino and Kaarlo, who have always believed in me, even when I didn't. It has always felt good to come home, no matter the circumstances. In addition to my dear parents, my aunt Pirkko and uncle Jorma have always supported me and carried me in their prayers. My cousin Hanna and her husband Juha-Matti have offered me understanding and advice, as well as invigorating discussions on various topics. I also want to thank the rest of my family for all the support. My dear friend Jonna has provided me a vast amount of common sense, food, and honest answers. Jussi, Sanna-Maria, Tommi, Tanu and Veera, and other great friends of mine, including my sweet goddaughters, have supported me through these years in various ways.

Last but by no means least; my beloved Vesa, who came into my life in the middle of the depths of a dark period, and who has been taking care of me and been my companion during these recent years. You have brought laughter and happiness into my life.

Tuula Kantola
Viikki, 13 May 2019

LIST OF ORIGINAL ARTICLES

This dissertation consists of the following six research articles. They are referred by roman numerals of I-VI in the text. The articles are reprinted with kind permission from the publishers.

I Kantola T., Vastaranta M., Lyytikäinen-Saarenmaa P., Holopainen M., Kankare V., Talvitie M., Hyyppä J. (2013). Classification of needle loss of individual Scots pine trees by means of airborne laser scanning. Forests 4(2): 386-403. https://doi.org/10.3390/f4020386

II Vastaranta M., Kantola T., Lyytikäinen-Saarenmaa P., Holopainen M., Kankare V., Wulder M., Hyyppä J., Hyyppä, H. (2013). Area-based mapping of defoliation of Scots pine stands using Airborne Scanning LiDAR. Remote Sensing 5: 1220-1234. https://doi.org/10.3390/rs5031220

III Kantola T., Lyytikäinen-Saarenmaa P., Coulson R.N., Strauch S., Tchakerian M. D., Holopainen M., Saarenmaa, H., Streett, D. A. (2014). Spatial Distribution and Pattern of Hemlock Woolly Adelgid Induced Hemlock Mortality in the Southern Appalachians. Open Journal of Forestry 4: 492-506. https://doi.org/10.4236/ojf.2014.45053

IV Kantola T., Lyytikäinen-Saarenmaa P., Coulson R. N., Holopainen M., Tchakerian M. D., Streett, D. A. (2016). Development of monitoring methods for Hemlock Woolly Adelgid induced tree mortality within a Southern Appalachian landscape with inhibited access. iForest – Biogeosciences and Forestry 9: 178-186. https://doi.org/10.3832/ifor1712-008

V Olsson P-O., Kantola T., Lyytikäinen-Saarenmaa P., Jönsson A. M., Eklundh L. (2016). Monitoring Insect Induced Defoliation in Nordic Forest Landscapes with MODIS derived Vegetation Indices. Silva Fennica 50(2): article id:1495. https://doi.org/10.1016/j.rse.2016.03.040

VI Kantola T., Tracy, J. L., Lyytikäinen-Saarenmaa P., Saarenmaa H., Coulson R. N., Trabucco A., Holopainen, M. (2018). Potential Range of the Hemlock Woolly Adelgid in North America under Historical Climate and Climate Change Induced Shift of the Range. iForest - Biogeosciences and Forestry 12(2):149-159. https://doi.org/10.3832/ifor2883-012

Author’s contribution

Tuula Kantola was the main author in the sub-studies I, III, IV, and VI. She had a leading role in designing, data processing, analysis, evaluations, writing, interpretation of the results, and writing of the respective articles. Ville Kankare was responsible for the LiDAR data preparation for the sub-studies I and II. Study design for the sub-study IV was created together with James L. Tracy. Mikko Vastaranta was the main author in the sub-study II, having a leading role in the study design, and analysis. Per Ola Olsson was the main author in the sub-study V and had the main role in data preparation, method development, and interpretation. Tuula Kantola made significant contributions in planning, writing, interpreting results, and writing of the sub-studies II and V. She inventoried all the field data with colleagues, except the Abisko field data (V). Kantola was also responsible for the reference data used in the sub-studies III, IV, and VI. All the articles were improved by the contributions of the co-authors at various stages of the planning, data collection, analysis and writing process.

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ABBREVIATIONS AND DEFINITIONS

3D	Three-dimensional
ACS	Adaptive cluster sampling
AISA	Airborne imaging spectrometer for applications
ALS	Airborne laser scanning
AUC	Area under curve
AVHRR	Advanced Very High Resolution Radiometer
AVIRIS	Airborne Visible/Infrared Imaging Spectrometer
CART	Classification and regression trees
CHM	Canopy height model
CIR	Color-infrared
CSR	Complete spatial randomness
DEM	Digital elevation model
DSM	Digital surface model
EIL	Economic injury level
ENM	Ecological niche modeling
ESA	European space association
ET	Economic threshold
EVI	Enhanced vegetation index
EVI2	2-band Enhanced Vegetation Index
FPR	False positive rate
GARP	Genetic Algorithm for Rule-Set Production
GBIF	Global Biodiversity Information Facility
GIS	Geographic information system
GPS	Global positioning system
HWA	Hemlock woolly adelgid
IPCC	Intergovernmental Panel on Climate Change
IPM	Integrated pest management
ISR	Infrared simple ratio
ITD	Individual tree detection
LiDAR	Light detection and ranging
LAI	Leaf area index
MaxEnt	Maximum Entropy
MODIS	Moderate Resolution Imaging Spectroradiometer
NAIP	National Agricultural Inventory Program
NBR	Normalized burn ratio
NDVI	Normalized difference vegetation index
NFI	National forest inventory
NIR	Near infrared
NOAA	National Oceanic and Atmospheric Administration
QA	Quality assurance
Radar	Radio Detection and Ranging
RGB	Red, green, blue
ROC	Receiver Operating Characteristics
SAR	Synthetic Aperture Radar
SPOT	Satellite Pour l'Observation de la Terre

SR	Simple ratio
SVM	Support vector machine
SWIR	Shortwave infrared
UAV	Unmanned aerial vehicle
USA	United States of America
USDA	United States Department of Agriculture
TLS	Terrestrial laser scanning
TPR	True positive rate
WDRVI	Wide Dynamic Range Vegetation Index

1. INTRODUCTION

1.1. Forest disturbances – a growing threat of the changing world

Numerous issues are threating sustainability of world's ecosystems, such as the diverse range of forests, and consequently, human welfare. Changing climate with elevating temperatures, continuously growing human population and the following increased demand of goods and services, as well as traffic and trade induced biological invasions of exotic species can be included into the most complex socio-economical threats. The existing forest resources are, at the same time, facing wider and more intense disturbances than before and increasing in their value for the world. The global change is exposing forest ecosystems to severe threats along with the increasing demand of the ecosystem services provided by forests (Seidl et al. 2016). In addition to forest products, forests have critical non-material values, including major effects on important regulating services, such as carbon storage and sequestration, flood control, and water purification (Boyd et al. 2013). Infestations by insect pests are threatening forest health and persistence of existing forested landscapes and the critical ecological processes. Forests and tree species are regarded resilient and well adapted to disturbance regimes (Gutschick and BassiriRad 2003). However, the disturbance regimes are also changing, and the magnitude of the future impacts include significant uncertainty (Westerling et al. 2006; Seidl et al. 2014; 2016). Magnified insect-induced forest disturbances have negative effects on, e.g., biodiversity (Beudert et al. 2015), various biogeochemical processes (Seidl et al. 2014), and economic return (Dale et al. 2001). Efforts for monitoring and protecting forests against damaging agents, especially insect pests, are growing in importance. Improved forest health monitoring and development of methodology for early warning would facilitate more effective mitigation of the negative impacts of forest insect pests. Relatively new and rapidly developing tools of remote sensing and spatial modeling should be included into efficient forest health monitoring and risk assessment. In this context, this dissertation contributes to forest health monitoring, particularly of insect induced forest damage. Relevant background and related scientific advancement are reviewed in the thesis and combined with six sub-studies focusing on methods of insect pest monitoring with different spatial and temporal resolutions.

1.2. Forest health and disturbances

1.2.1. Definitions for forest health

Healthy and sustainable forest ecosystems provide social and economic welfare. Healthy forests support important ecosystem services, i.e., beneficial functions and goods supporting directly or indirectly the quality of human life (Harrington et al. 2010; Díaz et al. 2015). Ecosystem services provided by healthy forests includes direct *provisioning services*, i.e., products used by human, indirect *regulating services* providing benefits resulting from modifications of the environment, and *cultural services* that improve human well-being (Boyd et al. 2013). These services include carbon storage and sequestration, habitats for species, maintenance of biodiversity, regulation of climate and mitigation of climate change, filtering and maintenance of water resources, erosion control, and supplying for energy, food, and materials (Trumbore et al. 2015; reviewed by Lausch et al. 2016). Forest health is a complex concept and challenging to define or evaluate. Despite the commonness of the term, *forest health* is often used without a clear definition. (Kolb et al. 1994). Further, human expectations are often inserted into the concept (Raffa et al. 2009). A healthy ecosystem is free from distress (Haskell et al. 1992). This distress can be characterized, e.g., by reduction in biodiversity, nutrition, and productivity, increase in fluctuation of key populations, and presence of retrogression and sever disease (Rapport 1992). Unfortunately, quantitative information for measuring these changes in indicators of forest health is lacking in most regions (Kolb et al. 1994). According to Trumbore et al. (2015), current measures of forest health vary from extreme practical aspects, based upon local human needs, to ecological characterizations associated with forest persistence within a landscape. Indicators of forest health range from pure utilitarian or economic (e.g., Adamowicz 2003) to ecological, preserving ecosystem resilience and stability (Kolb et al. 1994). The Food and Agriculture Organization (FAO) covers this variation with a definition of forest *health and vitality*. This definition combines presence of abiotic and biotic stressors and their impacts on tree growth and survival, yield and quality of forest products, wildlife habitats, as well as recreational, scenic, or cultural values (Trumbore et al. 2015).

A fully utilitarian view on forest health comprises conditions where no biotic or abiotic damage agent hinder obtaining satisfying management goals at the present, or in the future (USDA Forest Service 1993; Kolb et al. 1994). However, the ecological perspective of forest health should include information on ecological processes, structure, diversity, and productivity (Kolb et. al. 1994). They introduced four ecological indicators facilitating evaluation of forest health for a range of forest ecosystems, from those at natural stages to artificial settlements. (1) The abiotic and biotic environment, including the trophic networks should support productive forests during, at least some, seral stages of the ecological succession. (2) A forest ecosystem should have resistance to catastrophic changes or have the ability to recover from these changes at a landscape-scale. (3) A functional equilibrium should exist between the supply and demand of fundamental resources and (4) a diversity of seral stages and stand structures should provide for various native species and essential ecosystem processes. Edmonds et al. (2000) identified eight conditions characterizing healthy forest ecosystems. These qualifications include conditions were (1) current or future management targets are not threatened by biotic or abiotic factors, (2) plant and animal community and its physical environment are fully functional, and (3) the forest ecosystem is in balance. Further, the ecosystem balance has (4) to sustain complexity whilst providing for humankind, (5) be resilient to change, and (6) to be able to recover from various stressors (natural and anthropogenic), and at the same time (7) maintain and sustain its functions and processes. Finally, a healthy forest ecosystem (8) does not show symptoms of distress, including reduced productivity, loss of nutrients, reduced biodiversity, or widespread prevalence of disease or tree-killing insects.

The lack of a clear definition for forest health is hindering operational level decision-making and forest management (Kolb et al. 1994). For a comprehensive description of forest health, both utilitarian and ecosystem indicators should be included and implemented across varying spatial scales (Lausch et al. 2016). With increasing spatial scale, from the individual tree level to forested landscapes, the definition of forest health becomes more ambiguous, as the system increases in complexity (Kolb et al. 1994); health status of a tree is usually much easier to assess than that of a forest stand or landscape (Trumbore et al. 2015). Although the definition of healthy forest is binary and corresponds to absence of disease or damage, intervals or ratio scales are needed to assess forest health in practice (Lausch et al. 2016). Such scales often include subjective components. Further, it is good to keep in mind that healthy forest environments rarely remain constant over time (Berryman 1986) or space.

1.2.2. Forest disturbance regime

Forests face numerous natural and anthropogenic threats. Various forest disturbance factors include deforestation (Lewis et al. 2015), soil erosion (Pimentel 2006), land-use change (Foley et al. 2005), unsustainable management (Suorsa et al. 2003), air pollution (Kandler and Innes 1995), drought, water, fire, and wind (Millar and Stephenson 2015; Gauthier et al. 2015), pests and pathogens (Gauthier et al. 2015; Wingfield et al. 2015), climate change (Allen et al. 2010), and invasive species (Pyšek and Richardson 2010). External drivers may also alter ecosystem dynamics to transform native species into emergent threats (Raffa et al. 2009). Disturbance agents are divided into abiotic and biotic. In North America, insect pests, pathogens, and invasive plant species are regarded as primary biotic forest disturbance agents (Fike and Niering 1999; Logan et al. 2003). Examples of typical abiotic disturbance agents in forest ecosystems include fire, heavy winds, and drought. Often these abiotic and biotic disturbance agents act together intensifying the impacts on a forest, such as in case of a bark beetle infestation following a storm event; or trees suffering from defoliation can be highly susceptible to systemic pathogens (Dwyer et al. 2000). *Forest disturbance regime* includes the frequency, scale, and type of a disturbance (Asner 2013). These measures are considered, e.g., in the impact evaluation.

Illustrating complexity of the concepts of *forest health* and *disturbance*, natural disturbances have a fundamental role in forest ecosystem functions, referring to processes of resident species interacting among each other and their physical environment (Raffa et al. 2009; Asner 2013). Natural disturbances are essential to forest environments, as they induce forest succession, release plant growth, alter nutrient and water cycling, increase food resources, and affect plant and animal interactions (Vitousek and Denslow 1986; Dale et al. 2001; Folke et al. 2004; Asner 2013). However, this only applies when all the key processes of the forest ecosystem operate within the normative limits of resiliency (Folke et al. 2004); healthy forests are regarded as relatively resilient to various stressors and disturbance agents. Forest ecosystems with high resilience can recover faster to the stage preceding the disturbance (i.e., reach equilibrium) than more susceptible ones (Berryman 1986; Lausch et al. 2016). Consequently, factors compromising inherent processes and resilience should be emphasized in evaluation of forest health (Raffa et al. 2009). However, understanding the limits of forest resilience requires knowledge on patterns, processes, interactions, and responses to the external drivers (Raffa et al. 2009). Forest stability and resiliency are complex and continuous processes. Resilience can be defined as ecosystem’s capacity to absorb disturbance and go through change at the same time as persisting and maintaining the important functions, structures, identity, and feedbacks (Holling 1973; Walker et al. 2004; Drever et al. 2006). This means that a resilient forest ecosystem should be able to reconfigure itself without a significant change after disturbances or other stressors (e.g., Carpenter et al. 2001). The current understanding of ecosystem resilience is the strongest at smaller scales (Landis 2017). It is known that in general, more complex and diverse forest ecosystems are usually more stable. In diverse forests, other species may be able to compensate the decline of a particular tree species targeted by a forest pest (Hessburg et al. 2000; Boyd et al. 2013). However, in case of foundation (keystone) species, other tree species cannot serve as a replacement, and thus ecosystems and provided services can fundamentally change (Boyd et al. 2013). Further, biodiversity and the following functional redundancy are naturally lower in the boreal zone (Aitken et al. 2008). Disturbances targeting individual tree species may have a much higher impact in the North than elsewhere (Boyd et al. 2013). Further, relative stability of a forest ecosystem is mainly a long-term characteristic (Berryman 1986) and not to be evaluated at any given time. Maintaining stability includes interactions between species and trophic levels, as well as negative and positive feedback loops (Berryman 1986). The reactions are often timely delayed. Even though forest ecosystems are assumed to respond to gradual changes, such as in climate, dramatic switches in the resilience may occur (Scheffer et al. 2001). Loss of resilience may be resulting from, e.g., forest management or gradual environmental changes in the ecosystem when in coincidence with weather extremes and/or pest outbreaks (Scheffer et al. 2001; Bréda and Badeau 2008).

Whether the event in question exceeds the threshold of a *disturbance* and requires involvement is often matter of human expectations. For example, the term *forest pest* as such is anthropogenic and firmly tied to human anticipations. It has been defined as an organism that interferes with desired management objectives or have a negative impact on human survival or wellbeing (Berryman 1986; Raffa et al. 2009; Coulson and Saarenmaa 2011). A forest pest is acting as a parasite, transmits pathogens, competes with humans for resources, or is just an annoyance (Berryman 1986). Coulson and Saarenmaa (2011) defined forest management as ‘orchestrated modification or manipulation of landscape structure, function, or rate of change’. Various management strategies and intensities lead to specific types of forests, such as conservation areas, even-aged stands, mixed species or monocultures, Christmas tree plantations, urban forests, etc. Depending on management strategy and resulting forest type, impacts of disturbance, as well as the need for mitigation vary. For instance, if a bark beetle species induces high tree mortality in a commercial forest, the species is regarded as a pest; the species is usually not a pest when causing same level damage in a wilderness area (Raffa et al. 2009). Further, even minor damage within a small forest area with high value may exceed the threshold level of economic injury (Damos 2014), where as in conservation areas, disturbances are seen as normal processes of the forest environment. In general, the economic impact is often important in defining damage intensity. Greater losses are tolerated in low value forest environments than in more valuable ones, such as plantations or seed orchards (Berryman 1986).

Timing and locations of forest disturbances are highly unpredictable due to high number of organisms and ecological processes that may disturb forest environments (Dukes et al. 2009). When exceeding natural variation, the change in the structure and functions of a forest following a disturbance can be extreme (Ayres and Lombardero 2000). Major disturbances may affect sustainability and economic return even at a landscape level. Disturbances may interrupt ecological succession or even change the direction of succession, affect resources and the physical environment, and population structure (Attiwill 1994; Linke et al. 2007). At extreme, a disturbance agent is able to, e.g., eliminate a whole population of a tree species. A classic example is the ecological impact of the chestnut blight (*Cryphonectria parasitica* (Murrill) Barr.) infestations on the American chestnuts (*Castanea dentata* (Marsh.) Borkh.) in the early 1900s (Freinkel 2009). The chestnut blight drove the pristine host species almost to an extinction. In case of removal of the American chestnut, other tree species were observed to compensate for the loss (Elliot and Swank 2007). The major loss seems to be of social and esthetical values of the iconic tree species (Boyd et al. 2013).

1.3 Forest insects as disturbance agents

1.3.1. Insects in forest environments

Insects (Arthropoda: Insecta) comprise the most diverse and the largest group of fauna. Over two dozen separate orders of insects have spread and adapted into every ecological niche

(Berryman 1986). Myriad of insect species are also adapted to forest environments. However, only a small portion of them is considered as a problem (Berryman 1986). Insects, in general, are an important living component of any forest environment, playing many key roles, such as facilitating various ecosystem services (Millennium Ecosystem Assessment 2003; Schowalter 2013; Noriega et al. 2018). Although specific information on functional roles of most species is lacking (Hortal et al. 2015). Insects induce change in forest conditions, especially to the state of the abiotic and biotic environment, and forest configuration (Coulson and Stephen 2008). They influence the abiotic environment significantly by accelerating decomposition and nutrient cycling and maintaining forest productivity (Coulson and Stephen 2008). On the biotic environment of a forest ecosystem, impacts of insect are multitude. For example, in case of herbivorous species, impacts include tree mortality of selected species, alteration of species composition, weakening trees and predisposing to abiotic natural disturbances, modifying the form and appearance of trees, reducing food supplies, reducing or enhancing regeneration, influencing succession, and fertilizing the forest floor (Berryman 1986, Coulson and Wunneburger 2000; Coulson and Stephen 2008). In case of forest configuration, i.e., spatial forming of size, shape, number, and arrangement with a landscape, impacts of insects include alteration of structural and age class diversity resulting in from, e.g., insects killing trees in the older age classes or forming disturbance patches within the forest matrix. Many insect species are also beneficial for humans. For example, various predators and parasitoids act as natural enemies for potential pest species suppressing their populations (Berryman 1986). This function is included into the selection of ecosystem services (Sing et al. 2015). Insects can reallocate nutrients to healthy trees. Insect are normally more successful in attacking weakened trees, such as trees under environmental stress. After tree mortality, more nutrients become available and recycled to the remaining trees (Berryman 1986). Although insects can improve certain sites in long term, these processes can be in conflict with human's more short-term management goals (Berryman 1986). Insect are also important forest pollinators, ensuring cross-fertilization of flowering trees (Berryman 1986; Ollerton et al. 2011).

1.3.2. Insect-induced forest damage

Insect-induced disturbances during periodic oscillations or outbreaks occur naturally in forest environments and are involved in varying ecological processes. These disturbances are often included into natural processes that help maintaining health and heterogeneity of forests (Raffa et al. 2009). Insect-induced disturbances have also an important role, e.g., in long-term forest dynamics. However, pest insect infestations can threaten forest ecosystem sustainability, normal succession functions, and provided services (Boyed et al. 2013). Although trees have various defense strategies against forest pests and natural enemies control pest populations, certain species can overcome the tree resistance (Berryman 1986). A good example of this are several bark beetle species that can reproduce rapidly, colonize a host via aggregation pheromones and tree volatiles, and mass attack even healthy trees (Raffa et al. 2008). Tree mortality also promote fuel, increasing probability of forest fire (Berryman 1986: Hicke et al. 2012). However, from the ecological point of view, this is sometimes desired. For example, the mountain pine beetle (*Dentroctonus ponderosae* Hopkins) have a role in the fire ecology of lodgepole pine (*Pinus contorta* Douglas), important in maintaining current range of the pine species (Logan and Powell 2001). A few years after a mountain pine beetle outbreak, dead needles and trees serve as high combustible fuel for forest fire opening the serotinous pinecones.

Whether the impacts of insects on forests are positive or negative, they can be classified into ecological, economic, social, or political impacts (Coulson and Stephen 2008). Ecological impacts include functional roles, i.e., insect activities affecting forest environments at various spatial scales. Economic impacts refer to the effects on the economic return from products and services. Social impacts are difficultly quantified aesthetic, moral, or metaphysical values associated with forests, such as related educational or recreational use. Effects of insects on the forests that result in actions, practices, and policies comprise the political impacts. Economic impacts are in most cases the triggering factors for classifying an insect species as a pest. Most of the forest insect pests can attain high population densities causing serious economic losses, even occasionally (Berryman 1986). Because population density is such a critical attribute of most forest pests, understanding underlying causes inducing changes in insect population densities is important in forest health management (Berryman 1986). At endemic levels, pest insect population levels are typically low and do not cause significant damage. For example, sparse bark beetle populations attack successfully only weak trees. The change from stable and low population levels to unstable and dense populations are typically triggered by environmental disturbances, such as droughts, storms, or other stressors (Berryman 1986; Anderegg et al. 2012; 2015). Human actions may also trigger insect pest infestations (Berryman 1986). However, low and sparse insect populations can be harmful as well. For example, in cases when the insect species is affecting extremely valuable resources, such as ornamental and shade trees, or plantations and seed orchards. Further, insects, even at low population densities, acting as a vector for other species or pathogens, or inject toxin to host species can be damaging (Berryman 1986). For example, the smaller European elm bark beetle (*Scolytus multistriatus*) transmits *Ophiostoma novo-ulmi* fungus causing destructive Dutch elm disease (Menkis et al. 2016), and longhorn beetles (*Monochamus* spp.) act as a vector for pinewood nematode (*Bursaphelenchus xylophilus*) causing pine wilt disease (Vicente et al. 2012).

Outcomes and impacts of insect-induced damage are often difficult to predict (Dale et al 2000). Impacts of insect driven disturbances can be seen on varying spatial scales, such as at a branch, tree, stand, forest, or landscape level. Effect of insects on forests are typically related to site and stand conditions (Coulson and Saarenmaa 2011). Forest landscapes are consisting of differing site conditions that vary over the life cycle, rotation time, and/or tree species (Coulson and Saarenmaa 2011). Insects can cause damage to forests and forest products in various ways. The impacts of insect infestation may vary from tree mortality to growth reduction, can reduced timber value, stem deformity, or reduce seed crops. In addition to direct damage to trees, many species carry and spread, e.g., fungal species, as bark beetles, inducing reduction in timber quality. Insect infestation may have effects on recreation, wildlife, esthetics, or wildfire hazards (Berryman 1986). The economic impact can be considerable high. For example, tree removal and replacement after infestations by the emerald ash borer (*Agrilus planipennis* Fairmaire) was estimated to cost $26 billion dollars in the Midwestern states of USA (Sydnor et al. 2011). In Europe, between 1950 and 2000, an estimated average annual timber loss by bark beetles was about 2.9 million m^3 (Schelhaas et al. 2003). About half of the wood was damaged by the European spruce bark beetle (*Ips typographus* L.). Ecological impacts can also be extreme. Forest pest insects can fundamentally affect landscapes through altering, e.g., ecosystem composition, structure, and function (Hunter 2002; Coulson and Stephen 2008; Ford and Vose 2007; Ford et al. 2012). For example, elimination of hemlocks (foundation species) by the hemlock wooly adelgid (*Adelges tsugae* Annand, HWA) may result in an altered forest structure and ecosystem functions and services dominated by deciduous tree species (Stadler et al. 2006; Clark et al.

2012). Insect pests can also facilitate altering microclimatic conditions, including solar radiation (Classen et al. 2005).

Foliage-feeding insects, i.e., defoliators are economically very important group of forest pests (Berryman 1986). Defoliators attack forest stands of all ages, depending on the species in questions. However, defoliator outbreaks can often be linked to old or overstocked stands, or forests growing on poor site types (Berryman 1986). It is further believed that stands suffering from physiological stress are susceptible to defoliator outbreaks (Berryman 1986). The immediate effect is defoliation that further causes loss in tree vigor and growth (Lyytikäinen-Saarenmaa and Tomppo 2002), and even widespread tree mortality (Berryman 1986; Zhang et al. 2014). Substantial tree mortality typically occurs when the stand is exposed to other stressors, such as nutrient or water deficiency, intense competition, or high age (Berryman 1986). Even reduction in tree growth without significant mortality may cause substantial economic losses if wide areas are infested. Weakened trees by defoliators are also more susceptible to other damaging species and abiotic factors, such as heavy wind or drought. Additional tree mortality is often present when linked with the secondary stressors (Cooke et al. 2007). Survival of trees also depends on their distinctive properties or on the intensity and duration of defoliation. Typically, tree mortality occurs when the species is feeding for a few years in a row (Chen et al. 2017). However, some tree species may be killed after a single complete defoliation and others withstand defoliation for several years (Berryman 1986).

1.3.3. Population dynamics of forest insect pests

Forest insects can be divided into three groups based on their population dynamics: (1) relatively stable populations that do not have high fluctuations and remain close to equilibrium, (2) populations exhibiting violent cycles in abundance (cyclic pattern), and (3) populations that occasionally erupt and spread over large areas (eruptive pattern) (Berryman 1986). Insect pest outbreaks can further be classified into seven outbreak patterns (see Berryman et al. 1987; Singh and Satyanaryana 2009). Most forest insect pests have either cyclic or eruptive population dynamics, such as autumnal moth (*Epirrita autumnata* Borkhausen; cyclic), or common pine sawfly (*Diprion pini* L.), and European spruce bark beetle (*Ips typographus* L.; eruptive). Cyclic forest pests are typically feeding on tree foliage. They often cause severe defoliation but not extensive mortality to host trees (Berryman 1986). Local environmental conditions are critical in regulating magnitude of population cycles. Consequently, outbreaks of cyclic pests typically occur in the same areas and rarely spread into other areas (Berryman 1986). Cyclic changes in the population gradient often occur in intervals of eight to 12 years and are spatially synchronized over large areas (Berryman 1986; Myers 1998). Periodic intervals of infestations in every 8-12 years are observed for, e.g., larch budmoth (*Zeiraphera diniana* Guenée), western tent caterpillar (*Malacosoma californicum pluviale* Dyar), and gypsy moth (*Lymantria dispar* L.) (Baltensweiler 1989; Myers 1990; Johnson et al. 2005). An example of a longer periodic cycle is an interval of 30–35 years of the spruce budworm (*Choristoneura fumiferana* Clem.) (Williams and Liebhold 2000). The spatial synchrony regularly decreases with the distance (Peltonen et al. 2002; Tenow et al. 2007). These patterns of cyclic pests are most likely affected by the climate change (Jepsen et al. 2008). High-amplitude cycles are expected in forest environments that are favorable for reproduction and survival of the species and less favorable for the hosts or natural enemies (Berryman 1986). Eruptive species may stay at low population level, i.e., endemic phase for a long period and then start to increase in population density exponentially (e.g., Boone et al. 2011). Eruptions can be caused by either a sudden event or more gradual changes in the environment. Outbreaks of eruptive pest insects are often initiated in local environments (epicenters) that are very favorable for the reproduction and survival of the species (Berryman 1986). For example, endemic bark beetle populations may rapidly grow to epidemic outbreak levels when a heavy wind event provides plenty of fresh wind thrown trees for breeding material (Seidl and Rammer 2017). Triggering conditions for an outbreak may form as a combination of several factors (Boone et al. 2011), such as availability and quality of host species (Aukema et al. 2006; Hicke and Jenkins 2008), favorable weather conditions (Logan and Powell 2001; Powell and Bentz 2009), and avoidance of natural enemies (Turchin et al. 1999). The initiated outbreaks typically spread into less favorable neighboring forest stands or areas when emigrating insects exceed the outbreak levels of these stands. Several eruptive pests can also be associated with monocultures, i.e., conditions in which most trees within a stand or landscape are suitable hosts for the species (Mattson et al. 1991). In addition to the European spruce bark beetle, species, such as the mountain pine beetle and southern pine beetle (*Dendroctonus frontalis* Zimm.) are included to highly destructive eruptive forest insect pests.

Insect populations are naturally regulated by various density-dependent and -independent factors. These natural controlling factors include availability of food resources, natural enemies, and intraspecific competition. There are three trophic levels involved in the population dynamics of forest insect pests involving herbivore interactions with host plants and natural enemies (Price et al. 1980). It is generally agreed that herbivore populations are influenced by bottom-up forces (e.g., host plant quality and abundance, plant defense) and by top-down trophic effects (e.g., diversity and abundance of predators and parasitoids) (Price et al. 1980; Hunter et al. 1997; Gurr et al. 2017). These forces are also referred as hypotheses of recourse concentrations and enemies, respectively (Root 1973). Typically, high pest insect population levels decrease, and the effect of natural controlling factors can be seen even during one generation. However, many of the regulating factors, including natural enemies are delayed. This natural regulation may be too slow or inefficient for the forest practitioner. From the human point of view, mitigation of insect-induced forest damage often aims to reduce the impacts on economic return, e.g., timber value. Habitat management operations can be targeted to emphasize these trophic interactions to control pest populations. Methods include actions supporting population of natural enemies or providing additional pray or hosts (Gurr et al. 2017). Habitats can also be manipulated altering abiotic conditions, i.e., microclimate to favor natural enemies (e.g., Landis et al. 2000).

1.3.4. Forest protection and integrated pest management

Coulson and Saarenmaa (2011) defined a three-level hierarchical structure of management of forest environments. Forest protection is the foundation of the management hierarchy and is applied as a part of forest management. Further, forest management is a component of environmental management. Forest protection aims to mitigate impacts of agents causing undesirable changes in conditions or resources of a forest environment (Coulson and Stephen 2008; Coulson and Saarenmaa 2011). Main elements of forest protection include impact assessment, mitigation and prevention, forest health monitoring and management planning, problem solving, and decision-making (Coulson and Stephen 2008). Insect-induced disturbances can never be fully eliminated. An important role of sustainable forest management is to limit damage to acceptable levels.

Integrated pest management (IPM) is a component of forest protection that aims to reduce or maintain destructive agents, such as insect pests, at tolerable levels (Coulson and Saarenmaa 2011). The IPM concept includes various preventative, suppressive, and regulating means that are ecologically and economically efficient, as well as socially and politically acceptable (Coulson and Saarenmaa 2011). These actions should be fully integrated into comprehensive forest management and planning (Coulson 2003). Different tactics and strategies of IPM can be applied in various combinations according to the situation in hand. Effect of IPM should always be considered in the context of desired management goals (Coulson and Saarenmaa 2011). Effects on the surrounding environment have to be taken into account as well, i.e., the highest hierarchy level of environmental management (Coulson and Saarenmaa 2011). IPM consist of 11 different interrelated activities (Coulson et al. 2003). These activities include assessment of effects of climate on the forest environment, pest population dynamics, tree and forest dynamics, and impacts. Rest of the activities are evaluation of control alternatives, monitoring, database management, diagnosis, environmental assessment, management planning, and decision and execution. These steps should include methods for simulation and modeling, field surveys, remote sensing, and building up databases.

The focus of insect pest management should on preventive measures, since eradication is very difficult (Wingfield et al. 2015). Due to effective reproduction and high mobility, insect pests have very low extinction thresholds, and thus are unlikely to be driven to extinction by human actions (Berryman 1986). More realistic goal for forest practitioners is to specify the environmental conditions allowing populations to grow to very high densities, i.e., outbreak behavior from those maintaining endemic behavior (Berryman 1986). Concepts of economic injury level (EIL) and economic threshold (ET) are commonly used in the decision-making (Pedigo and Higley 1996). According to Peterson and Hunt (2003), concept of IPM is based upon the assumption that certain levels of pests are tolerable. Accordingly, the economic injury level (EIL) is a fundamental part of IPM. The EIL provides information on tolerable forest pest densities and intensity of damage (Peterson and Hunt 2003). Development of EIL facilitated development of modern IPM (Peterson and Higley 2002). The ET equals the level of pest population density at which management action should be taken to inhibit the pest population from reaching the EIL. Decision-making in IPM, however, is usually done under high uncertainty (Peterson and Hunt 2003).

Characteristics of a favorable environment for an insect pest population, include but is not limited to having high quality food resources (host abundance and quality), shelter and breeding sites, a low risk of mortality by natural enemies and low number of competitors, as well as a high probability of finding a mate (Berryman 1986). Characteristics of the physical environment are also affecting insect performance. Prevailing temperature and precipitation are related to other characteristics, such as latitude and topography. For example, south facing (i.e., sun facing) slopes are warmer and drier. In a simplified manner, birth and immigration rates usually exceeds those of death and emigration in favorable environments, inducing population growth (Berryman 1986).

Means of protection and mitigation of insect-induced damage should be chosen based on pest species, severity, and the forest and surrounding landscape in question. An outbreak is often a causality resulting in from other biotic factors, abiotic conditions, human actions, and their interactions. The human activities affecting insect populations include poor forest hygiene, storing harvested wood in wrong manner, or poor network of forest roads. Insect-induced disturbances typically occur at or close to the time when forest stands reach maximum biomass density or the greatest volume (Berryman 1986). At the maximum biomass phase, water, nutrient, and light resources are limited weakening the trees; forest owner should harvest or thin the trees in the end of maximum growth period, before the trees become susceptible to insect attack (Berryman 1986).

Managers can manipulate forest stands creating conditions where insect populations are relatively stable and densities are low (Berryman 1986). Insect pest populations can be controlled at low densities by interactions with their food resources, i.e., trees or by natural enemies, i.e., biological control (Berryman 1986; Duan et al. 2015). Biological control has been efficient in case of several introduced pests, such as in mitigation of emerald ash borer populations (Duan et al. 2015; Wingfield et al. 2015). Forest manipulation operations to control insect pest outbreaks may include thinnings and loggings, alterations in tree species, tree species composition, or age distribution, practicing forest hygiene, applying fertilizers, burning, grazing, pheromone trapping, or genetic manipulation, etc. In order to accomplish regulation successfully, forest manager has to understand the basic patterns of pest population dynamics and the feedback processes (Hunter and Price 1992; Berryman 1986). Further, if the type of exhibited outbreak pattern is identified, causal environmental variables can be managed in order to attempt to maintain insect population under outbreak levels (Berryman 1986). If a pest insect population reach outbreak densities and forest is under risk of severe damage, forest manager has three options; do nothing, try to limit spreading and/or try to reduce the population.

Forest insect pests have many advantages making controlling efforts difficult. These include (1) ability to flight, which enables insects to colonize widely dispersed resources, escape enemies, and find mates in sparse populations; (2) high fecundity and fast development enable them to rapidly exploit available resources and maintain high genetic diversity; and (3) genetic plasticity that enables rapid adaptation to environmental changes, including anthropogenic changes (Berryman 1986). Although insect advantages exceed weaknesses making them so successful organisms, insects have some disadvantages that can be taken into account in monitoring and controlling efforts. For example, insects' stereotype behavior force them to respond automatically to various stimuli, including pheromones, light, and host odors (Berryman 1986). Further, insect development is temperature/moisture dependent and environmental manipulation can make them vulnerable. Some stages of metamorphosis and transition between the stages, such as flightless immature stages or newly emerged adults are regarded more vulnerable. The more vulnerable stages, however, are seldom taken into account in forest health management planning.

1.4. Amplified threats of insect pests on forest ecosystems

1.4.1 Climate change in relation to insect pests

Changes in climatic conditions during the next century will substantially affect conditions, compositions, distributions, and productivity of various ecosystems (Easterling et al. 2000). Elevated temperature is the dominant feature of the climate change (Chung et al. 2013). The global mean annual temperature has increased by 0.85°C from 1880 to 2012, and it is anticipated to increase between 1.8°C and 4.0°C by the end of the 21st century (IPCC 2014). Globally, the number of colder days has decreased and that of warmer days increased. Further, the frequency of heat waves has increased in Europe, Asia, and Australia. Climate change also induce reallocation of water resources (Seager et al. 2007). Precipitation is anticipated to increase substantially in the North and South. Simultaneously, e.g., subtropical areas are turning into more arid (IPCC 2014). There also is an increasing number of regions with an elevated probability of heavy precipitation events, compared to those with decreased risk (IPCC 2014). Changes in precipitation patterns may also lead to earlier and longer dry seasons, as well as more frequent and longer droughts (Seager et al. 2007). Increased frequency and intensity of extreme weather events are associated with the changing climate. Ecosystems can be highly vulnerable to these events, including storms, heat waves, droughts, floods, cyclones, and wildfires (Bale et al. 2002; IPCC 2014). Gutschick and BassiriRad (2003) described extreme events as episodes, during which (1) the acclimatory capacities of an organism or population are significantly exceeded and (2) lead to death or prolonged recovery phase that impact both physiological and developmental responses. Although having a high impact on forest ecosystems, these events are stochastically unpredictable (Bréda and Badeau 2008). Unfortunately, it is uncertain, how, when, and where these events occur (Jentsch et al. 2005).

Impacts of climate change are most pronounced on natural systems (IPCC 2014). Climate change is regarded as one of the major environmental concerns threatening forest health (Lindner et al. 2010; Netherer and Schopf 2010; Ramsfield et al. 2016). Effects of the climate change on forests are moderated between prevailing climate, disturbances, and the forest environment itself (Dale et al. 2001). Ecological indicators of climate change in regards of forest environments include increased forest fires and infestations of pests and pathogens, moved treeline, and alteration of age, structure, and species composition (reviewed by Soja et al. 2007). The increased frequency of heavy winds, fires, and insect infestations in European forests has already resulted in signs of saturation of the carbon sink (Nabuurs et al. 2012). Further, the impacts include changes in forest conditions and ecological balance (Tkacz et al. 2008), ecological processes and biodiversity (Dale et al. 2000; Mantyka-Pringle et al. 2011), loss of ecosystem services (Schröter et al. 2005; Lee at al. 2015), and alteration in forest productivity and carbon balance (Dale et al. 2000; Houghton 2005).

It is projected that warmer climate will increase the impacts of insect-induced forest disturbances (e.g., Seidl et al. 2014, 2017). Climatic conditions are regarded as the main factors determining geographical distributions and affecting performance of insect pests (Berggren et al. 2009; Björkman et al. 2011; Jamieson et al. 2012). Insect species are directly connected with temperature and other abiotic factors. These factors can trigger outbreaks or biological invasions (i.e., expansion of a species geographical range to new areas) (Logan et al. 2000; Nativi et al. 2004; Parmesan et al. 2006). Insects are very sensitive to the prevailing temperature and respond rapidly to the changes in the temperature (Sharpe and DeMichele 1977; Lemoine et al 2014). Accordingly, temperature is considered as the most important abiotic factor that influences insect behavior, development, survival, and reproduction (Bale et al. 2002; Karban and Strauss 2004). Success of insect populations have also been directly linked to seasonal temperatures (Berryman 1986; Danks 2002; Glazaczow et al. 2016). Seasonal temperatures control, e.g., rates of life stage development (Preisler et al. 2012) or insect mortality. Warmer climate increases insect metabolism in the growing season and decreases the risk of winter mortality (Bale et al. 2002; Ayres Lombardero 2000). However, species fitness may decline if the temperatures are beyond its optimum level (Lemoine and Burkepile 2012). Rapid genetic adaptation of insects to seasonal changes in temperature has already been documented (Balanyá et al. 2006; Bradshaw and Holzapfel 2006), and numerous range expansions have occurred as species move into new niches created by the elevating temperature (Battisti et al. 2006; Nealis and Peter 2009). The effects of climate change are more pronounced in the North. The increase in temperatures in northern latitudes and high elevations, such as in boreal zone, is expected to exceed that of the global mean (Soja et al. 2007; IPCC 2014). Further, more frequent extreme weather events are expected in these regions. Forest ecosystems may be even more vulnerable to weather extremes while simultaneously adapting to more gentle changes by climate or forest management (Bréda and Badeau 2008). Extreme weather events cause severe forest damage, including selection against more susceptible species (Bréda and Badeau 2008).

The ongoing climate change affects forest insects and the related disturbance patterns in the forest ecosystems (Moore and Allard 2008; Klapwijk et al. 2013). Insect pests are flexible and rapidly adapting their survival, development, reproduction, dispersal, and geographic distribution as a response to the climate change (Régniére 2009; Lindner et al. 2010). Climate change is likely to influence the temporal and spatial dynamics, as well as intensity, frequency, and ranges of insect pest outbreaks (Logan et al. 2003; Vanhanen 2007; Battisti 2008; Jepsen et al. 2008; Netherer and Schopf 2012; Hicke et al. 2012; Chung et al. 2013; Tobin et al. 2014). Various insect species have already responded to the climate change by shifting their geographic ranges and altered seasonal activities, migration patterns, abundances, and/or species interactions (Parmesan 2006; IPCC 2014). An increasing number of insect species is expanding geographic ranges pole-wards or upwards (Logan et al. 2003; Battisti et al. 2006; Vanhanen et al. 2007; Hlásny et al. 2011) or turning into a serious pest species within the current distributions (De Somviele et al. 2007). In many cases, host tree availability is not a limiting factor defining insect pest distributions (Benz et al. 2010). Major northward and upward range shift can be anticipated for several insect pests, such as bark beetles (Benz et al. 2010), moths (Forsman et al. 2016), and diprionid sawflies (Virtanen et al. 1996). There are already indications that the climate change has induced or intensified severe insect pest outbreaks (e.g., Tenow et al. 1999; Battisti et al. 2005, 2006; Benz et al. 2010). Insect-induced forest disturbances are often related to warm and dry conditions (Berryman 1986); periods of draught or warm and dry springs and summers are significant factors increasing insect population levels and facilitating outbreak densities. In comparison, cool and moist summers and cold winters can mitigate populations considerably. Milder winters may also promote success of insect pests (Neuvonen and Viiri 2017). Increased minimum winter temperatures are associated with reduced bark beetle mortality (Benz et al. 2010). Insect pests may complete their life cycle faster than earlier. In northern parts of the ranges, pest populations are may be able to produce one generation per year compared to the earlier two-year cycle (Berg et al. 2006). Alternatively, they may be able to produce two or more generations per year in other regions. This can lead to shifting the balance between the insect and tree defense in favor of the insect (Berg et al. 2006). For example, the European spruce bark beetle have managed to produce two generations in some years during the past decade, in southeastern Finland (Lyytikäinen-Saarenmaa, personal observations). Only a little is yet understood about the potential consequences of climate change and elevated temperatures on the interactions between the trophic levels (Jamieson et al. 2015).

In addition to insect pests, climate change is affecting host trees and the insect-host interactions. The effects are often species-specific. Changes in temperature, precipitation, and atmospheric greenhouse gas concentrations are anticipated to affect host trees (McNulty and Aber 2001). For instance, elevated temperatures can affect tree species establishment and survival (reviewed by Chung et al. 2013). Increasing temperatures have an impact on all biological processes in forest ecosystems, such as tree growth and biomass allocation, photosynthesis, phenology, and nitrogen cycling (reviewed by Chung et al. 2013). Studies addressing impacts of climate change on host species phytochemistry and defense responses are scarce. Zvereva and Kozlov (2006) suggest that the elevated temperatures influence different groups of chemical defenses of host species either increasing or decreasing, and thus affecting insect-host interactions. Host plant quality influences insect pest performance, as well as attractiveness of the host plant (Coviella and Trumble 1999). Herbivorous insect pests are dependent on the concentrations of essential nutrients (such as carbon and nitrogen) and affected by defensive secondary compounds (such as phenolics and terpenes) in the plant tissue they are feeding on (Zvereva and Kozlov 2006). For example, herbivorous insects tend to benefit from higher nitrogen contents in foliage. Increased temperature may lead into increased carbohydrate contents in the host plant diluting nitrogen concentration (Zvereva and Kozlov 2006). Elevated CO_2 consecrations in the atmosphere also affect plant quality, e.g., lowering nitrogen concentrations and increasing allocation of phenolic defensive compounds (Coviella and Trumble 1999; Hunter 2001; Cornelissen 2011). Herbivorous insect pests respond to lower quality food resource by increasing consumption but may suffer from reduced fitness (Williams et al. 1994; Coviella and Trumble 1999; Hunter 2001). Climate change induced weather extremes, such as drought, may also influence tree defense (Raffa et al. 2008; Benz et al. 2010).

Individual tree species must either persist and adapt to rapidly changing environment, shift range, or go locally extinct (Aitken et al. 2008; Benz et al. 2010). McKenney et al. (2007) predicted an average northward range shift of 700 km with 12% decrease in distribution area, with full dispersal ability for 130 North American tree species by the end of this century. With no dispersal abilities, the mean shift was 330 km with 58% decrease in the distribution area. Simultaneously with direct effects of climate change on tree physiology and growth, indirect effects from the interactions between herbivores and their host trees may have high impacts on forestry (e.g., Logan et al. 2003). Ability of different tree species to adapt to expected climate change is still very much unclear (Hamann and Wang 2006; Bolte et al 2007) and severe infestations may inhibit the adaptation (Hastings et al. 2017). For example, in case of eastern hemlock (*Tsuga canadensis* L. Carriere) and Carolina hemlock (*Tsuga caroliniana* Engelmann), poor seed spreading, slow growth, and environmental preferences are hindering adaptation to climate change together with HWA infestations (Hastings et al. 2017). Furthermore, the low rate of adaptation of tree species to changes, compared to insects, increases forest ecosystems' vulnerability to insect pest outbreaks (García-López and Allué-Camacho 2010).

1.4.2. Invasive insect pests

Oceans and other natural barriers used to define distributions of Earth's biota (Liebhold et al. 1995). However, during the last century, mainly because of international travel and trade, species have been able to bypass these barriers and invade new geographical regions at an accelerated rate by globalization (Liebhold et al. 1995). These species include a multitude of insects and other arthropods, plants, and pathogens introduced to novel areas by accident or intentionally. Introduction of most of the plant and vertebrate species have been intentional, while most invertebrates and microbes have been introduced accidentally (Pimentel et al. 2005). The risk associated with biotic invasions have rapidly increased recently due to fast human population growth and movement, and rate of environmental change (Pimentel et al. 2005). For example, more than 2000 non-native insect species have established in North American forests or agricultural settings (Sailer 1983: Niemelä and Mattson 1996; Pimentel et al. 2005). Most of these species have maintained largely unnoticed, however, many of the species have turned into serious pests (Liebhold et al. 1995). According to a US Congress report (OTA 1993), 79 invasive species resulted in $97 billion in damage during 20th century.

Close to a half of the threatened or endangered species in the USA are considered to be at risk largely due to competition with, or predation by non-native species (Wilcove et al. 1998).

Biological invasions cause extensive disturbance to forest ecosystems and have high socioeconomic impacts (Liebhold et al. 1995). These invasions are often facilitated by very favorable new environments due to low host plant resistance, lack of competition, and/or absent or low number of natural enemies. These kinds of conditions may even trigger permanent outbreaks (Berryman 1986). Similar climatic conditions between native range and pristine environments are considered as a basic requirement for a successful invasion (Thuiller et al. 2005). A successful invasion process consists of three different phases: arrival, establishment, and spreading (Liebhold and Tobin 2008). Arrival occurs at the time of the initial transportation of a species to a novel area. Establishment comprises the process, during which the population grows enough to avoid extinction. During the spreading phase, the species expands infestation into adjoining uninfested areas. This range expansion may often last until the species have invaded its completely new ecological niche or the range of host species (Ramsfield et al. 2016). In the beginning, after the introduction to a novel environment, population dynamics of invasive species is often similar to eruptive because they tend to spread fast from the point of origin (Berryman 1986). However, over time, the species may subside and settle into a relatively stable pattern or exhibit one of the different outbreak patterns (Berryman 1986).

Invasive forest insects can have similar negative impacts to forest ecosystems that native insect pests. Invasive insects been observed to influence, e.g., evapotranspiration (Clark et al. 2012) and carbon dynamics (Clark et al. 2010). Climate change will further intensify the negative impacts of invasive insects (Zavala et al. 2008; Dukes et al. 2009). Liebhold et al. (1995) rated biological invasions as the most significant environmental threat to natural forest ecosystems. They called for more efforts to control and mitigate the high impacts of these invasions (Liebhold et al. 1995). Management of invasive insect pests targets on preventing either arrival, establishment, or spread (Liebhold et al. 1995). Typically, in case of invasive species, there is a need to predict the future spreading patterns (Liebhold and Tobin 2008). These projections can be used to estimate anticipated impacts and timeline for targeting mitigation (Liebhold and Tobin 2008).

Especially forests of North America have been suffering from major invasions of non-native invasive insect species. For example, in the USA, hundreds of non-native invasive forest insects, diseases, plants, and other organisms have already been established. Widespread tree mortality is occurring, e.g., by Asian longhorn beetle (*Anoplophora glaripennis* Motschulsky), emerald ash borer, gypsy moth, and hemlock woolly adelgid (*Adelges tsugae* Annand; HWA), just to name few. Although the total number of invasive species in Europe is lower, some highly destructive forest pests have established at the continent, including pinewood nematode and the Asian longhorn beetle.

1.4.3. Increased demand of forest health monitoring

Health of forest ecosystems is under a higher risk than ever before (Boyd et al. 2013; Santini et al. 2013; Roy et al. 2014; Wingfield et al. 2015). Climate change induced changes in performance of native insects and alien invasive species have relatively recently amplified impacts of biological outbreaks. Coupled with the amplified abiotic disturbance patterns, effects of climate change are posing a major threat on sustainable forests ecosystems (Dix et al. 2010; Wingfield et al. 2015). Joint impacts of climate change and insect pest outbreaks have induced increased tree mortality and wide-scale forest dieback during last few decades

(Raffa et al. 2008; McDowell et al. 2011; Jamieson et al. 2012; Ryan and Vose 2012; Weed et al. 2013). Various forest ecosystems suffer from increased intensity, frequency, and spatial scale of insect-induced disturbances and the recent disturbance activity well exceeds the levels of the 20th century (Millar and Stephenson 2015). The impacts are anticipated to intensify further in the future. Consequently, monitoring and mitigating the negative impacts of forest insect pests have become major topics (Pimentel et al. 2005; Dukes et al. 2009). Amplified insect-induced disturbances have raised concerns regarding the impacts on, e.g., biodiversity (Beudert et al. 2015; Müller et al. 2008), biogeochemical processes, such as carbon cycle (Kurz et al. 2008; Edburg et al. 2012; Seidl et al. 2014), and economic return (Dale et al. 2001).

In addition to monitoring climate change induce changes in the patterns of insect-induced disturbances; invasive species have increased the monitoring load. Already established and spreading species needs monitoring, as well as insect pests that have a high potential of establishment. Monitoring efforts are typically focused on international ports of transportation, such as harbors or truck and train stations close to border crossing areas. In addition to the species that have been transferred overseas, transportation of invasive species may occur within the geographic boundaries of a country. Invasive pests are often moved within a country with firewood and lumber, on vehicles, or on nursery stock.

Climate change scenarios, biological invasions, and associated range shifts are causing great uncertainty in the impact evaluation, risk assessment and forest management planning (Dukes et al. 2009; Liang et al. 2014). Because of the importance of forest ecosystems and the increasing risks, implementation of sustainable forest management is crucial (Lausch et al. 2016). Despite the importance, there are no consistent data sets on insect-induced disturbances through time and space (Kautz et al. 2016). This lack of data significantly hinders development of methods for accurate predictions, as well as sufficient management strategies (Kautz et al. 2016; Seidl et al. 2011). Because of the high impacts and high uncertainties, detailed information on forest disturbance is essential for a variety of applications, ranging from ecological modeling to global carbon budgets (Hilker et al. 2009). Remote sensing has been seen as a highly needed source of information for detecting and evaluating the disturbances (e.g., Potter et al. 2003; Linke et al. 2009).

Traditionally the focus on monitoring insect disturbances has been on field inventory and human observations. These methods are relatively expensive and time consuming. Very often, a field campaign can cover only a minor proportion of the infested area. This may lead to biased results and either under- or overestimation of the impacts. Furthermore, traditional methods can be impractical. For example, major outbreaks of forest insect pests may occur in areas with complex topography, sparse road networks, or human settlements inhibiting collection of adequate field data. Field inventories are also typically restricted to certain time or number of species (Homolová et al. 2013).

Modern information to support efficient forest management is complex, extensive, and constantly increasing (White et al. 2016). To support sustainable forest management, forest information has to be up-to date and available across a range of spatial and temporal scales (Turner at al. 2003; Wulder et al. 2008). Furthermore, accurate information is important for decision-making (Kangas and Maltamo 2006). The need for accurate and detailed information poses challenges for forest inventory (White et al. 2016). Further, reducing financial resources hold pressure on efficient forest monitoring (White et al. 2016). However, these needs and the subsequent pressure for method development provide an opportunity for new information sources (Alam et al. 2014). Inaccurate or biased estimates on the disturbance in question may result in inefficient of even bad decisions regarding forest health management operations (Talvitie et al. 2011). While enhanced forest information is required, this can also support development of improved applications for forest health monitoring and management (White et al. 2016). There is a high demand of accurate, efficient, and cost-effective methods for forest health monitoring. In an optimal situation, these methods should be included into comprehensive wall-to-wall forest monitoring systems. These systems should include improved methods of, e.g., accurate and timely disturbance detection, monitoring of infestations, and impact evaluation. Ideally, these systems would be able to identify damage agent, evaluate damage intensity, and provide information on disturbance trends and future projections.

2. EVALUATING INSECT-INDUCED DISTURBANCES

2.1. Forest health monitoring – an overlook

Methods for forest inventory are designed to assess the extent, quantity, composition, and condition of forest resources (Kangas et al. 2006). However, traditionally the focus has been often on the quantitative forest information, such as stand volume or growth. Most of the existing inventorying and monitoring schemes have not been developed to meet the needs of forest health monitoring. Forests inventories are carried for various purposes at varying scales. Reasons for gathering forest resource information include strategic, tactical, and operational forest planning and management (White et al. 2016). Typical small-scale forest inventories include, e.g., an area of a private forest property. National forest inventories (NFIs) are an example of wide-scale inventories. NFIs are carried to acquire nation-wide information on forest resources and to facilitate national strategic planning and development of policies (White et al. 2016). Acquired data may include information on forest cover, growing stock volume, biomass, carbon balance, and wood procurement (White et al. 2016). NFIs are not designed based on needs of forest health monitoring either. However, many NFIs collect some information related to forest health and disturbances, such as the Natural Resources Institute Finland (LUKE) carrying out the Finnish NFI. Information on forest health is collected as auxiliary information, and the health status is monitored at a coarse scale (Tomppo et al. 2006). However, the demand of precise information on forest health management cannot be obtained by the current forest health monitoring practices (Talvitie et al. 2011). Typical challenges of forest inventory tasks, despite the approach, are accuracy, consistency for subjective assessments, and high costs (Thompson et al. 2007; White et al. 2016).

Monitoring of insect-induced disturbances is an essential part of forest health management. Monitoring can be utilized in detecting initial symptoms of insect outbreaks, or evaluating intensity and spatial scale of damage, as well as changes of insect outbreaks. This information is also used to update forest inventories and databases (Sprintsin et al. 2011). Further, forest health monitoring can provide information for projecting future risks or trends in disturbance regimes. Information from the disturbance monitoring can also be utilized in other tasks, such as evaluating global carbon cycles or increasing understanding of spatial and temporal trends in forest management (Healey et al. 2005). Monitoring can be targeted on tree symptoms, insect population densities, or even indirectly, natural enemies of the insect pest in question. Spatial scale of monitoring vary form surveying an infestation in detail to landscape level or large area monitoring. Monitoring can be conducted in the field, including utilizing pheromone traps, employing remote sensing, or with varying combinations linked to the IPM. Road surveys and even fire towers have occasionally been used in insect damage monitoring (Berryman 1986). Used means of monitoring should be chosen based upon the needs. Field surveys (i.e., terrestrial forest monitoring) can be high in detail but time consuming and costly. Typically, only relatively small areas can be covered. Fieldwork is usually applied on small scales from tree- to stand-level, whereas remote sensing provides wall-to-wall information on multiple temporal and spatial scales (e.g., Jetz et al. 2016; Lausch et al. 2017). Developing remote sensing technology is covering part of the needs for forest information traditionally collected in the field. Although fieldwork cannot be fully replaced with remote sensing in the near future, it is most likely that the need of costly filed assessments is reduced further. Most likely field assessments are needed also in the future to, e.g., confirm the damaging agent for decision-making.

Typical indicators of health status of a tree or a forest stand are symptoms on tree crown or canopy, and tree trunks. Symptoms in canopy may include defoliation, foliage chlorosis and other discoloration, loss of buds, and dead branches. Trunk symptoms comprise emergency holes, sawdust, sap, and missing bark. Most of the indicators of damage are qualitative and include visible assessment of an infestation. Some quantitative metrics for assessment of canopy damage or deterioration exist, such as leaf area index (LAI), crown closure, numbers and volume of standing, dead, or fallen trees (Lausch et al. 2016). Changes in forest canopy, including tree mortality, are in many cases more visible from above than on the ground. With means of remote sensing, data for broad, remote, and even inaccessible forest areas can often be produced more rapidly at significantly decreased costs, compared to terrestrial inventories (Ciesla 2000; Hall et al. 2007; Morgan et al. 2010). At wider scales of regional or greater, remote sensing is the only reasonable means for regular monitoring of the changes in forest environments (Healey et al. 2005).

Means of remote sensing have proven to be effective in disturbance monitoring and impact assessment in forest environments (e.g., Hall et al. 2007; Lausch et al. 2013). Efficient pest management is typically dependent on timely detection of an infestation. Often, visual detection of outbreaks is not easy or straightforward (Rullan-Silva et al. 2013). The situation is pronounced with wide and inaccessible forests (Rullan-Silva et al. 2013). Remote sensing has been employed in disturbance monitoring for two main reasons: (1) remote sensing sensors have spectral abilities for symptom distinction with a wide spectral range beyond human eyes and (2) aerial or satellite perspective permits assessment of large areas different spatial and temporal scales (Rullan-Silva et al. 2013). The recent developments of remote sensing methodologies in forest inventories should be adapted into forest health monitoring systems. Remote sensing can be effective for varying spatial scales, depending on the sensor and platform. However, e.g., in case of aerial or satellite imagery, only symptoms in the canopy can be detected. In some cases, one-time monitoring produces the required information. However, often continuous monitoring that can be applied with various temporal scales is needed. Monitoring can be done for a continuous area or applying one of the many sampling methods and plot designs. The procedure can be done individually or as a part of comprehensive forest inventory or monitoring tasks. Choosing methods and platforms for forest health monitoring comes typically with tradeoffs, e.g., between resolution and spatial scale, or consumed efforts and precision.

2.2. Monitoring of insect-induced disturbances with means of remote sensing

2.2.1. Overview on remote sensing

Remote sensing is acquisition of information from a distance (e.g., Lillesand et al. 2015). Remote sensing refers to the detection of reflected and emitted electromagnetic energy. However, the concept of remote sensing usually comprises all the steps from sensing to processing and applying the information. Different objects have different spectral signatures based upon how they reflect and emit electromagnetic radiation (Hunt 1977). These spectral signatures enable detection, identifying, and classifying forest damage by various damage agents, including insect pests (Ciesla et al. 2008). The electromagnetic spectrum can be divided into wavelength ranges, from shorter gamma and x-rays to longer microwaves and broadcasting radio waves, of which several can be utilized in remote sensing of forest health, such as ranges of visible light (~0.4µm – ~0.7 µm) and reflected infrared (~0.7 µm – 3.0 µm). Suitable ranges are chosen based upon knowledge on the spectral signatures or traits. For example, chlorophyll, present in green vegetation is known to highly absorb the blue and red regions, and reflect green wavelengths (Govender et al. 2007). Under various stressors, normal growth and chlorophyll production is hindered and less adsorption in the red and blue regions occur. This also applies when the amount of green biomass is decreasing, such as in case of defoliation. Near infrared (NIR) region has proven to be very useful in projections of forest disturbance (Senf et al. 2017b). Radiation in the NIR region is scattered by the plants leaf structure (Myneni et al. 1995). Shortwave infrared (SWIR) may be very useful in detecting early stages of a bark beetle infestation (Foster et al. 2017).

Typically, various indices are used in remote sensing of insect disturbances. Vegetation indices, i.e., a variety of mathematical combinations or transformations of the available spectral bands have been created to highlight spectral properties of green vegetation in order to improve the distinction from other objects. Typical implications of vegetation indices are indications of greenness, relative density of vegetation, or the vegetation health status. The Normalized Difference Vegetation Index (NDVI) (Rouse et al. 1973; Tucker 1979) is probably the most utilized vegetation index in mapping and monitoring insect disturbance (e.g., Eklundh et al. 2009; Hilker et al. 2009; Spruce et al. 2011; Gärtner et al. 2016; Olsson et al. 2016a). Spectral bands of red and NIR are used in NDVI calculation. Vigorous vegetation has low red reflectance and high NIR reflectance resulting in NDVI values. Lower NDVI values are obtained from disturbed vegetation, such as defoliated trees. Other vegetation indices used for mapping or detection of insect disturbance are multitude, including Enhanced Vegetation Index (EVI) (e.g., de Beurs and Townsend 2008; Bateman et al. 2013), Red-Green Index (RGI) (e.g., Coops et al. 2009a; Meddens et al. 2011; 2013), Simple Ratio (SR) or Infrared Simple ratio (ISR) (e.g., Fraser and Latifovic 2005), and Carotinoid Reflectance Index (CRI) (e.g., Fraser and Latifovic 2005; Lausch et al. 2013), just to name few. In addition to vegetation indices, indices developed for other purpose can be utilized in insect disturbance detection. For example, Kennedy et al. (2010) used tasseled-cap wetness (Crist 1985) and normalized burn ratio (NBR; van Wagtendonk et al. 2004) from Landsat data, in addition to NDVI, in forest disturbance detection. These disturbances included insect damage. They suggested that both wetness and NBR were more sensitive to the disturbances than NDVI. The used index can also be a modified version of an index or a combination of indices, such as a disturbance index developed by Healey et al. (2005) that combined three indices of brightness, greenness, and wetness. Increasingly, ready-to-use remote sensing based vegetation index products are available, such as 8-day NDVI MODIS data.

Sensors are predominately categorized by their spectral sensitivity (Toth and Józ'ków 2016). Further, remote sensing can be divided into two principal types based upon sensor, into active and passive remote sensing. Passive sensors, such as digital cameras, only detect naturally occurring energy, i.e., when reflected by sun. Active sensors emit radiation toward the object and the reflected radiation is again detected and measured by the sensor. Active sensors are able to acquire information despite the season or time and are less dependent on the prevailing environmental conditions (Toth and Józ′ków 2016). Typical active sensors include Light detection and ranging (LiDAR) systems and Radio detection and ranging (Radar). LiDAR methodologies are based on repeated range measurements between the laser scanner and target. The range (distance) measurements are conducted by measuring the time a single laser pulse traveling from the scanner to the target and back (Wehr and Lohr 1999). Emitted laser pulses reflect from the target object resulting in a back-scattering signal, of which intensity varies as a function of time and the resulting intensity curve (waveform) is used for the range measurements. Two laser beams are taken into account, the emitted laser pulse and the received portion of the pulse (Wehr and Lohr 1999). The ranges (distances) are defined by multiplying light speed with the time the emitted laser beam travels to the object and returns (Bachman 1979; Lim et al. 2003). There are two different approaches to record the back-scattering laser data (Wehr and Lohr 1999; Lim et al. 2003). The discrete return approach has been so far more widely studied and utilized in forestry, including in forest health monitoring. In the method, the waveform is analyzed by seeking local maxima in order to reduce the amount of data. Further, Laser scanners are characterized by size of the footprint, sampling rate, and scanning patterns (Dubayah and Drake 2000).

Both passive and active sensors record signal intensity within specified wavelength intervals (bands or channels) of the electromagnetic spectrum. For example, LiDAR systems use wavelengths from visible to near infrared (typically 1.064 µm) and Radar emits longer microwaves (Lefsky et al. 2002). In general, active and passive sensors are available on all platforms (Toth and Józ′ków 2016). Further, remote sensing can be divided into optical and thermal. Many sensors record radiation in the thermal infrared region (3 µm to 15 µm), in addition to the optical range of the spectrum. Thermal sensors measure, in general, surface temperatures and thermal properties of the sensed objects. Traditional platforms for remote sensing forest applications are aircrafts or satellites (Turner et al. 2003; Schowengerdt 2007). Nowadays, however, almost any method for acquiring images or spatial data are considered remote sensing (Mikhail et al. 2001). Use of unmanned-aerial-vehicles (UAVs), i.e., drones, as a remote sensing platform is increasing in popularity, including in disturbance monitoring (Colomina and Molina 2014; Pajeres 2015; Näsi et al. 2015, 2018). Remote sensing data can also be acquired on the ground (e.g., terrestrial laser scanning; TLS), or from vehicles operating on terrain or water. Defining the margins for remote sensing is increasingly difficult as the observation space includes a growing number of new applications (Toth and Józ′ków 2016). Earlier, remote sensing was based on a single sensor on a single platform (Toth and Józ'ków 2016). With the development of remote sensing technology and decreasing costs, remote sensing systems have often adapted for multiple simultaneous sensors, such as more than one camera and/or LiDAR sensors (e.g., Nagai et al. 2009; Asner et al. 2012). In addition, data from two or more different platforms are combined.

Characteristics of remote sensing include spatial, spectral, temporal, radiometric, and directional resolutions. These characteristics influence the ability to detect symptoms of varying forest disturbances. Often, remotely sensed data are differentiated by the spatial and spectral resolutions (Govender et al. 2007). In case of forest disturbances, also temporal resolution is very important. These characteristics are affected by both the remote sensing sensor and the platform. Level of spatial detail is defined by spatial resolution (Govender et al. 2007). Remotely sensed data are commonly distributed in a matrix of pixels (Turner et al. 2003). The size of a pixel corresponds to the spatial resolution of the sensor (and platform). Spatial resolution defines the smallness of objects, i.e., forest characteristics or symptoms that may be distinguished, and thus being larger than the size of a pixel (Turner et al. 2003; Lausch et al. 2016a). Depending on the pixel size, each pixel may contain reflectance from multiple features in the forest (Lausch et al. 2016b). The spatial properties of data result in from the sensor's field of view and operation altitude (Smith 2001). Higher spatial resolution enables assessment of an environment in higher detail. Currently, spatial resolution of remote sensing data ranges from millimeters to 1000 m or even more. Very high spatial resolution data (millimeters) can be acquired, e.g., by drones. High spatial resolution data is often acquired from aircrafts or with high-resolution satellites. Spatial resolution from 0.5 m to 2 m include aerial imagery and hyperspectral sensors (e.g., airborne imaging spectrometer for applications; AISA). Modern high-resolution satellites, such as WorldView-2, RapidEye, and Sentinel-2 reach to spatial resolution up to 2–10 m. WorkdView-3 data reach spatial resolution of 1.24 m for multispectral channels. Medium to low resolution data is typically acquired from the space. These spatial resolutions range from 10–30 m (e.g., Satellite Pour l'Observation de la Terre; SPOT or Landsat data) up to 250–1000 m or greater (Moderate Resolution Imaging Spectroradiometer; MODIS and the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer; NOAA AVHRR). In airborne scanning LiDAR, pulse density that is calculated as a function of the footprint spacing on a flat surface, is regarded as the most consistent measurement of the spatial resolution (Gatziolis and Andersen 2008). When planning a LiDAR campaign, a minimum pulse density for the task should be determined (Gatziolis and Andersen 2008). Factors affecting resolution of an airborne LiDAR point could include Laser scanning speed, flying speed and altitude, and side-lap coverage. LiDAR pulse densities can be divided into low (<1 pulse/m^2), moderate (1-3 pulse/m^2), and high (>3 pulse/m^2). The selection of possible remote sensing application increases with the pulse density.

Spectral resolution refers to the sensors ability to define wavelength intervals. It also refers both to the number and width of the measured portions of the spectrum (Govender et al. 2007; Rocchini 2007). A sensor may record a large portion of the electromagnetic spectrum but still have a poor spectral resolution if only few wide bands are recorded. A sensor capturing a wide range of the spectrum and having several narrower bands has a higher spectral resolution (Govender et al. 2007). Higher spectral resolution, i.e., information in higher detail facilitates better distinction of unique traits from other components in the imagery (Jensen 2005). Sensors with high spectral resolution enable, e.g., tree species recognition at a higher precision than sensors with broader spectral bands (Fassnacht et al. 2016). Where multispectral sensors typically record energy over 3-10 separate wavelength ranges, hyperspectral sensors are able to detect hundreds of very narrow spectral bands from visible to mid-infrared ranges of the electromagnetic spectrum. The obtained spectral signatures of multispectral images are discrete, as contiguous signatures can be obtained with hyperspectral sensors (Govender et al. 2007). Higher multispectral resolutions up to 15 channels, that are often spaceborne, are also acquired for improved classification performance (Toth and Jóźków 2016). In addition to the spectral resolution, the position of the captured range on the spectrum is important. The chosen sensor should record the range or ranges important for the task in question. Spectral resolution is not often that critical in visual interpretation but increases in importance when using automated classification techniques (Horning et al. 2010).

Radiometric resolution is describing the sensitivity of a sensor. A sensor with higher radiometric resolution is more sensitive in detecting minor differences in reflected or emitted energy than a sensor with lower resolution. The potential range of values within a pixel is often referred as radiometric resolution (Horning et al. 2010). Radiometric resolution is measured in bits, where the number of bits is an exponent to the power 2. This number represents the maximum number of available levels of brightness recorded. For example, Landsat data values range between 0 and 255 (8 bits) and IKONOS data values range from 0 to 2048 (11 bits). The level of detail and precision increase along the increasing radiometric resolution. Temporal resolution, or a revisit time interval, refers to the period between repeated remote sensing acquisitions of an object or target area (Turner et al. 2003). For example, Landsat data is acquired from the same location on Earth in every 16 days, and MODIS in every eight days. Some spaceborne remote sensing platforms have high temporal resolution, such as time intervals of 1 or 2 days (TerraSAR-X, RapidEye, WorldView-2, 3) (Pause et al. 2016). For tailored remote sensing campaigns, such as acquiring remote sensing data from aircraft or drone, the temporal resolution and number of revisits can be assigned based on the needs. Revisiting the target location enables monitoring of change, i.e., change detection. They also facilitate timely detection of disturbances. Temporal resolution is further important with optical sensors in obtaining cloud free data over frequently cloudy areas (Turner et al. 2003). Higher temporal resolution increases the probability of cloud free imagery. Temporal resolution is also included into the decisive factors improving distinction of forest characteristics and quantification of spectral traits of an object (Lausch et al. 2016a). In addition to disturbance, factors, such as senescence, phenology, stress, and limited resources lead to changes in spectral traits at varying time intervals (Lausch et al. 2016a). It is important to have sensors recording various processes at different temporal frequencies (Lausch et al. 2016a).

Generally, there are tradeoffs in choosing between different sensors and platforms. Often, when spatial or spectral resolution of remote sensing data decreases, the spatial extent increases. Satellite sensors with a low spatial resolution typically have a high temporal resolution. Further, sensors with high spatial and spectral resolution have often a lower temporal resolution; remote sensing systems imaging wider areas may visit the same point every day in expense of spatial resolution (Turner et al. 2003). This, however, is changing with the development of remote sensing technologies (Lausch et al. 2016a). In addition, new techniques are developed to merge remote sensing data with differing spatial, spectral, and temporal resolutions in order to obtain needed information to accomplish various monitoring tasks (e.g., Hilker et al. 2009; Lausch et al. 2017). High spatial resolution spaceborne sensors (< 5 m) typically have a lower spectral resolution than the medium resolution satellites (Ørka and Hauglin 2016). Their revisit time-interval, however, is often higher due to adjustable image acquisition angle (Ørka and Hauglin 2016). Recent sensors, such as Worldview-3 provide over 10 bands high spatial resolution of 0.3–2.5 m (Lausch et al. 2016a). However, the limited coverage per image is restricting the spatial scale of mapping. Snetinel-2 acquire data from moderately high to medium spatial resolution (10-60 m) with revisit time of five days at equator. In addition to reasonable high spectral and temporal resolution, Sentinel-2 carries a multispectral instrument with 13 spectral bands enabling a variety of vegetation indices for monitoring forest disturbances (Drusch et al. 2012).

Under perfect circumstances, remote sensing characteristics would be chosen based on the needs. For example, it is often practical to use an optical sensor that enables use the lowest number of images covering the study area and providing needed level of detail (Horning et al. 2010). Further, every popular pixel by pixel-based classification method may not work well with a very high resolution data. Multi-spectral sensors usually have quite broad bandwidths providing a high signal-to-noise ratio (Horning et al. 2010). However, sometimes pre-selected narrow bands are needed to detect subtle changes within a similar forest canopy. While remote sensing data acquisition and processing costs are decreasing, there are still expenses to take into account. The relative costs of remote sensing is related to the costs of system (Toth and Józ´ków 2016). For example, total costs of spaceborne remote sensing exceeds those of airborne platforms. However, usually expenses for the final user are considered. Conversely, satellite imageries are usually the most cost-efficient. There are medium to high resolution satellite data available free of charge, such as Landsat and Sentinel-2. Further, commercial high-resolution satellite data, including RapidEye, Ikonos, and Geoeye, can be obtained at low costs of 1–14 € per km^2 (Ørka and Hauglin 2016). Costs of airborne data vary depending on the sensor: aerial imagery (35–62 € per km^2), hyperspectral data (120–180 € per km^2), and LiDAR data (62–240 € per km^2) (Ørka and Hauglin 2016). Some of the costs of remote sensing can be compensated with reduction of costly fieldwork (Fassnacht et al. 2016). These expenses can also be associated with more efficient management and improved decision-making (Fassnacht et al. 2016). It should also be kept in mind that remote sensing enables monitoring of larger areas and may lead to higher accuracy than more traditional methods. Further, while usually field inventory has fixed costs per unit, remote sensing become often less expensive are the target area increases (Franklin et al. 2002). In the future, the expenses related to remote sensing data acquisition can be expected to decrease and more data sources will be available free of charge.

2.2.2. Remote sensing of insect-induced disturbances

Rapidly growing number of scientific publications have demonstrated usefulness of remote sensing in various forest health monitoring tasks. Modern remote sensing and modeling approaches combined with geographical information systems (GIS) provide new means in monitoring and estimating impacts of insect induced disturbances. However, remote sensing of insect damage gives an extra challenge compared to traditional applications of these methods, such as forest inventory and forest management planning. Nevertheless, with suitable scale, resolution, and correct timing, these approaches can produce valuable information and reduce the amount of fieldwork. Remote sensing methods are more cost effective compared to the traditional field inventories and more easily adapted to remote areas with limited access (Heurich 2008). However, to understand full effects of different stressors, monitoring systems combining terrestrial observations and remote sensing are still needed (Wingfield et al. 2015; McDowell et al. 2015).

Remote sensing applications are key components of cost-effective, extensive, repeatable, and standardized forest health monitoring programs (Lausch et al. 2016a). While the information on insect pests gained from field or laboratory data is important, these data cannot be used in predicting outbreak patterns at a landscape-scale or wider (Seidl et al. 2015; Senf et al. 2017a; Simard et al. 2012). The requirements of sufficient data for evaluating large-scale impacts include (1) spatial explicit information, (2) wide geographic area coverage, (3) temporal resolution that is suitable for monitoring the life cycle of the insect pest in question, and (4) long enough time-series to assess natural fluctuations characteristic to the population dynamics (Senf et al. 2017a). With means of remote sensing, these criteria can be met (Senf et al. 2017b). Remote sensing provides an opportunity to study insect outbreaks throughout wide areas at high spatial and temporal scales (McDowell et al. 2015; Trumbore et al. 2015).

Lausch et al. (2016a) considered three research questions on remote sensing of stress and disturbances in taxonomic, structural, and functional diversity over the diversity of forest ecosystems. (1) How can forest health and the mechanisms, drivers and processes be defined, and which spatio-temporal scales should be used to measure forest health? (2) What are the reasons and under which conditions remote sensing approaches are applicable for observing forest health, and (3) what is the concept of spectral traits and the variation in the traits that enable quantifying, monitoring, and assessing forest health with means of remote sensing? How well means of remote sensing serve in forest health monitoring dependents on several factors (Lausch et al. (2016a): (1) shape, density and distribution of spatial and temporal forest characteristics, (2) spatial, spectral, radiometric, angular and/or temporal resolutions of remote sensing sensors or multi-sensor systems, (3) choice of modelling and representation techniques, and (4) how the chosen algorithm and its assumptions fit both the remote sensing data and forest characteristics.

There is a multitude of tree or forest characteristics indicating forest health, ranging from biochemical characteristics, such as nutrient and moisture contents, phenological, physiological, and functional characteristics to diversity, structure, and yield and production. Research on remote sensing on several of these characteristics have been conducted (reviewed by Lausch et al. 2016a). Not all the symptoms of various forest disturbance can be monitored by means of remote sensing. The symptoms that cannot be recorded by remote sensing can be referred to as "Non-Spectral Traits" (Lausch et al. 2016a). These include symptoms that are underground, cannot be detected by a certain sensor, current remote sensing characteristics are not able to record the symptoms directly or indirectly, or have not been detected yet. These include, e.g., some trunk or root symptoms, such as root rot. For example, typical bark beetle trunk symptoms cannot be assessed from above, while they are visible in the field. However, these damage for tree trunks affect also foliage chemistry, and thus may be detected from above, at least in the future. The main component of forest to observe health conditions through remote sensing is the tree crown or canopy. There are two especially important and reliable stress related variables to be observed, discoloration and defoliation (Innes 1993; Rullan-Silva et al. 2013). Although there are various factors that cause both discoloration and defoliation, insects are regarded as the most common source of defoliation (Ciesla et al. 2008). However, these additional factors induce uncertainty in detecting insect-induced damage (Rullan-Silva et al. 2013).

In case of monitoring insect disturbance, spatial scale is an elementary issue (Rullan-Silva et al. 2013; Lausch et al. 2016a). In addition to the practical aspect, the costs are affected by the scale of investigation. At the operational level, two scales should be considered (Rullan-Silva et al. 2013). A wide scale monitoring at low spatial resolution, at a level of early warning, to identify insect outbreaks at locations they can be suspected to occur. The second scale is more local and tactical. Higher spatial resolution is utilized for assessing the warning signs delivered by the first level (Spruce et al. 2011; Rullan-Silva et al. 2013). Thus, monitoring of insect disturbance should be considered as a hierarchy of data sources ranging from wider to smaller scales (Wulder et al. 2006b; Coops et al. 2009b). Low-resolution satellite-based remote sensing can facilitate cost-efficient monitoring of large areas (Rullan-Silva et al. 2013), while high resolution remote sensing (with field surveys) is critical for delivering detailed information on the disturbance in question (Eklundh et al. 2009). A variety of sensors with differing spatial resolutions permits multi-scale applications (Rullan-Silva et al. 2013). Multi-scale monitoring would contribute to detection of complex 'all-scale' dynamics of forest disturbances (Marceau and Hay 1999). Combining different remote sensing data is also increasing in popularity (e.g., Gao et al. 2006; Zhu et al. 2010; Fu et al. 2013). Data fusion have also been utilized in monitoring of forest disturbance (e.g., Roy et al. 2008; Hilker et al. 2009).

Timing of data acquisition is critically important in remote sensing of insect-induced damage. Right timing can enhance the monitoring results substantially. Data acquisition should be scheduled based upon the phenology of the tree species and other vegetation, as well as on the insect pest's life cycle. For example, utilizing the dates of maximum greenness may enhance separation of infested and uninfested stands (Fraser and Latifovic 2005; Frantz et al. 2017). Information on suitable timing could be also derived from insect population models (e.g., de Beurs and Townsend 2008). The timing during the season influences monitoring damage by both defoliators and bark beetles (Senf et al. 2017b). For example, in the case of bark beetles, best timing is often late summer, allowing detecting of spring infestations and avoid effect of regular needle loss in the fall (Senf et al. 2017b). Timing may be the most critical aspect in remote sensing of short ephemeral disturbance events with high recovery rates (Senf et al. 2017b).

In addition to the characteristics of remote sensing sensor and platform, methodology, such as modeling algorithm or classification method affect the accuracy of forest health monitoring (Lausch et al. 2016a). Depending on the required information, some attributes can be directly measured with remote sensing technologies, while other can be derived indirectly employing modeling techniques (Brosofske et al. 2014). A vast variety of classification and modeling techniques has been employed in detecting insect-induced disturbance or evaluating the severity or impacts of outbreaks. According to a review study by Senf et al. (2017b), classification models, such as random forest, maximum likelihood, and logistic regression have been the most often utilized. In addition, rule-based approaches, and regression models have been popular. Typical mapping accuracies have ranged from 60% to over 90% (Senf et al. 2016). Accuracies for detecting damage by defoliating insects have been higher than detecting those by bark beetles.

2.2.3. Main sensors and platforms in monitoring insect disturbances

Use of remote sensing in evaluating insect-induced disturbance begun to increase in the early 2000s and has been amplified ever since (Senf et al. 2017b). European and North American applications have been the most frequent. The emphasis in Europe has been on the Boreal zone (Senf et al. 2017b). Medium resolution remote sensing data have been the most utilized (57%), of which most of the studies utilized Landsat images (Senf et al. 2017b). The most frequently employed low-resolution data has been MODIS (75% of the 13% share). High and very-high resolution data have been equally often utilized (15% each). Senf et al. (2017b) found that low-resolution data was often applied for mapping damage by defoliating insects. Medium resolution was used for all incest pest types and high resolution was especially utilized for mapping bark beetle infestations. Use of single date data was the most common in mapping bark beetle damage (Senf et al. 2017b). Multi-temporal data was used to all types of insect pests but was more common in case of defoliators.

Aerial images have been the most frequently used remotely sensed data in forestry (Hall et al. 2003). High-resolution aerial photography facilitates assessment at fine scale, i.e., individual tree level for reasonable large areas, such landscapes. A variety of forest health monitoring tasks can be accomplished with digital aerial photography (Wulder et al. 2006a). Although the performance of aerial sensors has also advanced, satellite systems have taken a leap towards aerial systems and increased in popularity. The fact that US governmental restriction on commercial satellite spatial resolution (<50 cm) was lifted in 2014 and very high-resolution satellite imagery could be sold, decreased further the difference between airborne and satellite imagery (US Satellite Resolution Restrictions 2014; Toth and Józ'ków 2016).

Landsat images are historically probably the most widely utilized remote sensing data for forest health monitoring. Landsat data has further been employed in various tasks of monitoring forest disturbance (e.g., Healey et al. 2005; Masek et al. 2008; Hilker et al. 2009). Cloud contamination of Landsat images can be particularly problematic in humid environments (Ranson et al. 2003; Ju and Roy 2008). In temporal monitoring tasks, the minimum revisit time interval of 16 days can be significantly extended due cloudy imagery or duty cycle limitations (Ju and Roy 2008). This may hinder data acquisition for forest disturbance in a timely manner (Gao et al. 2006; Leckie 1990; Pape and Franklin 2008). A probability for acquisition of cloud-free Landsat imagery can be only 10% for a given year (cloud cover < 10%) (Leckie 1990). Higher temporal resolution sensors increase the probability of cloud-free images. Opening the Landsat archive in 2008 provided free moderate resolution remote sensing data over large areas (Woodcock et al. 2008; Wulder et al. 2012). This data has facilitated development of methods for mapping several types of forest disturbance (Cohen et al. 2010; Kennedy et al. 2010; Meigs et al. 2011; Wulder et al. 2012).

MODIS data is increasingly included to the selection of methods for general insect disturbance monitoring (e.g., Sulla-Menashe et al. 2014). Although the main weakness of MODIS data is the low-spatial resolution, it has advantages explaining the increasing popularity of the data in forest health monitoring applications. These advantages include reasonable high temporal resolution, low computational demand, and historical continuity in time. Accordingly, MODIS data may gain an important role in large area monitoring of forest disturbance, from regional to global scales (e.g., Hayes et al. 2008; Adelabu et al. 2012). The higher temporal resolution, compared to lower temporal resolution data, such as Landsat, facilitates the more efficient use in areas with frequent cloudy conditions.

Active remote sensing has not been as widely used in forest health monitoring as passive sensors. Airborne scanning LiDAR is relatively new compared to other remote sensing technologies used in monitoring insect disturbance. However, forest applications using LiDAR are rapidly developing and expected to increase in popularity. LiDAR applications have many advantages, including highly accurate registration of spatial information and the capability to penetrate vertical canopy profiles and quantify canopy structures (Gatziolis and Andersen 2008). LiDAR may contribute considerably to monitoring insect disturbances. The ability to measure tree-dimensional (3D) distribution facilitate investigation of vertical structure of forest canopy (Lefsky et al. 1999; Wehr and Lohr 1999). Accordingly, LiDAR could be used to monitoring disturbance driven structural changes in forest canopies. These may include detection of defoliation (Solberg et al. 2006; Kantola et al. 2010).

2.2.4. Monitoring of defoliating insects

Detection of insect-induced defoliation with means of remote sensing is regarded to still be in its early stage and the spectral responses to damaged vegetation are not completely understood (Zhang et al. 2010; Wang et al. 2010). Further method development is needed before comprehensive adaptation at the operational level (Jepsen et al. 2009; Rullan-Silva et al. 2013). More challenging than the detection of needle loss is assessing the severity of defoliation (Rullan-Silva et. al 2013). Although classification accuracies of 70%-80% for three severity classes have been observed (Rullan-Silva et al. 2013), it has to be kept in mind that especially low intensity defoliation is very difficult to monitor (Zhang et al. 2010). Further, detection of defoliation within a sparse canopy cover is even more difficult (Dennison et al. 2009), such as in typical boreal pine forests.

Healthy and green vegetation results in a well-known pattern of spectral signature over the electromagnetic spectrum (Rullan-Silva et al. 2013). The pattern reveals the highest absorption and lowest reflectance in the visible range of the spectrum, followed by a plateau of highest reflectance in the NIR range. Within the range of visible light, a peak in the reflectance occurs in the green band (~0.54 µm), corresponding to the green color of a healthy crown (Rullan-Silva et al. 2013). It is suggested that the visual range is the most consistent indicator of plant stress shown in foliage (Carter 1993; Jensen 2005). A tree is regarded to suffer from stressors, when there is indication on change in the health condition in the foliage (Rullan-Silva et al. 2013). Under stress, reflectances of green and red are increased as the foliage turn into yellowish or chlorotic. Increase in reflectance in the NIR region seems to be consistent only at extreme stress levels (Rullan-Silva et al. 2013). Healthy foliage has a high reflectance of the NIR range. That is partly due to additional reflectance from the energy transmitted through the leaf and re-reflected by the leaves below (Jensen 2005). Hence, changes in the NIR region may be utilized in detecting defoliation (Rullan-Silva et al. 2013). The region of 0.65-0.7 µm may be suitable for early detection of forest damage; the first indicators of stress are seen as increase in reflectance of the red edge (0.7 µm), sifting towards shorter wavelengths (Jensen 2005). Remote sensing sensor's ability to record narrow sensitive ranges, such as hyperspectral data, may improve the detection accuracy (Carter 1993, 1996; Jensen 2005; Mutanga et al. 2009). Hyperspectral data may also be suitable to assess levels of chlorophyll absorption and photosynthetically active radiation related to, e.g., insect-induced defoliation (Jensen 2005). Shortwave infrared (SWIR) wavelengths have been useful in detecting insect-induced needle loss (Skakun et al. 2003; Wang et al. 2007; Goodwin et al. 2008; Coops et al. 2010). There are two peaks in the SWIR reflectance in case of healthy vegetation (~1.6 µm and ~2.2 µm) located between atmospheric water absorption bands (Rullan-Silva et al. 2013). These ranges are reflecting water content of healthy foliage tissue, which is correlated with plant transpiration rates. With decreasing moisture, the infrared energy becomes scattered and the reflectance increases (Jensen 2005). Timing of data acquisition is also very important in case of defoliating insects. One key to a successful assessment of defoliation is the biological window referring to an optimal period for 'visual expression of major forest pests and related damage' (Wulder et al. 2004). The period vary depending on factors, such as host tree phenology, climate conditions, and natural enemies. It is typically in accordance with the peak foliage period of the host (Rullan-Silva et al. 2013). Further, this period is often short emphasizing the role of high temporal resolution. Typical cases are ephemeral outbreaks by defoliators especially in areas with frequent cloud cover (Hicke et al. 2012; Rullan-Silva et al. 2013).

Most of the remote sensing studies on defoliating insects have utilized low to medium resolution data (Senf et al. 2017b). Medium-resolution Landsat and SPOT satellites have been the most widely utilized. Landsat data has been the most popular sensor (e.g., Luther et al. 1997; Radeloff et al. 1999; Franklin et al. 2003; Hall et al. 2003; Babst et al. 2010; Paritsis et al. 2011; Meigs et al. 2011; Olsson et al. 2012; Townsend et al. 2012; Thayn 2013; Sangüesa-Barreda et al. 2014; Rullan-Silva et al. 2015; Senf et al. 2015). MODIS data have been utilized in, e.g., mapping defoliation by pine sawflies (Eklundh et al. 2009), gypsy moth (de Beurs and Townsend 2008; Spruce et al. 2011), and geometrid moths (Jepsen et al. 2009;

Olsson et al. 2016a). SPOT data have been utilized by, e.g., Muchoney and Haack (1994), Fraser and Latifovic (2005), and Gilichinsky et al. (2013). Kharuk et al. (2004, 2007, and 2009) have utilized NOAA AVHRR, MODIS, and SPOT VEGETATION data in monitoring Siberian silk moth (*Dendrolimus superans sibiricus* Tschetverikov). High-resolution satellite data has been so fat less utilized in monitoring insect defoliation. RapidEye images have been utilized by Adelabu et al. (2014) and Sentinel-2 based vegetation indices by (Hawryło et al. 2018).

Although aerial photographs are the most utilized data in forestry (Hall et al. 2003), they have not been as widely utilized as lower resolution satellite-based images in needle loss detection. Aerial digital photography has been used in some studies detecting insect-induced defoliation, such as by pine looper (*Bupalus piniaria* L.) (Långström et al. 2004) and common pine sawfly (Ilvesniemi 2009). Haara and Nevalainen (2002) classified non-specified Norway spruce (*Picea abies* L. Karst.) defoliation from aerial images. Aerial video data was used by Franklin et al. (1995) to detect defoliation by the western spruce budworm (*Choristoneura occidentalis* Freeman). Leckie and Ostaff (1988) tested use of 11 band multispectral scanner data in classification of spruce budworm induced defoliation. Kantola et al. (2010) combined aerial images with high pulse density LiDAR data to classify Scots pine (*Pinus sylvestris* L.) defoliation.

Even though use of LiDAR enables assessment of vegetation structure it has not been widely utilized so far in mapping of defoliation. Further, the features on LiDAR data that could be associated with insect defoliation are less investigated than the associated spectral traits. It has been observed, however, that various metrics calculated form LiDAR point clouds, such as canopy-based quantile metrics, can be linked to foliage biomass (e.g., Magnussen and Boudewyn 1998; Lim and Treitz 2004). Foliage biomass have been directly estimated from point clouds (Riaño et al. 2004), or full waveform data (Lefsky et al. 1999). LiDAR have been utilized before in detection of defoliation by pine sawflies (Solberg et al. 2006, 2010; Kantola et al. 2010; Hanssen and Solberg 2007). Use of terrestrial laser scanning in classification of defoliation was tested by Huo et al. (2019). In contrast to LiDAR, active remote sensing SAR data seems to contribute only modestly to defoliation assessment (Rullan-Silva et al. 2013).

There is an increasing trend in comparing vegetation indices from different times to evaluate the changes by defoliators (Senf et al. 2017b). Multi-temporal satellite data derived vegetation indices have been utilized in, e.g., studies on defoliation by western spruce budworm (Meigs et al. 2015; Senf et al. 2015), Hungarian spruce scale (*Physokermes inopinatus* Danzig and Kozár) (Olsson et al. 2012), and pine processionary moth (*Thaumetopoea pityocampa* Denis and Schiffermüller) (Sangüesa-Barreda et al. 2014). The used vegetation indices utilized NIR or SWIR regions. Changes in NIR and SWIR enables detection of chlorosis and structural changes in the canopy, however, the relationship between the changes in spectral signature and insect defoliation is not as well understood as for bark beetles (Senf et al. 2015). Use of dense time-series may improve detection of defoliation with information on insect peak performance periods within a season (Fraser and Latifovic 2005). In case of broadleaved tree species, dense time-series may even compensate coarse spatial resolution (Senf et al. 2017b). Fusion of remote sensing data with different spatial and temporal resolution may be used to enhance the mapping of defoliation (Gärtner et al. 2016).

2.3. Species distributions

2.3.1. Concept of an ecological niche for species

A niche in ecology refers to a particular range of environmental conditions under an organism can survive and reproduce, or to the functions or positions the organism has in an ecological community (The American heritage dictionary 2018). Every organism has a certain set of physiological, morphological, and behavioral traits that is suitable to occupy particular spaces in nature (Grinnell 1917). It is usually agreed that the concept of niche is one of the central concepts of ecology; although, it is not fully understood (Real and Levin 1991; Leibold 1995). Ecological niches are widely utilized in, e.g., identifying set of environmental conditions affecting species performance, or limiting factors affecting population dynamics (Leibold 1995). Grinnell (1917) included microhabitats, abiotic factors, resources, and natural enemies into the limiting factors comprising the ecological niche. Hutchinson (1957, 1978) introduced a concept of fundamental niche which is a multidimensional space having all the environmental variables affecting the species on the multiple axes. This fundamental niche would be occupied by the species in the absence of other species. The realized niche is a part of the fundamental niche within the species is restricted resulting from interspecific interactions. Elton (1927) addressed the importance of the functional role of a species in the environment, such as in relation to the trophic levels.

2.3.2. Ecological niche models

As the forest health monitoring gives often answers on the current situation or near future, risk assessment is often needed in evaluating potential of damage events occurring or reoccurring in the future. In here, risk is defined as product of hazard and exposure, i.e., probability of disturbance occurrence in certain time and location. Risk assessment may facilitate prediction on, e.g., a set of conditions where outbreaks of an insect pest may occur in the future (Berryman 1986). Modeling techniques are often used as part of efficient risk assessment. Various modeling approaches can be employed in, e.g., projections of future disturbance trends, determining outbreak threshold levels, evaluating level of impacts, such as growth losses or tree mortality, and species distributions.

Ecological niche modeling (ENM, species distribution modeling) is a popular group of techniques for predicting species distributions and changes in the distributions (Soberón and Peterson 2005; Soberón 2007; Peterson et al. 2011). ENMs are contributing to forest health management, especially in decision-making and risk assessment. In ENM, a wide range of environmental layers can be used to predict species distributions. ENMs enable projections of species distributions across space and time, facilitating estimates on changes in the distributions over a range of spatial extents (Pearson and Dawson 2003; Gontier 2007). ENMs are based on the niche concept and are targeted to describe the range of suitable habitats for a species. This is accomplished by identifying environmental conditions associated with the species occurrence observations (Peterson et al. 2011; Halvorsen 2012). ENMs comprise a wide selection on algorithms, of which Maximum Entropy (MaxEnt) and Genetic Algorithm for Rule-Set Production (GARP) are the most widely used. Factors affecting accuracy of ENM projections include selection of predicting environmental variables and delineation of the background evaluation extent (Peterson et al. 2011; Merow et al. 2013). In addition, to projecting current ranges, of species, popular ENM applications include future predictions of distribution according to various climate change scenarios. The selection of predictors is affected by the goal, whether it is to project the current distribution or the potential distribution through time and space (Peterson et al. 2011).

A multitude of different factors affect species distribution, composition, and abundance (Hodkinson 2005). However, the potential distributions describing the current suitable abiotic environment can be projected with a reasonably small number of variables (Leidenberger et al. 2015). Further, the importance of varying environmental factors in identifying species distributions is highly scale-dependent (Peterson et al. 2011). Abiotic factors tend to be more important variables at large spatial scale over biotic and anthropogenic factors (Menke et al. 2009). Climate and topography are seen as the most important factors at the regional scale between 200 km and 2000 km (Pearson and Dawson 2003). At even wider continental scale, climate is the most important factor limiting species distribution (Thuiller et al. 2005). Out of the climatic factors, temperature and humidity has been suggested as the main drivers for species distribution (Grinnell 1917; Peterson et al. 2011). Climatic factors have, in addition to direct impacts on insects, indirect impacts via host plant quality, including nutrient balance and levels of secondary metabolites (Ayres and Lombardero 2000). Population dynamics of insect herbivores can respond to a variety of interactions between species and their natural enemies. However, it can be assumed that these interactions are also sensitive to climate, especially to temperature (Björkman et al 2011; Weed et al. 2013). In reality, distributions are never defined by abiotic factors only. With decreasing of spatial scale, other environmental factors increase in significance, such as biotic interactions, e.g., competition, dispersal, and soil and microclimate, as well as anthropogenic factors, including landscape change (Ehrlén and Morris 2015). These factors, however, are often difficult to incorporate into the models.

Ecological niche models utilizing presence data are not very suitable for assessing abundance of species, or the related impacts. Further, future projections are more suitable for estimating potential ranges than probability or timing of an establishment (Fitzpatrick et al. 2012). However, often, close to the ranges of the suitable conditions, the impacts can be milder than in the middle of the ranges. For example, pronounced genetic constrains and asymmetric gene flow on the edge areas may lead to lower survival (Parmesan 2006). On the other hand, ENMs can be further linked to other models, such as population growth and dispersal models to be used to in impact evaluation. New versions for ENM are also developed that include an estimate on species abundance as well. For example, exponential raw output can be used as an estimate of relative abundance within species distributions in the new version of MaxEnt (3.4.0; Phillips et al. 2017).

2.3.3. Potential distributions of invasive species

The main emphasis of ENM has been on native species and their future ranges according to various climate change scenarios. However, ENMs for invasive species have increased in their popularity due to the high impacts of these species on ecosystems and economic return (Menke et al. 2009; Kulhanek et al. 2011). Typically, ENMs are calibrated within the species' native range and the results are transferred into the novel environments. Often, in case of invasive species, results are presented as an ensemble of different modeling methods. However, that does not guarantee higher accuracies (Elith et al. 2010). However, ENMs can be created also within the introduced regions. This is particularly encouraged if the information from the native range is limited or biased. Use of information from the area of introduction in the model calibration requires careful delineation of the background evaluation extend and information on species history in the novel environment (e.g., Elith et al. 2010; Barve et al. 2011). In case of species that are not at the equilibrium and still spreading, the maximum distance of spreading under optimal conditions could be used to delineate the area for model calibration (Barve et al. 2011). However, varying condition outside the invaded area may induce additional error and uncertainty to the models (Menke et al. 2009).

There are more uncertainties present when calibrating ENMs for invasive species, compared to native and more stable insects (Peterson 2003). Two main concerns include: (1) the species occurrence data does not correspond to the stable relationships between the insect and environmental factors and (2) future combinations of suitable environmental factors cannot be sufficiently sampled (Menke et al. 2009; Elith et al. 2010). Various biotic interactions may influence successful invasion and pattern of distribution (Bruno et al. 2003; Suttle et al. 2007). Further, obtaining a good quality data within an expanding range is challenging (Guisan and Thuiller 2005). Other sources of uncertainty include species adaptation during range expansions. The rate of adaptation of invasive species can be very fast (Butin et al. 2005).

Significance of the impacts of invasive species cannot be determined only by their presence (Bradley et al. 2012). Further, the impacts are difficult to predict, and they may vary substantially within the area of invasion (Kulhanek et al. 2011). Impacts may be less severe at the edge of the suitable range, as for native species. However, if the area provides lower suitability for the host species as well, there is a risk of high impacts. When ENMs are used with abundance data, the technique can be utilized for risk modeling as abundance correlates stronger with risk that just presence (Kulhanek et al. 2011). Unfortunately, suitable abundance data for ENM purposes is not often collected, particularly in case of invasive species (Bradley et al. 2012).

3. OBJECTIVES OF THE THESIS

The dissertation aims to contribute to the development of efficient future forest health monitoring systems. Forest health monitoring is in transition and traditional methods are insufficient to cover all the current and future demands; new modern approaches are needed. These systems must operate at different spatial resolutions and scales over a gradient of different forest ecosystems and disturbance agents combining remote sensing and spatial models. The topic is wide and complex, and an immense amount of research is still needed to accomplish the major goal. In this context, the main goal of this dissertation is to evaluate and improve various methods for forest health monitoring at different scales in regard to insect pest disturbances. Improved methodology can lead to, inter alia, cost-efficiency, decreased fieldwork, increased accuracy of detection and monitoring, and improved evaluation of impacts of forest disturbances. Focusing on foliar insect pests, use of various remote sensing methods and ecological niche modeling are discussed. The thesis is adding information on issues related to forest health monitoring under varying conditions, such as on the use of proper spatial and temporal resolution in the monitoring. Influence of landscape heterogeneity, topography, and available information are also discussed in the context of remote sensing of insect-induced disturbances.

In the six sub-studies, use of remote sensing and ENM were investigated as components of forest health management. Remote sensing was employed in the sub-studies I-V. The scale of investigation ranges from individual tree level to forested landscapes and spatial resolution form high pulse density LiDAR to low resolution MODIS data. Most of the sub-studies are using singe date data and in the sub-study V, use of time-series are investigated. Several modeling techniques were applied on remote sensing data sets. In the last sub-study (VI), MaxEnt algorithm was applied for projecting continental scale distribution of an insect pest. Geographic information system software, such as ArcGIS (Environmental Systems Research Institute - ESRI, Redlands, CA, USA) and R environment for statistical computing (R core team 2019) were important components of the sub-studies. Study species include native insect pests and an invasive alien species. The main study species are common pine sawfly (*Diprion pini* L.) and hemlock woolly adelgid. Additional study species in the sub-study V were European pine sawfly, autumnal moth, and winter moth (*Operophtera brumata* L.). The specific objectives of the six sub-studies were:

I To investigate use of LiDAR in assessment of tree level defoliation after needle consumption by the common pine sawfly in Ilomantsi, North Karelia. Classification of defoliation was conducted for several different classification schemes to study how the number of classes and the class thresholds affect the classification accuracy. An additional objective was to investigate the effect of LiDAR pulse density on the classification accuracy.

II To develop and evaluate an area-based LiDAR method for assessing plot-level needle loss caused by the common pine sawfly in the Ilomantsi district. Hypotheses of LiDAR pulses penetrating deeper to the canopy was also evaluated by comparing penetration related LiDAR metrics. Impact of pulse density on classification accuracy was also tested.

III To demonstrate additional tools in investigation of broad scale impacts of hemlock mortality to HWA herbivory in Linville River Gorge, Southern Appalachians, NC, USA. The specific objectives included visual detection of dead trees from high spatial resolution aerial images and estimation of an area of the canopy cover surface occupied by dead trees. Furthermore, hemlock mortality in relation to topography, as well as the spatial pattern of the hemlock mortality were investigated.

IV To develop methodology for assessing insect-induced tree mortality within inaccessible forest landscapes. High spatial resolution aerial imageries and LiDAR driven canopy height model were employed in remote sensing of HWA-induced hemlock mortality in the Southern Appalachians. A two-phase semiautomatic method was developed to map dead trees and conifer patches comprising the living hemlock component.

V To investigate use of low spatial resolution satellite data in stand level detection of defoliation in Fennoscandia. Potential of time-series methodology applied to high temporal resolution data for insect disturbance was examined to investigate accuracy of regional or global disturbance monitoring methods based upon low-resolution data. The method was developed and tested in different Fennoscandian forest landscapes in North Karelia and North Sweden, characterized by different defoliating insect, level of fragmentation, and outbreak history.

VI To project potential current and future range for non-native HWA in the Eastern North America. Ecological niche models were calibrated within the introduced range of HWA. Statistically best subsets of explanatory features were chosen amongst over 100 environmental variables. An unusually high spatial resolution of 1 km was used in the models enabling use of topographic and soil features in addition to climatic variables. Habitat suitability for the species was reverse-casted to the native ranges in East Asia and Western North America and projected under several future climate change scenarios in the Eastern North America.

4. MATERIALS

4.1. An overlook on study areas and data sets

Sub-studies of the thesis comprise four different study areas (Figure 1). Three of the study areas are located in Fennoscandia. Two partly overlapping study areas in the Southern Appalachians, NC, USA. There were no specific study areas in the sub-study VI, but species occurrence observations are gathered within the eastern North America (and East Asia). Information measured and assessed in the field in the Palokangas study area, in Ilomantsi of eastern Finland, was used in sub-studies I, II, and V, Outokumpu and Abisko areas in V. Study areas in the Linville River Gorge served as bases of the sub-studies III and IV. The study areas differ in total area, disturbance agent and history, climate, vegetation, as well as in the scale of investigation (Table 1). The main focus is on the Palokangas and Linville areas, and thus described in more details.

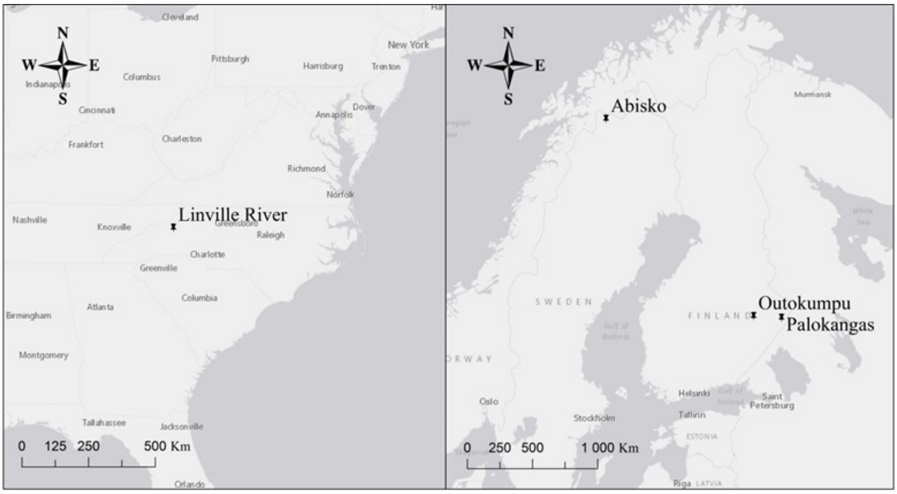

Figure 1. Locations of the specific study areas in the sub-studies; the Linville River Gorge area of western North Carolina (left) and Palokangas, Outokumpu, and Abisko study areas in Finland and Sweden, respectively (right). (Map by ESRI/HERE©)

Table 1. Summary of the study areas, scales, field data, and data sets in the sub-studies.

Study	Area	Scale of investigation	Main methods	Remote sensing data
I	Palokangas	Tree-level	Random Forest	LiDAR
II	Palokangas	Plot-level	Random Forest	LiDAR
III	Linville	Tree/landscape	Ripley's K	Aerial photography
IV	Linville	Landscape	CT/SVM[b]	Imagery/LiDAR
V	Fennoscandia[a]	Stand/region	Z-scores	MODIS
VI	North America	Continent	MaxEnt	N/A

[a] Fennoscandia comprises Palokangas and Outokumpu study areas in Finland and Abisko area in Sweden.

[b] CT refers to classification trees, and SVM to support vector machines.

Remote sensing was utilized in the sub-studies I-V. High pulse density LiDAR was utilized the sub-studies I and II. A canopy height model (CHM) was produced from low pulse density LiDAR data in the sub-study IV. Airborne photography enabled sub-studies III and IV. The sub-study V was conducted using spaceborne MODIS data products. Instead of remote sensing global climatic, topographic, and edaphic environmental layers were utilized in the ENM task in the sub-study (VI). The scale of investigation in the sub-studies ranged from individual tree level (I) to continental scale projections (VI).

4.2. Target insect pests and their main impacts

4.2.1. Pine sawflies (I, II, V)

Pine sawflies (Hymenoptera: Diprionidae) include some of the most common pine defoliators of Europe (e.g., Larsson and Tenow 1984; Geri 1988). There are eleven sympatric pine sawfly species in Northern Europe feeding on Scots pine (Kontuniemi 1960). Out of them, outbreaks by five species have been recorded in Finland (Kangas 1963). In here, defoliation by the larval stage of the two major pine sawfly species in Finland, the common pine sawfly, and the European pine sawfly are discussed. Of these, the focus is on the common pine sawfly. Berryman (1987) described a common type a of pine sawfly outbreak as sustained and eruptive. This kind of pattern is characteristics for the common pine sawfly (Geri 1988). Kangas (1963) raised a possibility that the European pine sawfly may have a 30-year cycle in the regional outbreaks. However, this cyclic pattern has not been confirmed (Hanski 1987). Pine sawfly outbreaks often start in forests growing on dry and poor soils (e.g., McLeod 1970; Nevalainen et al. 2015). Outbreaks can spread into large areas from epicenters and sustain for several years. For both of the species, outbreak levels are usually followed by long periods of endemic population levels. The endemic phase may last even for several decades (Viitasaari and Varama 1987; Herz and Heitland 1999, 2003).

Both European pine sawfly and common pine sawfly are currently regarded as forest insect pests in Finland causing declined tree vitality and growth on Scots pine due to defoliation during consecutive years. Outbreaks by these sawfly species in Finland are often accompanied by secondary pests, such as by pine shoot beetles (*Tomicus* spp.) (Annila et al. 1999). Damage by the secondary pests is often difficult to distinguish from that of pine sawflies. Local outbreaks by the European pine sawfly occur almost annually somewhere in

Fennoscandia, spreading sometimes into wide areas causing defoliation at regional scale (Virtanen et al. 1996). In Finland, the common pine sawfly used to cause only small-scale and low intensity damage (De Somviele et al. 2007). Outbreaks typically covered only few hundreds or thousands of hectares (Kangas 1963; Juutinen and Varama 1986). The outbreak pattern of the common pine sawfly has evidently changed during past few decades in Finland (De Somviele et al. 2007). Factors, such as elevated temperatures and Scots pine monoculture have facilitated the change. It was not until 1997-2001, when a massive outbreak of the common pine sawfly initiated in western Finland and spread throughout the central Finland, causing damage within an area of about 500,000 ha (Lyytikäinen-Saarenmaa and Tomppo 2002). The outbreak was so far the largest in the recorded history of the Finnish forest health (De Somviele et al. 2004).

The European pine sawfly seldom causes mortality to Scots pine in Finland. The common pine sawfly, however, may cause substantial tree mortality under current climatic conditions affecting further recovery of forest and economic return. Capability of the common pine sawfly to cause more intense damage compared to European pine sawfly, is mainly due to different timing of the larval stage. In Finland, both species are univoltine and their life cycles are regulated especially by prevailing temperatures. The European pine sawfly larvae usually feed on Scots pine needles during early summer. Common pine sawfly larvae hatch later in the season and typically feed on Scots pines during the late summer in August and September (Viitasaari and Varama 1987; De Somviele et al. 2007). The later timing of the larval stage facilitates consumption of needles of all age-classes and increases the probability of tree mortality. At peak population densities, the needle consumption may lead to total defoliation (Geri 1988). Tree mortality typically occur if the heavy needle consumption continues two or more subsequent years. The species ability to stay in diapause for several years can even prolong the outbreak phase (Viitasaari and Varama 1987; Talvitie et al. 2011).

Common pine sawflies have been observed to prefer mature and maturing Scots pine (Geri 1988; Dajoz 2000), as well as stands growing on shallow, low fertility, and well-drained soils (Viitasaari and Varama 1987). Despite the preference on more mature pine stands, at gradation phase, the species can spread into sapling and seedling stands (Geri 1988; De Somviele 2004). A typical pattern of common pine sawfly defoliation is that the taller and older dominant trees are more severely defoliated than the shorter and younger, i.e., suppressed trees. Females prefer laying eggs on needles of the uppermost parts of the tree crowns and canopy, due to higher carbohydrate synthesis in the needles than under more shaded conditions (Lyytikäinen 1994; De Somviele et al. 2007). The common pine sawfly typically attacks suppressed understory pines only after completely consumption of the needles of taller trees.

4.2.2. Hemlock woolly adelgid (HWA) (III, IV, VI)

Hemlock woolly adelgid is a non-native invasive insect in eastern North America that infests and induces tree mortality to eastern and Carolina hemlock communities. This piercing-sucking aphid-like insect is native to East Asia and the strain of HWA in the eastern North America originates from Japan (Havill et al. 2006). Recently, it was also confirmed that the species is also native in the western North America (Havill et al. 2016). All the ten hemlock species can serve as hosts for HWA. Excluding the eastern North American species, HWA causes only minor damage to hemlocks (Havill et al. 2006). Both eastern and Carolina hemlock seem to have low to no resistance against HWA (Eschtruth et al. 2006). The high susceptibility of the host species combined with lack of natural enemies, rapid reproduction, and several vectors have provided for the successful performance and fast spreading of HWA in the eastern USA (McClure 1987; McClure and Cheah 1999; Trotter and Shields 2009). The species was recorded for the first time in the eastern USA in Richmond of Virginia, in 1951 (Stoetzel 2002), although the introduction has most likely been much earlier (McAvoy et al. 2017). In the beginning, HWA spread slowly in ornamental settings and was not considered as a pest. In the 1980's, HWA begun the rapid and aggressive spreading (Spaulding and Rieske 2010). This was most likely due to reaching the native range of the eastern hemlock, accompanied with climatic factors (Ward et al 2004; Spaulding and Rieske 2010).

HWA has a complex life cycle that includes two annual generations and hosts (McClure and Cheah 1999). On hemlock species, it has an overwintering asexual generation (*sistens*) and a spring generation (McClure 1987). The spring generation develop into two morphs; asexual *progrediens* and winged *sexuparae* that pursue host spruces (McClure 1987). In the eastern North America, no spruce species is suitable for HWA as a host and the morph acts as a population sink (Fitzpatrick et al. 2012). HWA feed on hemlock parenchyma cells during cooler months and is inactive during hot summer months (McClure 1987; Ward et al. 2004). Exact timing of the stages depends on various factors, including temperature, latitude, and elevation (Ward et al. 2004). The life cycle of HWA is described in detail by e.g., McClure (1987), McClure and Cheah (1999), and Ward et al. (2004).

HWA remains stationary most of its life cycle. Only the crawler stages are mobile. HWA eggs spread by various means, such as with phoresy by wind, wildlife, and human activities (Ward et al. 2004; McClure et al. 2001). Both short and long-distance dispersal of HWA occur (Morin et al. 2009). New colonies have been observed far ahead of the main front of the invasion. The spreading pattern of HWA is anisotropic (e.g., Evans and Gregoire 2007; Morin et al. 2009); HWA has spread towards south and north much faster than to the West. This may be due to phoresy by migratory birds, as well as pattern and abundance of the eastern hemlock (McClure and Cheah 1999; Morin et al. 2009). Annual rates of range expansion vary between 12.5 km (Evans and Gregoire 2007) and 20-30 km (McClure et al 2001; Morin et al. 2009). By the year 2012, the species was observed to reach the most southern part of the eastern hemlock range (USDA 2015). Novel areas within the eastern hemlock range are available in the North and West.

The early symptoms of HWA infestations are defoliation and reduction in shoot growth (Kohler et al. 2008). Infested hemlocks often die in a span of four to 10 years (McClure et al. 2001; Spaulding and Rieske 2010). Complete mortality of a hemlock stand may occur as fast as in two to three years, particularly in the South (Trotter and Shields 2008). Infested hemlocks are also susceptible to secondary damage (Cheah et al. 2004). Herbivory by the HWA has various effects on forested landscapes. Impacts of hemlock mortality include alternations in carbon and nitrogen cycling (Orwig et al. 2008; Albani et al. 2010; Templer and McCann 2010), decomposition (Cobb 2010), landscape structure, composition, and function (Ford et al. 2007; Ford et al. 2012). HWA also affect other plant species and wildlife (e.g., Ward et al. 2004; Rohr et al. 2009). Influence of hemlock mortality reach beyond forest ecosystems, to riparian areas, stream ecosystems, and urban settlements (Ford and Vose 2007; Templer and McCann 2010). The high performance of HWA in the eastern USA results in from rapid parthenogenic reproduction, lack of natural enemies, high dispersal potential, and very susceptible host species (Trotter and Shields 2009).

4.2.3. Geometrid moths (V)

Mountain birch (*Betula pubescens* ssp. *Czerepanovii* [Orlova] Hämet-Ahti) forests in northern Fennoscandia, at the upper boarder of the Boreal zone, are regularly suffering from defoliation by geometrid moths (Lepidoptera: Geometridae; Tenow 1972, 1996). Large areas of mountain birch forests are defoliated in periodic cycles of about 9–10 years, usually around mid-decades, by autumnal moth and a more recent winter moth, especially in the Scandes (Bylund 1995; Tenow et al. 2007). Autumnal moth and winter moth are present in most of Fennoscandia but they differ in their regular outbreak distributions (Tenow 1972; Neuvonen et al. 1999). Autumnal moth outbreaks often occur in heath birch forest on the eastern side of Scandes as the outbreaks of winter moth typically occur in meadow birch forests in the western Scandes (Tenow 1972). Further, outbreaks of the autumnal moth are more common in the northernmost parts of Fennoscandia and in the continental regions (Tenow and Nilssen 1990; Bylund 1999). This difference in the outbreak ranges is regarded to result from the difference in cold tolerance between the species (Jepsen et al. 2008). The species overwinter as eggs that are placed on birch branches and twigs, and thus are exposed to the weather extremes (Tenow et al. 2007). Autumnal moth suffers from high mortality in temperatures below −36°C (Tenow and Nilssen 1990). Winter moth is a little more sensitive to low temperatures (−35°C; MacPhee 1967; Tenow 1996). Winter moth also seems to be less tolerant to extended periods of cold temperatures than autumnal moth.

These moth species can have substantial ecological impacts resulting from growth reduction and tree mortality (Tenow 1972; 1996; Ammunét et al. 2015). Even widespread birch mortality may occur from the foliage consumption by the larval stages in the spring (Kallio and Lehtonen 1973; Tenow et al. 2007). Typically, older forests are attacked and the recovery time of the trees from these outbreaks may be long, even for decades before the full recovery (Tenow 1996; Ruohomäki et al. 1997). Sometimes local autumnal moth outbreaks have occurred simultaneously throughout the Scandes, while other times outbreaks have been spreading like a wave through Fennoscandia (Tenow 1972; Tenow et al. 2007). Outbreaks by autumnal moth can also be synchronized with those by winter moth (Tenow 1972; Tenow et al. 2007). It has been assumed that low summer and winter temperatures may have synchronizing influence on the outbreaks regionally (Niemelä 1980; Bylund 1995). Outbreaks by these moth species in North Fennoscandia have been reported since late 19th century (Tenow 1972). Most likely, the species have been persistent notable longer in the region (Tenow 1972). Warming climate, particularly lower number of extremely cold winters has a high impact on these birch moth populations (Babst et al. 2010; Callaghan et al. 2010). Expansion towards North and Northeast have already been documented for both species in Fennoscandia (Jepsen et al. 2008). Distribution of autumnal moth outbreaks is expanding into colder areas with more continental conditions; winter moth is ranging towards areas previously dominated by the autumnal moth (Jepsen et al. 2008). Winter moth has also been rapidly spreading into outbreak ranges of autumnal moth, such as in northern Finland, and may even outcompete the ‘true native’ species (Ammunét et al. 2010). Winter moth has a capability to adapt for a range of host plant qualities potentially causing severe cascading effects on the northern ecosystems (Ammunét et al. 2011, 2012). In addition to these moth species another geometrid moth, the scarce umber moth (*Agriopis aurantiaria* Hübner) has been able to reach outbreak densities in Fennoscandia (Jepsen et al. 2011), posing a novel threat to the Fennoscandian mountain birch forests (Ammunét et al. 2012).

4.3. Study areas

4.3.1. Palokangas area (I, II, V)

The Palokangas study area, totaling of 34.5 km^2, is located in Ilomantsi of eastern Finland (62°53′N, 30°54′E, Figure 2). Managed Scots pine forests, owned by the Tornator Ltd are mainly growing on dry and dryish forest site types. The relief within the area is relatively flat with a mean elevation above the sea level of 170 m. In 2009, the majority of the stands were young and middle-aged, with average age of 53 years and diameter-at-breast-height (dbh) of 14.7 cm (Talvitie et al. 2011).

The initial outbreak by the common pine sawfly was already visible at the area in 1999. The outbreak initiated when the widespread outbreak spread to the east and reached the region (section 4.2.). Within the region, the common pine sawfly caused growth losses and Scots pine mortality within an area of circa 10,000 ha. The population density, damage intensity, and spatial extent have been fluctuating ever since. Peak population densities at gradation phase were observed during 2000-2002, and again at 2005. After 2005, population densities have remained at relatively high postgradation phase, showing some chronic nature. Last time the area was visited in the spring of 2016, new defoliation from the previous year was apparent (Kantola T., personal observation). The forest owner has conducted large salvage loggings within the area due to the prolonged outbreak. Typically, the infested Scots pine in the Palokangas area were also infested by secondary pests of pine shoot beetle (*Tomicus piniperda* L.) and lesser pine shoot beetle (*Tomicus minor* Hartig) (Kantola T., personal observations).

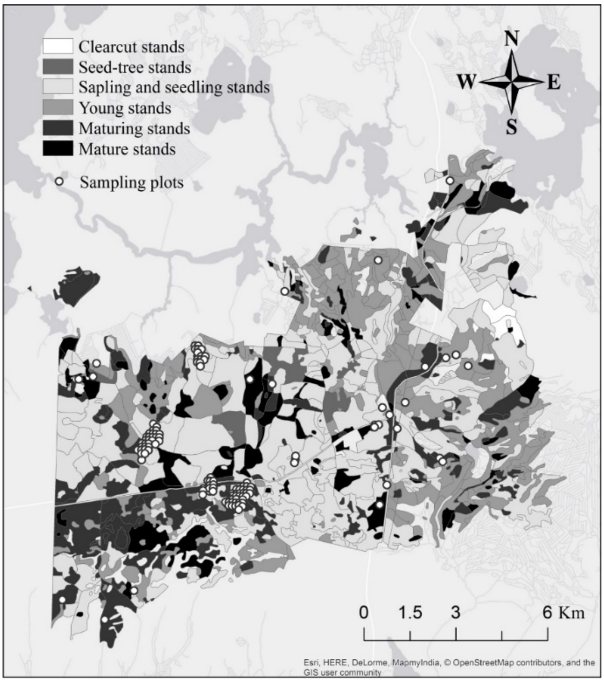

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Figure 2. Locations of Palokangas study area and locations of Adaptive cluster sampling plots and clusters within the study area. (Map by ESRI/HERE©)

4.3.2. Outokumpu area (V)

Outokumpu study area is located in eastern Finland (62°46′N, 28°57′E), west of the Palokangas area (Figure 1). The landscapes are generally flat and highly fragmented. The landscape mosaics are comprised by agricultural fields, lakes, and residential components in addition to forests. The forested areas are mainly Scot pine dominated intensively managed commercial forests, targeting for fiber and timber production. Similar to the Ilomantsi area, the main site types comprise poor and dry heath (*Calluna* type), quite poor and dryish heath (*Vaccinium* type) (Cajander 1926). However, medium fertile fresh heath (*Myrtillus* type) is more predominant in Outokumpu than in the Palokangas area. In general, the forest stands in Outokumpu are more fertile than in the Ilomantsi area. A typical size of a forest stand varies between one and three ha. Regarding the most recent pine sawfly outbreaks in these regions, the forests in the Outokumpu study area have a shorter disturbance history than in the Ilomantsi district. The most recent gradation phase of the European pine sawfly initiated in 2008 within an area of circa 50,000 ha. The sawfly population obtained the peak densities in 2011 and started to collapse into postgradation phase since then.

4.3.3. Abisko area (V)

The Abisko study area is located in Northernmost Sweden, near Norwegian border (68.35°N, 18.82°E, Figure 1). These sub-alpine forest landscapes are featured by mountain birch forests, mires, and heath vegetation with high abundance of dwarf shrubs, grasses, and lichens (Wielgolaski 2001). The Abisko region has a history with outbreaks by both autumnal moth and winter moth (Bylund 1995; Tenow 1996). The unmanaged mountain birch stands are characteristically infested by these species in a time interval of 9−10 years. Two most recent moth outbreaks occurred in 2004 and 2012−2013 (Heliasz et al. 2011; Olsson et al. 2016b). The subarctic region, including Abisko area has been subjected to increasing temperatures in the last decades causing, e.g., disappearing of permafrost and changes in the vegetation communities (Callaghan et al. 2010; Johansson et al. 2006). Elevated temperatures during this century have led to mean annual temperatures above 0 °C in the area (Callaghan et al. 2010) Warming climate, particularly less frequent extreme winter temperatures support the overwintering egg survival (Tenow 1972; Callaghan et al. 2010). The magnitude of climate change driven impacts on the population dynamics of these moth species and further their impact on the mountain birch ecosystems are still unknown (Jepsen et al. 2008; Heliasz et al. 2011).

4.3.4. The Linville River Gorge area (III, IV)

Target areas of the sub-studies III and IV are located in the Lower Linville River area, in the Grandfather Ranger District (35˚56’N, 81˚55‘W) of the Pisgah National Forest, Southern Appalachians, NC, USA (Figure 3). In the sub-study III, the study area comprised the Lower Linville River Watershed, with the spatial extent of approximately 60 km^2. For the sub-study IV, the study area was delineated by available remote sensing data sets (section 4.4.). The area of 40 km^2 is located in the northern part of the Lover Linville River area and much of it (in the center) overlaps with the study area of the sub-study III.

The Linville Gorge wilderness comprises most of these two study areas. The great majority of the wilderness area have been left unlogged and the wilderness is included to the greatest old-growth forests within the region. The area has suffered from frequent forest fires

(Newell and Peet 1998; Wimberly and Reilly 2007). Topography in the area is very complex and prominent cliff-like bluffs are dividing upper and lower slopes (Wimberly and Reilly 2007). The elevation of terrain ranges from 350 m to 1300 m, from the southern part and the river basin to the upper ridges in the north. Three major ecological zones comprise the area: Acidic Cove, Xeric Pine-Oak Heath and Oak Heath, and Mesic Oak-Hickory (Simon et al. 2005). The region's climate is humid and temperate. Characteristics of the area provide a wide range of habitats that are suitable for over 400 vascular plant species and a vast diversity of tree species (Schafale and Weakley 1990; Simon et al. 2005). Both of the susceptible hemlock species, eastern and Carolina hemlocks are abundant in the area (Jetton et al. 2008). Hemlock woolly adelgid was observed in the area for the first time at the early beginning of this century (Koch et al. 2006). The species have caused substantial hemlock mortality in the region.

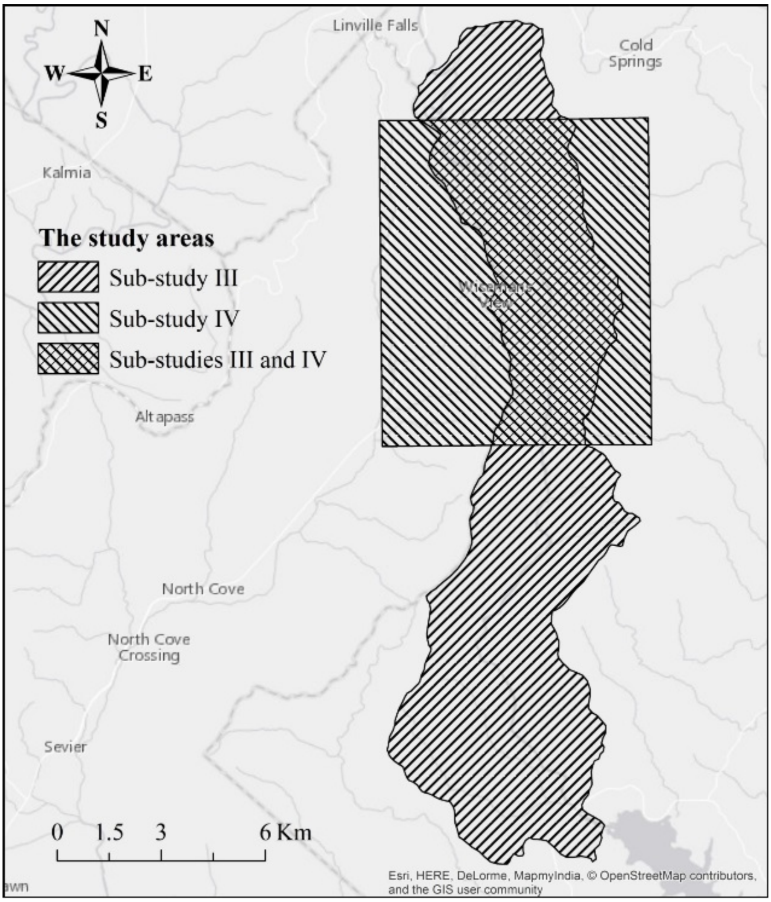

Figure 3. Locations of the two study areas, and the overlapping area in the lower Linville River region, North Carolina, USA. (Map by ESRI/HERE©)

4.3.5. Introduced and native ranges of the hemlock woolly adelgid (VI)

The in ENM modeling task (sub-study VI), areas for background evaluation extent and model projections have to be delineated (Figures 4 and 5). Background evaluation extent describes the area, within the niche model is calibrated while the projection areas comprise the extent to with the calibrated models are projected under contemporary or future climatic conditions. Normally, ENMs for invasive species are calibrated within the native range and then projected into the novel environments. However, in case of limited number of species occurrence observations within the species' native distribution may fail to cover the extent of suitable habitats and the developed models may lack transferability to new ranges or spatial scales (Menke et al. 2009; Peterson et al. 2011). Further, ENMs calibrated in highly differing areas with different environmental gradients are prone to errors when projected elsewhere (Menke et al. 2009). Errors can be even more pronounced if models of alien invasive species altering their niche requirements are projected under future climate scenarios (Urban et al. 2007). Due to the inadequate, sparse, and clustered pattern of available HWA observations in the continental East Asia, the models were calibrated within the introduced range in the eastern North America, were plenty of information in regard to the species exist. The HWA observations, described in the section 4.5., were utilized in the delineation of the background evaluation extent. It is not yet known if the HWA is yet in equilibrium and have invaded its whole range in the eastern North America. For that reason, we delineated the background evaluation extent with a narrow 20 km buffer from a convex hull polygon of the species occurrence observations (Figure 5). The calibrated models were projected to the eastern North America and reverse-casted to the native ranges of the species in East Asia and western North America. The projection areas in the both eastern and western North America were buffering 800 km and 2000 km in East Asia around the available presence points.

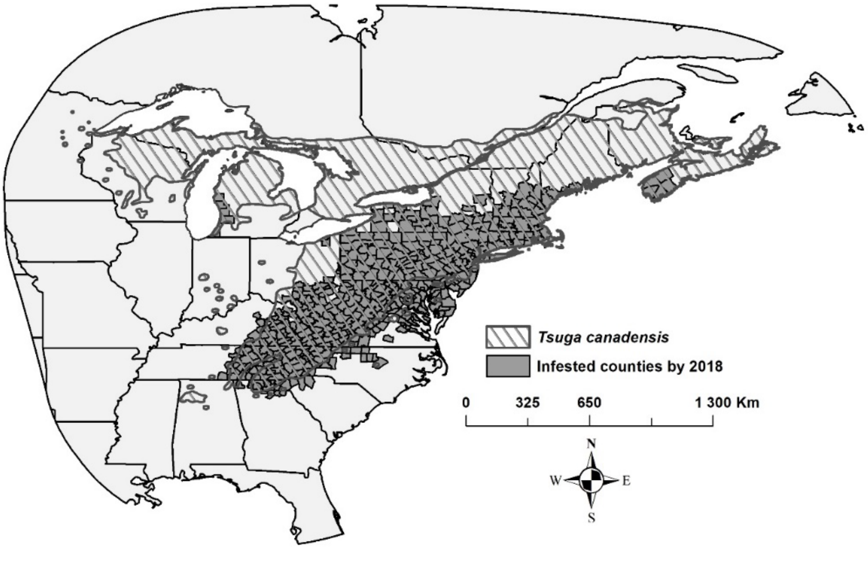

Figure 4. Counties with at least one HWA observation by 2018 and native distribution of eastern hemlock (Little 1971) within the eastern North America.

4.4. Remote sensing data sets

4.4.1. LiDAR data sets (I, II, IV)

The high pulse density Airborne-scanning LiDAR data set used in the sub-studies I and II was acquired in October of 2008 with a Leica ALS50-II SN058 laser scanner (Leica Geosystem AG, Heerbrugg, Switzerland). The obtained pulse density was circa 20 pulses per m^2 and footprint size was 0.11 m. The LiDAR data was classified into ground and non-ground returns according to the standard TerraScan methodology described by Axelsson (2000). Further, a digital elevation model (DEM) was generated from the classified ground returns. Laser heights above the ground, i.e., normalized heights or canopy heights, were computed by subtracting the obtained ground elevation from the corresponding laser measurements.

Airborne-scanning LiDAR for the sub-study IV was with a Leica Geo-Systems Aeroscan system in 2003 during the North Carolina Floodplain Mapping Program (phase II). The pulse density of less than one per m^2 was obtained. A LiDAR point cloud for an area of 40 km^2 was obtained from the USGS Earth Explorer (USGS 2012).

4.4.2. Aerial Photography (III, IV)

Aerial images used in the sub-studies III and IV consisted of 1 m spatial resolution color-infrared (CIR) imagery and a color aerial imagery of red, green, and blue bands (RGB) with 15 cm spatial resolution. Color-infrared imageries were acquired with a Multiple Intergraph Digital Mapping Camera (DMC) (Intergraph Corporation, Huntsville, AL, USA) system at an altitude of approximately 9000 m in the summers of 2010 (III) and 2012 (IV) under leaf-on conditions. Images were captured simultaneously from four-pixel multispectral (MS) cameras with 30 mm lenses to produce red, green, blue, and NIR bands. The data sets were acquired by the National Agricultural Inventory Program (NAIP).

Color aerial imagery of RGB had a very high spatial resolution of 15 cm. Data for ranges of red, green, and blue were acquired by the Sanborn Map Company Inc. (Colorado Springs, CO, USA) with a large-format Zeiss (Carl Zeiss AG, Oberkochen, Germany) / Intergraph DMC, at a flying altitude of about 1,500 m. The data acquisition was done in the winter of 2010 with leaf-off conditions.

4.4.3. Satellite images (V)

Two different Terra/MODIS data time-series products were utilized in the sub-study V. These were the MOD09Q1 (ver. 5), that includes surface reflectance in red and NIR bands in 8-day periods. The spatial resolution of the data is 250 m (LPDAAC 2012a). The second data set was the MOD09A1 (ver. 5). This data set includes surface reflectance in 8-day periods with 500 m spatial resolution (LPDAAC 2012b). Further, 250 m resolution 16-day vegetation index data (LPDAAC 2012c) was obtained for the second vegetation layer of the Enhanced Vegetation Index (EVI).

4.5. Reference data sets

4.5.1. Palokangas and Outokumpu areas (I, II, V)

The field campaigns were carried out in May and early June of 2009, in the Palokangas area (I, II, IV), and in May of 2010 in the Outokumpu area (V). Timing of the field assessments was chosen the way that they were accomplished before elongation of the season's needles. Accordingly, defoliation status of the trees represented the situation of the fall 2008 and 2009, respectively. The used sampling method in the Palokangas area was Adaptive cluster sampling (ACS; Thompson 1990), discussed in more detail in Talvitie et al. (2011). The method has an advantage for sporadic and aggregated phenomena, focusing on areas with the inventoried characteristics, i.e., defoliation by pine sawflies. In Outokumpu, a restricted ACS was used (Brown and Manly 1998). In this method, the total number of sampling plots is assigned a prior to the field campaign. Both of these methods consist of initial sample of plots and additional sampling plots, forming clusters, are established when the sampling criterion is met, i.e., plot level mean defoliation level of 20% or more. This is considered as a level of defoliation that already cause substantial decrease in radial growth of infested trees (Lyytikäinen-Saarenmaa et al. 2006).

A total of 55 permanent sampling plots and 125 additional plots were established and inventoried in Palokangas (a total sample of 180 plots). The corresponding numbers in Outokumpu were 39 and 91, yielding 130 sampling plots. The Trimble Pro XH (Trimble Navigation Ltd., Sunnyvale, CA, USA) was used to locate centers of the plots. All the trees were located from the plot center by distance and azimuth to the tree. After the establishment, various tree- and stand-wise characteristics were assessed on the plots (Talvitie et al. 2011). The visual needle loss assessment was done for each tree. The defoliation intensity of a single tree was visually assessed from different directions, according to method by Eichhorn (1998). Intervals of 10% were used to classify the trees into needle loss classes.

In addition, defoliation assessment over a larger area was performed in June 2010 (V). The assessment was done stand-wise at course level. Stand-wise defoliation level was visually assigned into two classes with the threshold of 20% of defoliation. The data consists of 87 Scots pine stands in vicinity of Palokangas (65 healthy and 22 defoliated) and 43 in Outokumpu (8 healthy, 35 damaged).

4.5.2. Abisko (V)

The field survey was performed during the last week of June of 2013. The sampling scheme was designed to represent the used MODIS satellite data. The size of the sample units was corresponding to the nominal extent of one pixel (250 m x 250 m). The sampling units were located with a Pocket LOOX N520 PDA (Fujitsu Siemens Computers, Darmstadt, Germany). The units were chosen subjectively to cover a large area and ensure even spatial distribution. The defoliation level was assessed visually for the sampling units and classified into two classes using a threshold value of 50% of average defoliation. Defoliation assessment was assumed generally accurate. Most of the birch sites were either heavily defoliated or nearly healthy. Eighty 250 m x 250 m sampling units were assessed, yielding 48 damaged and 32 healthy units.

4.5.3. Linville river gorge area (III, IV)

Due to a very complex topography, the study areas are mostly inaccessible. Consequently, the reference data was created utilizing remote sensing in both of the sub-studies (III, IV; Figure 4). For the sub-study III, forested areas within the lower Linville River watershed areas were analyzed (about 57 km^2). All the visible dead trees within the watershed were identified from the CIR imagery using the very high spatial resolution RGB imagery as a reference when needed. All together 9,881 dead trees were identified and located. The vast majority of the dead trees were assumed hemlocks as HWA was the only major damage agents present at the time of data acquisition. Generally, the detected dead trees were located in the upper canopy cover layers due to visibility. Potential gap size of 1977 individual dead trees was digitized, corresponding with 20% of all the detected dead trees. The areas within the surrounding dominating trees were estimated rather than the widths of the tree crowns. An area distribution of the canopy surfaces with bins of five m^2 was created and generalized for all the dead trees to assess their occupied surface area.

Testing and training data sets for the sub-study IV were also created by visual assessment of the CIR and RGB imageries. Corresponding pixels of the 3 x 3-image mosaic were chosen for the training and testing sets. A 200 m × 200 m systematic point network was for testing the accuracy of the created forest mask. Totaling of 1,080 pixels (3 m x 3 m) were classified into the forest or non-forest pixels (792 forest and 288, respectively). Separate data sets for train and evaluate the classification of forest cover were created. A sample of 7,925 pixels was subjectively chosen for the data sets (5,701 for training and 2,224 for testing). These pixels could be classified correctly with low uncertainty into conifers, hardwood species, and dead trees. Additional canopy cover classes would have increased the level of uncertainty considerably.

4.5.4. Introduced and native ranges of the hemlock woolly adelgid (VI)

A reasonably high spatial resolution of 1 km^2 was used in the ENM task to include other environmental factors, in addition to the climatic features. Consequently, high spatial accuracy was also a requirement for the species occurrence observations. Hemlock woolly adelgid occurrence observation records with at least three decimals in the geocoordinates were gathered from different sources. Some of the records were downloaded from the open data sources of Global Biodiversity Information Facility (GBIF) and iNaturalist. A small number of presence points were also georeferenced from HWA maps available online. However, the vast majority of the data was received from scientists and forest managers in North America. Totaling 4.219 HWA occurrence observation with high spatial accuracy and unique location were gathered form the eastern North America (Figure 5). With this information county-infestation map was also updated to the situation of 2018 (Figure 4). Occurrence observations on the Pacific Northwest and East Asia were obtained from GBIF, iNaturalist, and scientific publications. These observations were not utilized in the modeling efforts, but they were used in evaluation and as reference within native ranges (Figure 12B, C).

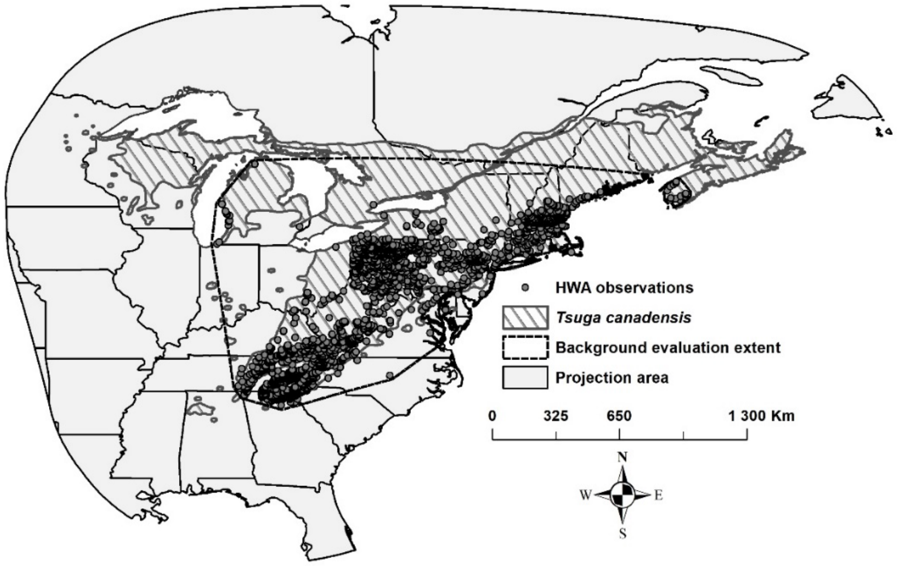

Figure 5. Hemlock wooly adelgid occurrence observation, MaxEnt background evaluation extent, and distribution of the eastern hemlock (little 1971) within the MaxEnt projection area.

5. METHODOLOGICAL OVERVIEW

5.1. Tree- and plot-wise Scots pine defoliation (I, II)

5.1.1. Tree-level classification of defoliation (I)

A digital surface model (DSM) is a 3D representation of the ground surface in non-vegetated terrain or aboveground features, including vegetation and buildings. In forestry, 3D representations of vegetation are often referred as CHMs. Individual tree detection (ITD) was achieved using watershed segmentation of a smoothened 0.5 m grid CHM (Hyyppä et al. 1999, Yu et al. 2011). The resulting segments were verified with the trees on the plots and these data were combined. Segments including more than a single tree crown were excluded due to varying defoliation levels and overlapping canopy cover layers. Totaling of 701 watershed segments were considered as single Scots pine crowns. The majority of the trees (n = 603) were mild to moderately defoliated (10%–30%). The ITD segment data was classified further into five classification arrangements for testing needle loss classification accuracy. The number of defoliation classes ranged from two to four in the classification schemes. Classification scheme DEF1 (two classes, threshold = 20% of defoliation) was assumed as the starting point and used as foundation for all the computations. The threshold values for the other schemes were 30% (DEF2), 30% and 60% (DEF3), 20% and 50% (DEF4), and 20%, 30%, and 40% (DEF5) of defoliation.

LiDAR returns were extracted for each tree segment. Hits below 2 m were considered as ground or forest floor vegetation. Canopy heights were used to derive LiDAR features for each tree. Only the *first* and *only* returns were used in the analysis due to the highest reflections and because they are less affected by intra-crown transmission losses (Korpela et al. 2010). The physics involved in the interactions between other LiDAR returns and canopy is more complicated. Furthermore, more uncertainties are related to later returns. Twenty-six laser point metrics were calculated from the canopy returns: maximum height (*Hmax*), mean height (*Hmean*), and standard deviation of heights (*Hstd*), penetration (*pene*), ten height percentiles (*h*10-*h*90), proportions of canopy returns at relative heights (*p*10-*p*90), and the mean return intensity (*Int*). The intensity was not calibrated.

5.1.2. Plot-level classification of defoliation (II)

The sampling plots were classified into classes of healthy and defoliated using a threshold of 20% of mean defoliation. A novel approach was used in predicting defoliation level of forest stands. The prediction was done with airborne scanning LiDAR data, plots combining ITD and stand-based techniques at plot level. LiDAR features were not calculated for the entire sampling plots, but only for the particular area, within the returns are reflected from the upper forest canopy (50% and above). Other factors may hinder accurate prediction of defoliation, such as overlapping branches and understory vegetation. Forest canopy cover is known to influence LiDAR penetration, which should be taken into account in area-based projections of defoliation. The area of forest canopy cover was delineated with an ITD procedure, similar to that of in the sub-study I, i.e., using watershed segmentation from a smoothed CHM. To minimize the influence of these factors, only LiDAR returns reflected below the mean plot height were excluded, corresponding to 50% of the *Hmax*. This stratification by mid-canopy was unique in relation to use of LiDAR in forest monitoring. The resulting canopy cover segments consisted returns from the crowns in the upper canopy cover layers (Figure 6). After the segmentation, LiDAR point clouds were extracted separately for each canopy cover segment. Similar to the sub-study I, only *first* and *only* returns were used. In addition to *Hmax*, *Hmean*, and *Hstd*, *p*60-*p*90 were computed. The LiDAR metrics were linked to the field inventory data by using the plot center coordinates located in the field.

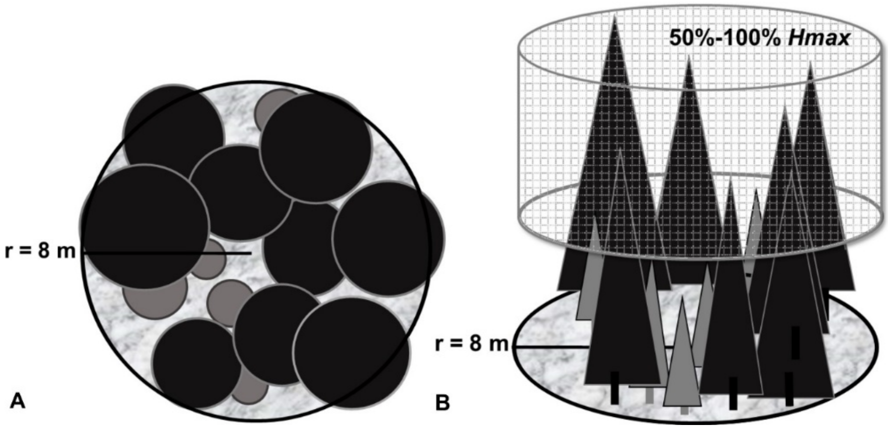

Figure 6. Illustration of the LiDAR data lineation and canopy cover surface creation for the analysis of plot-wise defoliation A) from above and B) from the side. LiDAR returns above the top 50 % of the area based maximum height (*Hmax*) of the black trees are included into the analysis. Gray trees represent the suppressed trees that were excluded from the analysis.

5.1.3. Effect of pulse density (I, II)

The high pulse density of the LiDAR data set used in the sub-studies I and II (~20 pulses/m^2) facilitated simulation of influence of varying pulse densities on the classification accuracy. In both of the sub-studies, the original segments were used, since the pulse density may not influence the ITD performance (Kaartinen et al. 2012). The original LiDAR data was thinned with simple random sampling procedure at 10% intervals, yielding 10 varying pulse densities from two to 20 pulses/m^2. Densities of two pulses/m^2 was assumed as minimum for an ITD method (e.g., Kaartinen et al. 2012). For the sub-study II, additional data sets for pulse densities of 1 and 0.5 pulses/m^2 were created. Laser metrics and classifications were conducted with these thinned data. The same metrics were used for the thinned data sets. The thinning, metric calculation, and classifications were repeated 10 times for each data.

5.1.4. Random forest (I, II)

In a previous study to the sub-studies I and II, Kantola et al. (2010) tested three different methods for tree-level classification of defoliation: random forest, logistic regression, and most similar neighbor search. All the methods were proven quite suitable for the task. However, best accuracies were obtained with random forest and it was selected for the sub-studies II and III to classify tree- and plot-level Scot pine defoliation. Random forest is a nearest neighbor approach by Breiman (2001). The method has shown to be robust and flexible in prediction of forest characteristics (Hudak et al. 2008; Latifi et al. 2010). In addition to classification, random forest can be used for feature selection (Cutler et al. 2007). The method has been increasingly used in various airborne scanning LiDAR applications to predict forest characteristics (e.g., Falkowski et al. 2009, Korpela et al. 2010; Yu et al. 2011), including defoliation (Kantola et al. 2010, 2011).

In Random Forest, several regression or classification trees are generated for training and testing (see Crookston and Finley 2012; Falkowski et al. 2010 for description). Several classification or regression trees (CART) are created and the prediction is made by averaging the results of each tree. The data is split at all nodes, until the data at leaf nodes contain a number of samples that is less than a preselected value, or the sum of the squares of the distances to the mean of the respective group fall below the threshold. Nearness is defined based upon the probability of observations to end up to the same terminal node during the classification. The obtained output is the percent increment of misclassification rate compared to the out-of-bag rate. Multiple regression or classification trees are computed recreating sets of two thirds and one third for training and testing, respectively, for each tree.

Although random forest is considered robust, the set of variables was kept low in order to minimize over-fitting, which may occur, particularly with noisy data, as in case of visual assessment of tree defoliation. In the sub-studies, tree- (I) and plot- (II) specific LiDAR metrics were used to predict defoliation intensity. Two thousand CART trees were fitted for each random forest run. Further, to reduce impact of randomness, the models were fitted 10 times for the sub-study I and 50 times for the sub-study II. The results were the mean values of these repetitions. The results were evaluated with classification accuracies and kappa-values (Cohen 1960). The R statistical computing environment (2018) and yaImpute library (Crookston and Finley 2012) were applied in the random forest searches. In forestry applications, stable results have been obtained assigning the number of neighbors (k) between two and seven. The smallest bias is obtained with k=1. Parameter k values of three (I) and one (II) were used.

5.2. Landscape-level hemlock mortality (III, IV)

5.2.1. Incorporating topographic information to the dead tree observations (III)

Topographic features of aspect and slope were derived from the DEM raster in order to investigate topography in relation to the tree mortality. The DEM raster was classified into elevation classes by every 100 m, aspects by cardinal and ordinal compass directions, and slopes by every 10 degrees. The three topographic features were extracted to each dead tree separately and density of dead trees was calculated for each topography class.

Euclidean distances from all of the dead trees to the banks of the Linville River were measured in order to investigate the tree mortality in the riparian zone. Euclidean distance was considered to describe the functional grain of HWA regarding its perception of distance within the complex landscape better than the ground distances along the terrain. A sample of 99 dead trees (0.1%) was taken in order to contrast the two measures of distance. The distances were observed to differ from 9.1 m to 1,304.3 m. Percentage of the differences varied between 0.02% and 51.9%. However, the mean difference between the distances was only 10.1%.

5.2.2. Spatial pattern analysis (III)

An overall spatial pattern of the hemlock mortality was investigated employing Ripley's K-function (Ripley 1976, 1977, 1981). This second order statistic is based upon the distribution of pairs of points and it tests the deviation from complete spatial randomness (CSR). Observed point patterns can be compared at different spatial scales with point patterns generated by known processes, such as a homogenous Poisson process (Bailey and Gatrell 1995). Ripley's K-function detects pattern over a range of spatial scales, which facilitates detection of mixed patterns as well (Wiegand and Moloney 2004). However, the method is regarded to detect only large-scale of clustering (Dale 1999). Description of the method can be read in detail from e.g., Goreaud and Pélissier (2003) or Wiegand and Moloney (2004). Ripley's K-function has been utilized before in forest research (e.g., Zenner and Hibbs 2000; Youngblood et al. 2004; Wolf 2005), including tree mortality (Aakala et al. 2006, 2012), and monitoring of forest pests (Kelly and Meentemeyer 2002; Liu et al. 2007; Lynch and Moorcroft 2008).

A grid of one km^2 was created and each grid cell represented a sub-area for the analysis (section 6.2.; Figure 7). The sub-areas bordering the watershed were clipped to the perimeter. The analysis was conducted to the sub-areas having at least 10 dead trees. The linearized square root transformation of the K-function, the L-function, was employed in the analysis. The L-function is easier to interpret, and the variance is stabilized. Under the CSR, the L-function equivalents zero (Goreaud and Pélissier 2003). Statistical significance was evaluated with Monte Carlo simulation (95% confidence level) (Haase 1995; Wiegand and Moloney 2004). Spatial scales from 1 m to 250 m with 1 m intervals were analyzed. The R statistical computing environment (The R Project 2018), Spatstat library (Baddeley and Turner 2005), and Translation correction (Ohser 1983) were used in the implementation.

5.2.3. Mapping hemlock mortality within forest landscapes (IV)

A forest mask was created first to exclude non-forest areas and deep shadows from the study extent. The forest mast was created with decision tree classification. Without this step, surface of dead trees would be a great overestimation resulting from the similar spectral reflectance associated with certain non-forested objects, including bare ground and roadways. Furthermore, number of cover classes were kept in minimum to improve the classification accuracy. In the second phase, the remaining forest canopy cover was classified with Support Vector Machine (SVM) classification. Accuracies of the both phases were evaluated with classification accuracies and Cohen's kappa-values (Cohen 1960). The ArcGIS (), FUSION (FUSION/LDV, USDA Forest Service, Seattle, WA, USA; McGaughey 2009), and ENVI (EXELISVIS Inc., Boulder, CO, USA) were employed in the analysis.

5.2.4. Forest mask creation (IV)

A CHM and NDVI layer calculated form the CIR imagery were used in the forest mask creation. The CHM was derived from the LiDAR data set. The highest returns of each grid cell were assigned as local maxima. The ground elevation was computed with a ground filter algorithm (see Kraus and Pfeifer 1998). Laser heights above the ground were computed by subtracting ground level from the equivalent local maxima. The CHM with a spatial resolution of 3 m was smoothened with a 3 × 3 pixel median filter.

Decision-tree classification is a non-parametric method and regarded as a practical approach for land-cover classification (Tooke et al. 2009). In the procedure, a data set is repetitively partitioned into smaller subdivisions based upon tests defined at each node (Friedl and Brodley 1997). The method has no required assumptions on the distribution of a data, and may provide improved accuracies compared to, e.g., maximum likelihood or neural networks (Mahesh and Mather 2003, Tooke et al. 2009). The method can deal with missing values and facilitates use of numerical and categorical inputs (Friedl and Brodley 1997; Mahesh and Mather 2003). The method is flexible and enables processing of non-linear relationships (Mahesh and Mather 2003). Suitable threshold values were search through testing. CHM heights greater than 1.2 m were considered objects above the ground, including vegetation. This decision was acceptable since the goal was to simply separate vegetation from the ground. A small NDVI threshold value of 0.05 was determined to exclude deep shadows, water, and other non-vegetation elements, but not the dead trees, also having a relatively low NDVI values. The resulting classification layer was extracted and filtered to smoothen the forest mask, using a neighborhood-majority-filter.

5.2.5. Forest cover classification (IV)

The extracted area of the forest mask was utilized in the second phase, i.e., classification of the forest cover. The aim of the second phase was to detect dead hemlocks and living conifers, i.e., potential hemlock patches from hardwood species. Support vector machines is a group of supervised non-parametric learning techniques (Cortes and Vapnik 1995). These classification techniques are not as well-known as many other classification methods. The performance of SVM can outcompete, however, those of other classification procedures (Gualtieri and Cromp 1999; Mountrakis et al. 2011). The SVMs aim to define the location of optimal decision boundaries that separate classes and results in a hyperplane (Vapnik 1995). The nearest observations to the hyperplane are determining the margin, and thus called the support vectors (Pal and Mather 2005). Kernel functions enable mapping non-linear data into a higher dimensional space and a linear surface that separates two classes is searched for (Gualtieri and Cromp 1999). SVMs are regarded robust to noise and high-dimensional data. Further, it is seen suitable for remote sensing procedures with restricted training data

(Mantero et al. 2005; Mountrakis et al. 2011). Support vector machines has been successfully utilized in ecological applications of remote sensing (e.g., Gualtieri and Cromp 1999; Huang et al. 2008; Lardeux et al. 2009), including tree species identification (Heikkinen et al. 2010). Radial basis function (RBF) kernels are frequently utilized in various remote sensing-based SVM applications (Kavzoglu and Colkesen 2009). The RBF kernel was employed in the classification. The used layers are the spectral bands of red, green, NIR, and NDVI. The LiDAR data was not utilized in this step since it was too outdated for this task.

5.3. Insect-induced defoliation in Fennoscandia (V)

5.3.1. Overall workflow and vegetation index data

An overall workflow for the sub-study V consisted of four steps. These include (1) computation of vegetation indices from the extracted reflectances of red and near infrared (NIR) of the MOD09Q1 data, (2) creation and processing of time-series from the vegetation indices to search for a metric representing the forests health condition during a season, (3) calculation of mean and standard deviation of healthy conditions, and (4) classification of MODIS pixels based upon z-scores.

MODIS data with the highest resolution of 250 m only was used due to level of landscape fragmentation in eastern Finland. Despite the popularity, NDVI can reach saturation in areas of high biomass, e.g., forests (Huete et al. 1997). This may limit the usability of the index. Therefore, use of Enhanced Vegetation Index (EVI), 2-band Enhanced Vegetation Index (EVI2), and the Wide Dynamic Range Vegetation Index (WDRVI) were also tested. These indices also are calculated from the channels of red and NIR. Enhanced Vegetation Index is a two-band version of EVI, which was developed to boost the signal from vegetation in areas of high biomass (Huete et al. 2002; Jiang et al. 2008). Wide Dynamic Range Vegetation Index was developed for high biomass areas as well (Gitelson 2004). This index has been previously used to detect Scots pine defoliation with similar results to NDVI (Eklundh et al. 2009). Initial testing indicated that defoliation by pine sawflies using EVI (LPDAAC 2012c) or WDRVI did not gain high accuracies, and thus only NDVI and EVI2 were studied further.

5.3.2. Creation and processing of time-series

TIMESAT 3.2 was used to create time-series of NDVI and EVI2 with 8-day temporal resolution for the years 2001−2011 (Jönsson and Eklundh 2002, 2004). Seasonality parameters, such as beginning and end of a growing season were extracted. Noise in the data was reduced by fitting smooth functions to the time-series of data. A seasonality parameter of *season max* comprised the season's maximum value of the fitted function and was used to define forest condition of each season. The *season max* was computed from weighted data of the complete growing season. This way the data it is not very sensitive to noise or outliers. The weights were assigned to each data value based upon MODIS data quality. The quality was based upon quality assurance (QA) flags from the data sets of MOD09Q1 and MOD09A1. The QA flags indicate, e.g., disturbance, cloudiness, or low solar zenith angle. Potential outliers were removed and no adaptation to the upper envelopes were performed. All three fitting functions of Savitzky-Golay filtering, asymmetric Gaussian, and double logistic functions were tested. Gaussian and logistic functions result in smooth curves and only few parameters have to be set. Savitzky-Golay fitted function follows data sets more directly and may be better for detecting smaller deviations. However, the fitted function using a higher number of parameters requires more work. Further, this function is not as easy to generalize to other regions as the other two.

5.3.3. Z-scores and decision criteria

Disturbance detection was based upon z-scores. Studies on employing z-scores in remote sensing of forest is scarce. However, the method has been successfully used before in drought monitoring (Peters et al. 2002). The method can be generalized to other areas and is not dependent on absolute thresholds for damage. Z-scores from data with different means, ranges, and standard deviations can be combined. Z-score is s number of standard deviations from the mean value of the data, i.e., *season max*. The mean and standard deviation of the *season max* are estimated for each pixel under reference conditions (i.e., healthy conditions) before z-scores can be computed. The reference conditions are unique for each pixel. High vegetation index values were assumed to correspond to healthy conditions. The reference condition for each pixel was computed accordingly: (1) the number of years with the highest *season max* values that gives the highest detection accuracy was identified, and (2) the mean and standard deviation for *season max* were estimated based on the identified number of years.

The z-score method development was done with the field data from the Outokumpu area. Palokangas field data included a longer time-series of defoliation assessment than the Outokumpu field data. However, the duration of the common pine sawfly outbreak in the Palokangas area extended as far back as the entire MODIS time-series data, until the beginning of this century. In Outokumpu, only the sampling plots located in forest stands covering nearly an entire MODIS pixel were included, resulting in 10 sampling plots. Separate assessments of defoliation were considered as independent observations, i.e., every sampling plot gave three values between 2009 and 2011, resulting in 30 observations. The observations were classified into two classes of damaged and healthy, with the threshold value of 20% of defoliation.

Z-scores were computed for each observation. Receiver Operating Characteristics (ROC) graphs were utilized to define the number of years comprising the reference conditions and to assign z-score thresholds for the disturbance. In the ROC graph, the ratio of damaged pixels correctly assigned as damaged (True Positive Rate, TPR) is plotted against the ratio of healthy pixels assigned as damaged, i.e., false alarm (False Positive Rate, FPR) (Fawcett 2006). The ROC curves were created by calculating TPRs and FPRs for a range of z-score thresholds. The ROC curves were calculated for all the observation, from the lowest to the highest z-score, with percentage increases of 0.1. To define the number of years of the reference conditions, z-scores were computed with varying number of years. It was assumed that the reference conditions should be based on a high number of years to obtain reliable metrics. However, including additional years increases the risk of including years of previous disturbance, affecting detection accuracy. Four years was assumed as the minimum number of years for reliable reference. ROC curves with additional years were created until the accuracy begun to decrease. In case of the European pine sawfly outbreak in Outokumpu, the maximum number of healthy years was seven (2001−2007). The z-score value on the ROC curve closest to point (1, 0), i.e., closest to the perfect classification was chosen as a threshold. This approach is objective and can be used in automated systems. The classification method was developed with EVI2 data and applied to NDVI data in order to compare the performance of the two vegetation indices. After defining the reference conditions and a z-score threshold value, z-scores were computed for each pixel for each season separately. According to the threshold, each observation was classified as damaged or healthy. The method was evaluated in Outokumpu, with a shorter history of defoliation and in Ilomantsi (around Palokangas area), where the infestation had persisted for entire time-series of MODIS data. The evaluation data consisted of the stand level data assessed in June 2010. To test generalization, the same method was also applied to the Abisko study area. Time-series of EVI2 for the years 2001–2013 was created. Instead of using the same threshold z-scores as in Eastern Finland, new ROC graphs were computed. In Abisko, no separate testing data was used.

5.4. Species distribution modeling (VI)

5.4.1. Environmental predictors and future climate change scenarios

Environmental factors predicting habitat suitability for HWA were chosen amongst a large set of 119 environmental features at 1 km spatial resolution. Seventy-nine climatic variables, 16 topographic variables, 12 soil physical properties, and 12 soil suborders were screened for the niche models.

Minimum temperature is the most studied factor affecting HWA survival (McClure and Cheah 1999; Parker et al. 1999; Skinner et al. 2003). It is also regarded as the most limiting factor for HWA range. Cold temperatures from −25°C have been observed to affect HWA survival (Parker et al. 1999; Skinner et al. 2003). Temperature of −35°C was observed as a threshold of HWA survival. Cold tolerance, however, may be affected by geographic location and season (Skinner et al. 2003). Furthermore, long cold periods may influence the tolerance (Skinner et al. 2003). Although an increasing temperature often have positive effects on insect performance, high temperatures may restrict species distribution. Species typically have a range of temperatures supporting their survival (Speight et al. 2008). Hemlock wooly adelgid have been observed to tolerate extreme temperatures over 40°C within the native range in Japan (McClure and Cheah 1999). However, other studies indicate that heat-exposure and high temperatures over 30°C may threat species survival (Mech 2015; Sussky and Elkinton 2015).

There is not much available information in the influence of precipitation or humidity on HWA. Precipitation may have both direct and indirect effects on the species (Speight et al. 2008; Jamieson et al. 2012). Rainfall may affect HWA by host plant distribution and quality (Evans and Gregoire 2007; Speight et al. 2008). An example of direct impacts is insect dehydration and mortality resulting from lack of rain (Jamieson et al. 2012). Elevation influence performance of insect pests (Niemelä et al. 1987; Hodkinson 2005; Kharuk et al. 2007), including HWA and its host species (Trotter and Shields 2009; Narayanaraj et al. 2010; sub-study III). Effects of elevation, however, are mainly indirect. Species may mainly respond to associated changes in temperature, oxygen levels, and air pressure (Peterson et al. 2011). Topography and soil characteristics and are regarded important modifiers of climatic conditions, such as soil water holding capacity or topography related sun exposure, in future climate projections (Ehrlén and Morris 2015). Hemlock woolly adelgid is dependent on hemlocks as host species, the interactions of soil properties and topography with the prevailing climate can be important for identifying environmental conditions suitable for hemlock, and further for HWA. Soil characteristics, including the distribution of soil suborders, have been previously associated with hemlocks and were observed to overlap with global *Tsuga* spp. distributions (Burns and Honkala 1990; Farjon 1990).

5.4.2. MaxEnt niche model calibration and feature selection

MaxEnt algorithm (Phillips et al. 2006) was chosen for model calibration after preliminary trials of several popular algorithms. MaxEnt is regarded as robust and it is well documented (see e.g., Elith et al. 2011). The algorithm has been widely employed in species distribution modeling tasks (Merow et al. 2013), including projections of invasive species within their introduced ranges (Roura-Pascual et al. 2009; Gormley et al. 2011; Barbosa et al. 2012; Zhu et al. 2012; Kumar et al. 2014). MaxEnt supports features of six types of mathematical transformations of the original predictors. Models can be calibrated with several features or produce simpler models with only few features (Merow et al. 2013). While all the features are often chosen, a modified version may be more suitable in many cases (Merow et al. 2013). Simpler models using only hinge features may be more appropriate in case of range-shifting species (Elith et al. 2010).

In order to reduce sample bias and spatial autocorrelation, the HWA occurrence observation data was spatially thinned to 10 km using a spatial filter (Boria et al. 2014). MaxEnt niche models were calibrated with the introduced range HWA occurrence observations using R “dismo” package (Hijmans et al. 2016). About 10.000 pseudoabsence points were created within the background evaluation extent. These points were buffered at 20 km from the presence points. Pseudoabsence-based versions of the True Skill Statistic and Area under the Curve statistic (AUC) for evaluation were calculated using the “PresenceAbsence” package by Freeman and Moisen (2008). In order to reduce model complexity and overfitting, the MaxEnt beta regularization was adjusted to two and only quadratic and hinge features were used (Warren and Seifert 2011; Tracy et al. 2018). MaxEnt models were calibrated to binary presence/absence format using a threshold at maximum True Skill Statistic (Liu et al. 2013).

To create relatively small subsets of environmental factors predicting HWA habitat suitability in the MaxEnt niche models, all the predictors (n=119) described in *section 5.4.1.,* were screened using the random subset feature selection algorithm (RSFSA) by Tracy et al. (2018). In the feature selection method, hundreds of random subsets of the potential environmental predictors of pre-specified sizes are created. Inter-correlated variables were restricted from the same subsets using a correlation filter of $r = |0.7|$ as a maximum correlation (Dormann et al. 2013). These random feature subsets were then ranked in performance by subset wrappers of AUC and/or the corrected Akaike information Criterion (AICc). Performance of the subsets with varying number of variables were compared to select an optimal subset size. The optimal number of variables were that of beyond no significant improvements in AUC, AICc, and overfitting values was observed (Warren and Seifert 2011). Statistical performance between RSFSA-selected and random MaxEnt models was then evaluated. This was done by generating and ranking 3000 models for the selected subset size using held out model training and testing data (Tracy et al. 2018). Instead of one final MaxEnt models, statistically 12 best RSFSA-selected models were chosen, binary calibrated, and combined by frequency consensus forming feature subset ensemble (FSE) models.

5.4.3. MaxEnt projections and future range shifts

The 12 final MaxEnt models were projected over a wider extent in eastern North America (Figure 12A, section 4.3.5.). The FSE models were also reverse-cast projected to the known native ranges of East Asia and western North America (Figures 12B-C). To assess the MaxEnt niche model performance that were generated within the introduced range and projected into the native range, sensitivity statistic was used (Jiménez-Valverde et al. 2011); a sensitivity reverse transferability index (sensitivity native range - sensitivity introduced range; Heikkinen et al. 2012) was calculated. This method does not require use of pseudoabsence data. The existing presence data within most of the native HWA range, in the continental regions of East Asia was not available. This patter would have made use of pseudoabsence data more prone to error.

Future projections for the potential HWA range were only done for the introduced range in the eastern North America, where the species is causing substantial damage. The final FSE models were projected onto four different climate scenarios based on the Hadley Centre's HadGEM2-ES general circulation model with low and high representative concentration pathways for CO_2 emissions (RCP 2.6 and RCP 8.5) for the years 2050 (2050he26 and 2050he85) and 2070 (2070he26 and 2070he85). In addition to future range maps, change detection maps between the contemporary climate and the future climate scenarios were created (Figures 13A-D). The MaxEnt FSE projection under historical climate was subtracted from each of the four future MaxEnt FSE projections. The resulting maps demonstrate the change in the number of models projecting suitable habitat for HWA in any given location within the projection area. Furthermore, each of the 12 MaxEnt models under contemporary climate was paired with the future climate models and the north/south and east/west shifts in centroids were computed. Mean elevations within historical and future climate models were also compared.

6. RESULTS

6.1. Classification of pine defoliation by the common pine sawfly (I, II)

6.*1.1. Tree-level classification (I)*

Random forest classification was ran first for the scheme of DEF1 (two classes, threshold = 20% of defoliation) with all the 26 laser metrics to derive the scaled importance of the metrics. Mean return intensity was observed to be the most powerful predictor. However, because this metrics was not calibrated it was excluded from the following analysis. It is anticipated that dominant Scots pines are often more severely defoliated by the common pine sawfly than suppressed trees (section 4.2.). To classify defoliation level instead of tree size, *Hmax* and *Hmean* were also eliminated. Based upon the preliminary runs, the three most important features were *h*10, *Hstd*, and *p*70. These three metrics were used in all further classifications. The highest overall accuracies for defoliation classification were obtained with the schemes DEF2 (86.5%, SD ±6.1%) and DEF3 (85.4%, SD ±4.6%). As assumed, DEF5 with a highest number of defoliation classes (four) gave the lowest overall accuracy (71.0%, SD ±10.1%). In general, classification of healthier trees was more successful. Nevertheless, most of the trees were classified at least to an adjacent class. In case of the thinned LiDAR data, classifications were done only for the classification scheme DEF1. Random forest classification performance did not seem to be sensitive to the pulse density.

6.1.2. *Plot-level classification (II)*

Approximately a half of the sampling plots (n = 106) were healthy and the other half defoliated. Inspection of the LiDAR *Hmean* and *Hmax* showed some differences between these groups. The preliminary predictors were chosen based on available research (e.g., Solberg et al. 2006; Kantola et al. 2010, 2011; Solberg 2010), correlation coefficients, and preliminary modeling results (i.e., based upon biological plausibility and statistical significance). On average, trees on the defoliated plots were taller than those of on healthy ones. In order to minimize the influence of stand structure, potential explanatory features having a high correlation with tree size were excluded, i.e., *Hmean* and *Hmax*. Percentages of the LiDAR returns from the upper canopy (*p*60, *p*70, *p*80, and *p*90) are relative features and cannot be directly associated with the tree size. The same metrics were also identified as eligible classifiers for pine defoliation. The mean values varied significantly in Student's t-test between the two defoliation classes (p = 0.00); on healthy plots, a higher number of LiDAR returns was reflected from the upper canopy.

Based on the preliminary random forest runs, the most important classifiers were proportions of the upper-canopy LiDAR returns of *p*80 and *p*90. These LiDAR metrics were used in the further analysis. Defoliated plots were classified with an accuracy of 84.3% (kappa = 0.68). The same metrics were used in examining influence of LiDAR pulse density in assessment of pot-level defoliation. The classification result was not very sensitive to the pulse density, ranging seemingly randomly from 77.1% to 89.3%.

6.2. Landscape-level hemlock mortality (III, IV)

6.2.1. *Effect of topography on hemlock mortality (III)*

Totaling of 9,881 dead trees were identified within the watershed (Figure 7A). The vast majority of the trees was found in the northern part of the area, as well as reasonable nearby the river. The digitized canopy surface areas for potential gaps of the 1977 dead trees ranged from three m^2 to 88 m^2 (mean of 36 m^2), with a positively skewed frequency distribution. When the gap size distribution was generalized to the whole dead tree population, a canopy surface area of 7.2 ha was estimated, corresponding 0.1% of the investigated areas within the watershed.

There is a drastic North-South directional difference (~1000 m) in elevation within the area. The slope angles varied from flat (0 degrees) to very steep slopes of 80 degrees, facing all the directions. Distributions of topographic features of the dead trees differed from those of the whole study area (Figure 8). Dead trees were the most abundant in the high elevations of 900 - 1000 m and 1000.1 - 1100 m, as well as on slopes to north and northwest. Not distinct pattern for slope could be detected, however, a mild trend of increasing density along with steepening slope. Noteworthy is that much of the terrain in the area is on mild to moderate slope. A vast majority of the tree mortality occurred close to the Linville River; with distances ranging from zero to 2,760 m (Figure 9). Twenty five percent of the cumulative distribution of dead trees were located less than 60 m from the riverbanks (50% and 75% of were met at 94 m and 577 m, respectively).

Spatial pattern of the dead trees was analyzed for 54 sub-areas (Figure 7B). The spatial pattern was clustered at all spatial scales from one to 250 m in 36 sub-areas and random at all the scales in three (Figure 7C). Mixed spatial pattern, varying between random and clustered, was detected in 15 sub-areas. No dispersed (even) pattern was observed. Clustered pattern of dead trees was mainly observed on higher elevations and in the proximity of the stream. The number of dead trees within the one km^2 sub-areas ranged from zero to 1192 (Figure 7D).

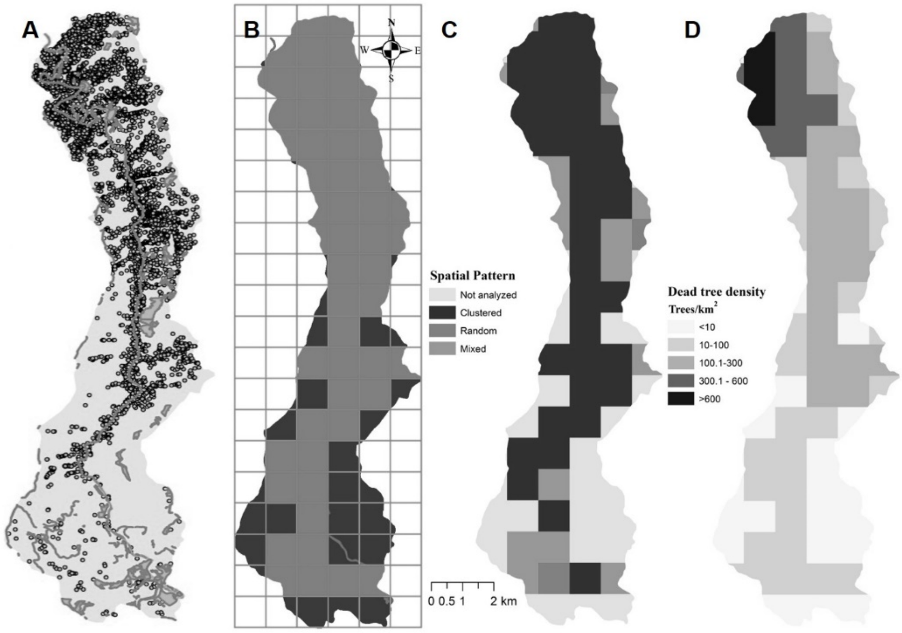

Figure 7. A) Identified dead trees within the Lower Linville River watershed, B) Subdivisions for the Ripley’s K analysis, C) Spatial pattern within the subdivisions, and D) the related dead tree density.

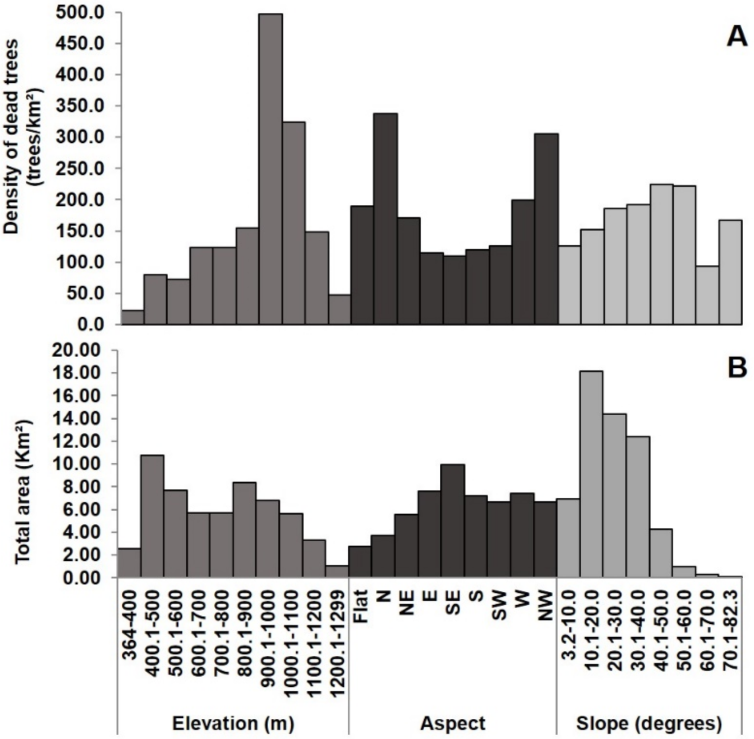

Figure 8. Frequency distributions related to topographic features of elevation, aspect, and slope in relation to A) density of dead trees within the study area, and B) for the whole study area.

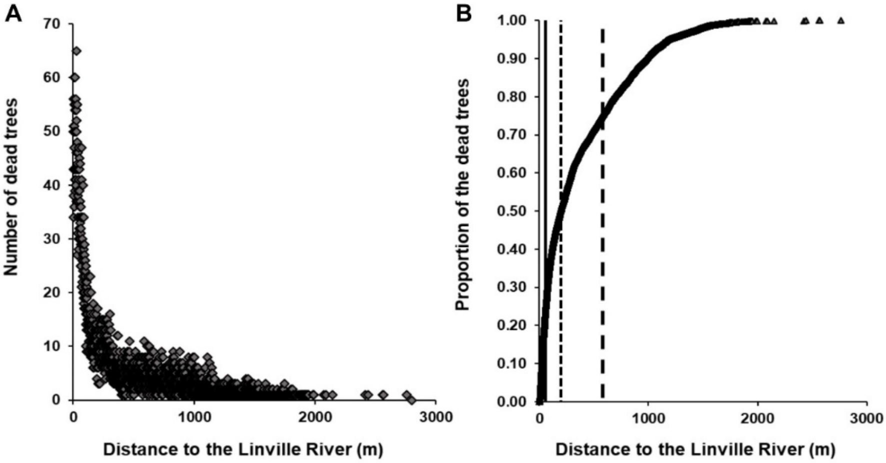

Figure 9. A) Distribution of distances of the detected dead trees in the Lover Linville River Watershed, and B) A cumulative distribution of the distances of the dead trees. Black solid and dashed lines represent threshold distances of 25% (60 m), 50% (194 m), and 75% (577 m) of the cumulative distribution.

6.2.2. Mapping hemlock mortality within forest landscapes (IV)

The forested area was extracted within the extent of the LiDAR point cloud. The obtained classification accuracy was 93.5% (κ = 0.84). The resulting forest canopy cover, totaling 30.2 km^2, represented 76.9% of the classified area. The forest canopy cover was classified into dead trees, conifers, and hardwood with an overall classification accuracy of 98.1% (κ = 0.96).

Coverage by broadleaved species was the greatest of the classes, over 55% of the total classified area. Conifers occupied 42.6%, and dead trees 2.1% of the area. Dead trees represented over 0.6 km^2 of the forest canopy cover and conifers covered 12.9 km^2. The resulting classification image linked with a DTM showed that coniferous species were mostly located in drainages and on northern and western slopes (Fig. 10). Dead trees were mostly aggregated either in the proximity of the river, along drainages, or at higher elevations.

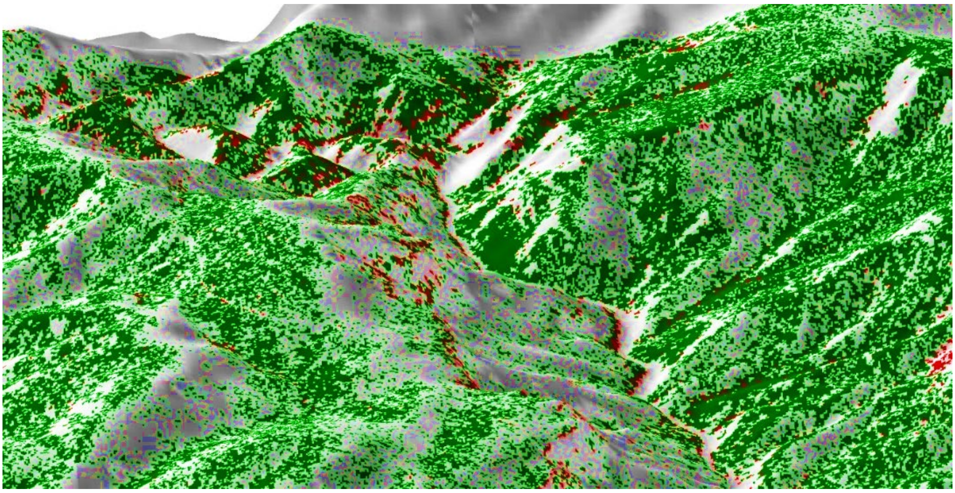

Figure 10. Classification image combined with digital elevation model at the Linville River Gorge. Classified conifer patches show as green and dead trees as red.

6.3. Insect-induced defoliation in Fennoscandia (V)

Five years was chosen as the number of years for the reference conditions. The ROC curve for EVI2 data resulted in an optimal z-score threshold of –2.9. With this z-score threshold, 50% of the damaged observations were correctly detected with no misclassification of healthy observations. The method was also tested with levels of 15% and 20% of defoliation. The results indicated that the detection accuracy was not highly affected by the used defoliation threshold. The ROC curves of the NDVI data showed a zigzag pattern. This inhibited selection of the number of years for reference conditions, as well as optimal z-score threshold. Because use of NDVI also resulted in extensive misclassification of healthy plots with low TPR rate, EVI2 was assumed to outcompete NDVI in this sub-study. However, the preference may depend on the goals of a monitoring task.

Evaluation was done for the analysis with EVI2 data only. In Outokumpu, 50% of the defoliated stands used in the evaluation were detected with a misclassification rate of 22%. Only 27% of the damaged stands were detected (misclassification rate of 54%) in Ilomantsi. To demonstrate the ability to tailor the method according the purpose, the z-score threshold was adjusted. A higher threshold (z = –2.1) was applied. This resulted in misclassification of the healthy stands of 50% and 35% for training and testing data set respectively, in Outokumpu. In Ilomantsi, the corresponding rates were 46% and 70%. In Abisko, six years was assigned as a number of years for reference conditions with the z-score threshold value of -6.0. The point closest to (0, 1) suggested a detection rate of 75% with a misclassification of healthy sampling units of 19%.

6.4. Projecting potential distribution of the hemlock woolly adelgid (VI)

6.4.1. Feature selection for the MaxEnt niche models

The random subset feature selection algorithm showed that only minimal gain in AUC, AICc, and/or overfitting was achieved in the MaxEnt niche models for HWA using subsets of more than six out of 119 environmental predictors (Figure 11A-C). Maxent models with subsets of six variables, selected based upon AUC, performed significantly better regarding to AUC, AICc, and overfitting than randomly chose six-variable models (Figure 11D-F). Forty-two variables out of the original 119 were used in the top 12 six-variable MaxEnt models (Table 2). Nineteen of these variables were used more than once. From one to three of the variables in each model were climatic factors enabling future climate projections. Out of the selected variables, 41.7% were edaphic indices, 37.3% climatic indices, and 20.8% topographic indices. The edaphic indices included 25% soil properties (e.g., silt % on top soil from 0-5 cm), and 16.7% soil taxonomy indices (e.g., % of Ochrepts suborder per 1 km^2 pixel). The evapotranspiration layers (actual and potential evapotranspiration: AET-PET) were the most often used climatic predictors (15.2%). In addition to these climatic predictors, monthly temperature/precipitation indices (13.8%), and Bioclim indices (8.3%). The six top ranked variables by permutation importance and frequency of appearance in the 12 models were: (1) Mean November PET; (2) Slope; (3) Inceptisols Order Ochrepts %; (4) Silt %, 5cm; (5) Inceptisols Order Udepts %, and (6) Mean February maximum temperature (Table 2). Eight out of the 12 top ranked climatic predictors were from the winter season. The variable response curves indicated that intermediate levels of November PET, February maximum temperatures, deeper slopes, and higher percent of Ochrepts and Udepts soils were optimal for HWA. Furthermore, suitability of silt percent of the top soil to 5 cm peaked at about 45%.

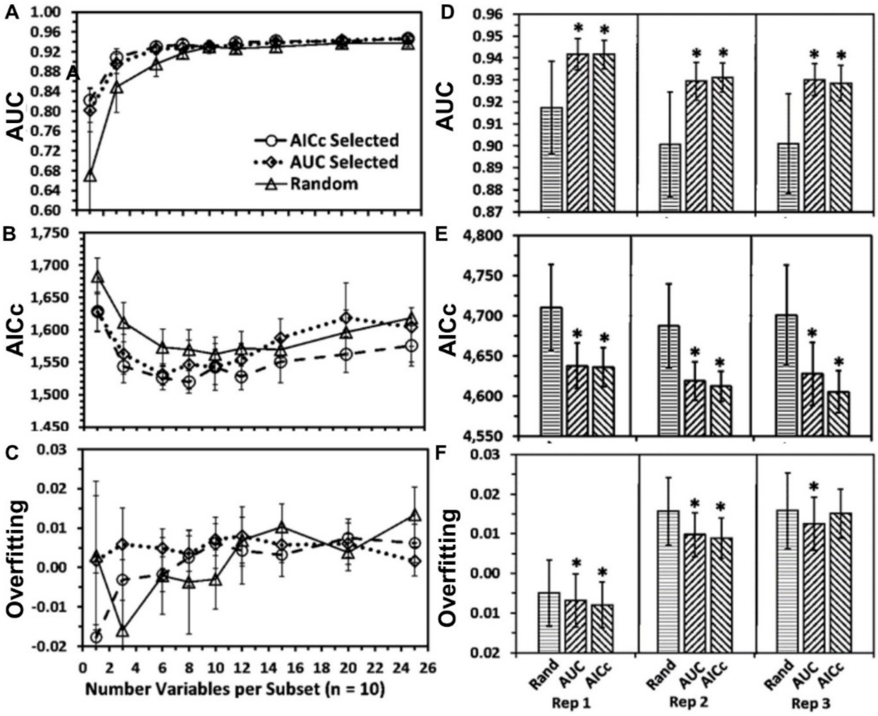

Figure 11. Evaluation statistics for the HWA MaxEnt models (mean ± SD) of AUC (A, D), AICc (B, E), and (overfitting; C, F). The statistics are computed for top ten models, based upon AUC, AICc, and 10 best random subsets out of 250 (A-C). Top 250 six-variable subsets of 3,000, based upon AUC or AICc, and top 300 out of 3000 random six-variable subsets (D-F). Means with an asterisk are significantly better than random models ($P < 0.05$; Welch t test with Holm correction, preceded by significant Welch ANOVA test, $P < 0.05$).

Table 2. MaxEnt model variable permutation importance, ranking, and number of models used in for 42 of 119 variables that we used in the top 12 six-variable hemlock woolly adelgid models, selected with the random subset feature selection algorithm.

Variable	**MaxEnt Model Permutation Importance, Mean ± SD (number of models)**	**Ranking by Mean Permutation Importance[b]**
*Mean November PET**	43.4 ± 4.8 (4)	1
Slope	33.4 ± 6.4 (4)	2
Inceptisols Order Ochrepts	19.4 ± 7.1 (4)	3
Silt %, 5 cm	12.7 ± 3.3 (5)	4
Inceptisols Order Udepts	44.3 ± 8.9 (2)	5
Mean February maximum temperature	40.2 ± 5.4 (2)	6
Coarse Fragments, 5cm	35.5 ± 5.2 (2)	7
Ph, 5 cm	19.5 ± 7.4 (2)	8
Bulk Density, 5 cm	18.7 ± 4.7 (2)	9
Mean January rainfall	9.1 ± 9.1 (3)	10
Elevation	8.7 ± 7.1 (3)	11
Sand %, 30 cm	11.8 ± 3.5 (2)	12
Silt %, 30 cm	7 ± 0.9 (2)	13
Entisols Order, orthents	5.3 ± 1.1 (2)	14
Mean February rainfall	4.5 ± 2.2 (2)	15
Mean temperature of wettest quarter (Bio 8)	3.5 ± 1.2 (2)	16
Distance to Low Flow Accumulation Areas	2.5 ± 0.1 (2)	17
*Mean July AET***	1.9 ± 0.8 (2)	18
Site Exposure Index	0.4 ± 0.5 (2)	19
Mean January PET	39.5 ± 0 (1)	20
Temperature seasonality (Bio 4)	38.3 ± 0 (1)	21
Mean March PET	36.5 ± 0 (1)	22
Mean February AET	35.6 ± 0 (1)	23
Mean January maximum temperature	33.2 ± 0 (1)	24
Mean March maximum temperature	33 ± 0 (1)	25
Bulk Density, 30 cm	16.2 ± 0 (1)	26
Ph, 30 cm	14.6 ± 0 (1)	27
Spodosols Order, Orthods	13 ± 0 (1)	28
Inceptisols Order, Aquepts	12.2 ± 0 (1)	29
Mean July PET	7.7 ± 0 (1)	30
Mean July Minimum temperature	7.6 ± 0 (1)	31
Alfisols Order, Udalfs	5.3 ± 0 (1)	32
Sand %, 5 cm	4.8 ± 0 (1)	33
Distance to Streams	2.3 ± 0 (1)	34
Topographic Position Index, 9 km circular	1.6 ± 0 (1)	35
Precipitation of coldest quarter (Bio 19)	1.6 ± 0 (1)	36
Topographic Position Index, 3 km circular	1.4 ± 0 (1)	37
Distance to Medium Flow Accumulation	1.2 ± 0 (1)	38
Mean June AET	1.1 ± 0 (1)	39
Precipitation of warmest quarter (Bio 18)	0.5 ± 0 (1)	40
Entisols Order, Psamments	0.5 ± 0 (1)	41
Precipitation seasonality (Bio 15)	0.1 ± 0 (1)	42

[b] Multi Multi-Objective Optimization Ranking by Mean Permutation Importance (0.6 weight) and Number Appearances in Top 12 Models (0.4 weight). Variables ranked using weighted joint criteria with MCDM R package.

* PET = potential evapotranspiration, ** AET = Actual evapotranspiration

6.4.2. MaxEnt feature subset ensemble model projections

The final MaxEnt FSE models projected habitat suitability HWA over most of the native range of the eastern hemlock (entire range of Carolina hemlock) in the USA and the southernmost Canada under contemporary climatic conditions (Figure 12). The area of 100% model consensus ranged roughly from 44° N in the northeast to 34° N in the South. Within the southern part of the range, higher elevation areas of the Southern Appalachians seem to be more suitable for HWA than the low elevation areas in the region. A lower number of models projected suitability within the westernmost hemlock range and Nova Scotia, Canada. The northernmost part the range of eastern hemlock, above 45° N, was mostly projected as unsuitable for the species under contemporary climate. The temperature limits according to the final MaxEnt models were averaging -15.80 ± 0.47 °C for minimum values for the minimum temperature of the coldest month, -7.97 ± 0.46 °C for the minimum values for the mean temperature of the coldest quarter. Corresponding values for the maximum values for the maximum temperature of the warmest month were 34.24 ± 0.63 °C. The equivalent extreme values of the HWA occurrence observations in eastern North America were quite similar at -15.00 °C, -7.20 °C, and 32.00 °C, respectively.

The reverse-casted MaxEnt projections to the native ranges in Asia and western North America overlaid with the available HWA occurrence observations and distributions of the host *Tsuga* spp. (Figure 12B-C). The MaxEnt FSE model projection for East Asia projected high suitability within the known native HWA regions in Japan, Central Taiwan, and Ulleung Island of, Republic of Korea (Figure 12C). High suitability highly correlated with the species occurrence observations in these regions. Within the continental Asia, the MaxEnt models also projected suitable habitats, but the habitat suitability was not as highly correlated with the available HWA occurrences. In the western North America, model suitability was generally high among the HWA records in the Cascade Mountains. Lower suitability was projected for the HWA occurrences eastwards of -121.5° W in Washington, Oregon, and Idaho. Sensitivity analysis showed that the sensitivity of the MaxEnt model projection to Asian islands did not significantly differ from that of in eastern North America, however, it was lower for the projections to the continental Asia and western North America. There was high variability in the sensitivity reverse transferability indices from the introduced range over the Asian continental, Asian islands only, and western North American ranges. No significant differences were observed.

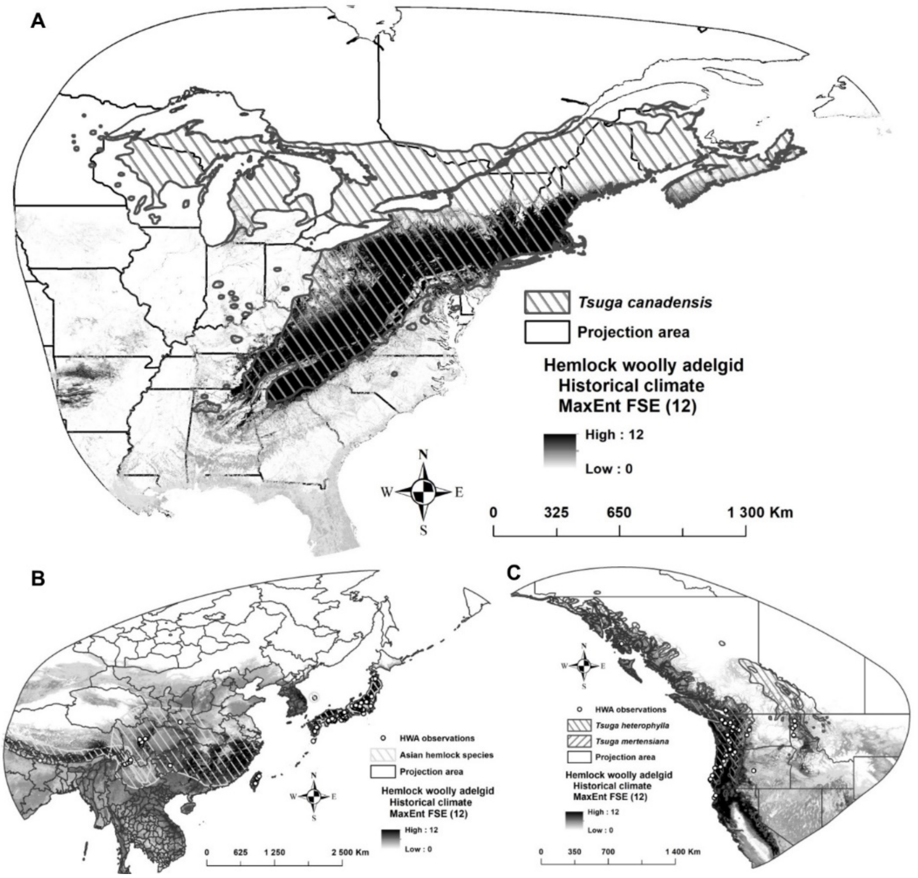

Figure 12. MaxEnt feature subset ensemble (FSE) projections for A) the introduced range in eastern North America and native ranges in A) continental Asia and Asian islands, and C) western North America. *Tsuga* spp. ranges according to Little (1971), Farjon (1990), and Holman et al. (2017).

Each of the four future climate MaxEnt FSE models projected range expansion northwards and eastwards in the eastern North America (Figure 13A-D). Shifts of the 12 MaxEnt projection centroids towards north and east differed significantly from zero, in case of all four climate scenarios ($p < 0.02$; Welch t-test with Holm correction). The range shift to north under the high CO_2 emission climate change scenario for 2070 (2070he85) was significantly greater than the other scenarios ($p < 0.05$; paired Welch t-test with Holm correction). Under this most extreme climate change scenario of 2070he85, vast majority of the northern range of the contemporary native eastern hemlock distribution was projected highly suitable for the HWA. The mean projected northward range shift of HWA ranged from 222.12 ± 92.45 km (2050he26) and 467.64 ± 198.85 km (2070he085). Corresponding expansions to east varied between 110.32 ± 66.24 and 164.03 ± 152.99 km, respectively. Contrary to the range shifts, are of potential distribution did not differ significantly among the contemporary climate and future climate scenarios. The projected areas were quite variable for the projections under future climate scenarios. The mean elevation for the

MaxEnt projections did not differ significantly either in the North or South ($p < 0.05$, paired Welch t-test with Holm correction).

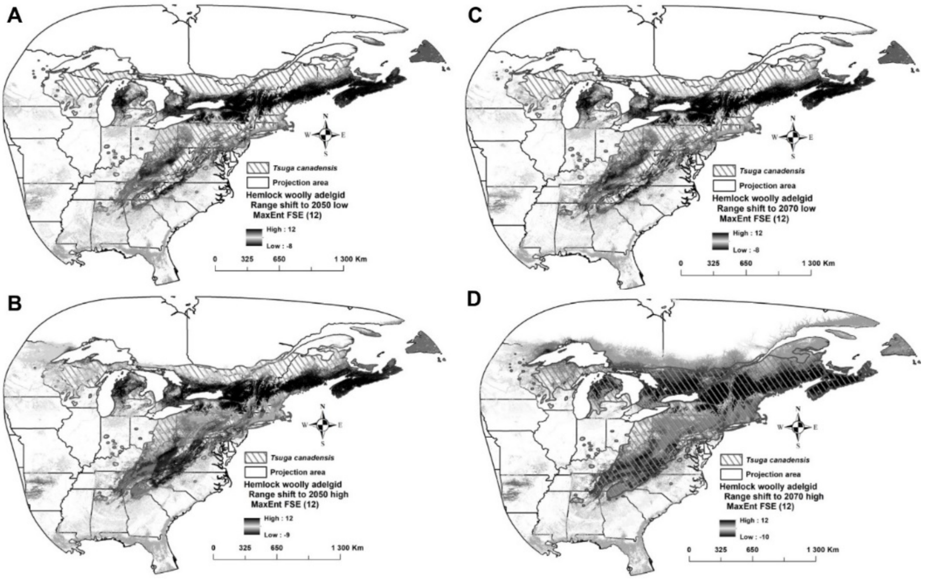

Figure 13. Hemlock woolly adelgid future range shifts in the eastern North America showing range addition and range loss under the four different climate change scenarios (A-D). Change maps were created by subtracting final MaxEnt models for contemporary climate from the corresponding models under future climate scenarios: (A) 2050he26; (B) 2050he85; (C) 2070he26, and (D) 2070he85. The scale indicates change in the number of models in agreement on habitat suitability for HWA.

7. DISCUSSION

7.1. Classification of pine defoliation by the common pine sawfly (I, II)

7.1.1. Tree-level classification (I)

Random forest classification results were promising for the schemes with two to three defoliation classes. For these schemes, laser metrics differed between the healthy and defoliated Scot pines. Similar level of accuracy could be obtained for varying pulse densities. While the accuracy was somewhat lower for the four-class scheme, most of the trees could be assigned at least to the neighboring class. The results are comparable with those of Kantola et al. (2010). They combined the same airborne LiDAR data with aerial imagery acquired form the area. A classification accuracy of 88.1% was obtained for two defoliation classes employing random forest classification. The NIR band of the aerial imagery was the most important feature. However, they excluded trees having equal defoliation level to the exact threshold value of 20% of defoliation. Aerial images have been utilized before to detect tree-wise defoliation of Norway spruce (Haara and Nevalainen 2002). An overall classification accuracy of 68.9% was obtained with four classes.

There are uncertainties in the needle loss assessment affecting the classification accuracy. Visual defoliation assessment is sensitive to errors. Development of more accurate methods for the assessment would also improve needle loss classification and damage detection. Defoliation levels were unevenly distributed among the sample trees. Due to cold and wet weather, *D. pini* performance suffered in the summer of 2008, leading to milder defoliation and underrepresentation of severely defoliated trees. This influenced the classification of defoliated trees, as well as the overall accuracies.

The raw mean intensity showed as a powerful predictor amongst the 26 LiDAR metrics. In theory, intensity based upon wavelength of 1064 nm in the NIR region, should differ between healthy and defoliated trees. The intensity of LiDAR returns should be lower for stands suffering from defoliation than for healthy stands. In practice, the use of intensity is often problematic, because of the need of feature calibration. Classification accuracies of 81.74% and 83.59% were gained for two classes, both schemes DEF1 and DEF2, respectively, when only *Int* and *pene* were used as predictors. This may suggest that a full waveform LiDAR could be successfully used in detection of defoliation. Further research should include evaluation of influence of forest characteristics on defoliation classification from LiDAR, such as site type (Vehmas et al. 2009). Distribution of laser metrics probably vary based upon size and hierarchy level of a tree (e.g., Korpela et al. 2010).

7.1.2. Plot-level classification (II)

Proportional LiDAR features were the best indicators for plot-level defoliation. Results of the analysis supported hypothesis that a larger proportion of LiDAR pulses would penetrate deeper into the canopy on the defoliated stands. The obtained classification accuracy with two variables of *p*80 and *p*90 for two defoliation classes (84.3%) was at the same level as for the tree-wise classification (section 6.1.1.). Again, classification results were not highly dependent on the pulse density. As in the sub-study I, a classification test with raw intensity was done. Classification accuracy of 86.9% was obtained, when *Int* was incorporated to the model. Similarly, to the tree-level study, full waveform data may provide additional explanatory power in needle loss detection. The results are, in some degree comparable to the studies conducted within the same region. Ilvesniemi (2009) classified plot-level defoliation from aerial photographs. The classification accuracies varied between 38% (9 classes) and 87.3% (2 classes).

The subjective method for assessment of defoliation is also a weakness at plot-level. However, if the error is random, the effect should be milder at this scale than at single tree-level. The study area mainly consisted of stands on similar site types and most likely, the variation in site types did not hamper the results. It should be kept in mind that a specific insect pest prefers certain site conditions. In case of the common pine sawfly, stressed pines on dry sites are preferable. These kinds of stands are often areas of initial infestations.

The novel ITD method to estimate the forest canopy cover can also be considered as a forest canopy mask. Instead of the method, canopy cover can be estimated also by thresholding the CHM. The approach was assumed, however, computationally more demanding. Variation in the forest canopy cover has seen as a major problem in mapping insect defoliation (i.e., Kantola et al. 2010, 2011). With the method used her, the effect of variation in defoliation in the forest canopy cover can be taken into account with a relatively uncomplicated approach. However, in practice, area-based mapping methods may often be more suitable than ITD based methods.

7.2. Landscape-level hemlock mortality (III, IV)

7.2.1. Evaluating landscape-scale hemlock mortality (III)

Previous studies on HWA induced hemlock mortality include plot- and stand-level studies (Orwig and Foster 1998; Paradis et al. 2008; Elliot and Vose 2011; Krapfl et al. 2011; Trotter et al. 2013), and medium to low spatial resolution remote sensing (Bonneau et al. 1999; Royle and Lathorp 2002; Wimberly and Reilly 2007; Kong et al. 2008). The level of investigation has been either small-scale or over a large area. Landscape-scale detailed information on the hemlock decline is needed. The high-resolution imagery and rather large spatial scale of the investigation facilitated interpretation of ecological impacts in the context of landscape functional heterogeneity (Coulson and Tchakerian 2010), i.e., how other living organisms may be affected by the removal of hemlock as a component of the forest vegetation community.

The sub-study revealed a high number of dead hemlocks in the upper canopy cover layers unevenly scattered throughout the landscapes. Additional mortality that could not be observed was present in the suppressed canopy cover layers (Orwig and Foster 1998; Krapfl et al. 2011; Kantola, T., personal observation). Topography have been observed to affect forest condition and further insect pests and host species (Niemelä et al. 1987; Ruohomäki et al. 1997; Kharuk et al. 2007; Baltensweiler et al. 2008). This has also been observed for the eastern hemlock (Orwig et al. 2002; Narayanaraj et al. 2010). The distribution of HWA infestations is affected both by the distribution of host species and environmental conditions. For example, on the contrary to the distribution of living hemlocks (Narayanaraj et al. 2010), dead hemlocks were often located at higher elevations. Narayanaraj et al. (2010) observed that eastern hemlock was absent above 1250 m in a Southern Appalachian landscape. Similar pattern was observed within the native range. Hemlocks outside their optimal range in Japan were, e.g., more susceptible to scale insects (McClure 1985). A relatively short-term period of infestation in the Southern Appalachians may have been a critical factor contributing to the HWA dynamics.

Over seven hectares of gaps in the canopy cover surface was observed. These gaps in the canopy surface can facilitate, e.g., establishment and spreading of invasive plant species, such as great rhododendron (*Rhododendron maximum* L.) or mountain laurel (*Kalmia latifolia* L.). However, Kantola et al. (unpublished data) noticed that the majority of the canopy gaps observed from the 2010 imagery significantly shrunk or disappeared by 2012.

Trotter et al. (2013) suggested that effects of HWA on hemlock community are not apparent at larger scales. However, at a landscape scale or smaller, influence of HWA-induced hemlock mortality to ecosystems may be substantial, particularly to the riparian areas, where a high number of dead trees could be identified. The overall reduction in plant biomass within the landscapes was modest. However, as keystone species, hemlocks have a range of functions within forested landscapes, including moderating environmental conditions, and providing resources for wildlife. Stream ecosystems are also substantially influenced by the hemlock decline (Ross et al. 2003; Ford and Vose 2007). The aggregated pattern of hemlock mortality, especially in riparian areas, may amplify the impacts of HWA within the landscapes and removal of hemlocks has more pronounced ecological impacts than could be assumed based upon removal of biomass.

7.2.2. Mapping landscape-scale hemlock mortality (IV)

Landsat Thematic Mapper (TM) is the most popular sensor in mapping both living hemlocks and hemlock mortality (Bonneau et al. 1999; Royle and Lathrop 2002; Wimberly and Reilly 2007; Kong et al. 2008). Lower resolution remote sensing may not succeed in providing detailed information on hemlock mortality taking into account the pattern of hemlocks within the Southern Appalachian landscapes. This kind of two-phase classification strategy could be adapted for monitoring infestations by other insect pests, such as gypsy moth, southern pine beetle, or emerald ash borer. Similar approach can be applied for large area inventories with lower-resolution remote sensing data sets and used in teaching a lower-resolution data.

The two-phase classification scheme was mandatory in this case to avoid great overestimation of the magnitude of tree mortality. The obtained classification accuracies of 93.5% and 98.1% were high. The accuracy for forest cover classification may be an overestimation due to subjectively created testing data set and exclusion of uncertain pixels. LiDAR acquired at the same time than the aerial photography may have increased accuracy as well as enable a wider selection of classification approaches. The result of 2.1% proportion of dead trees within the analyzed area is difficult to compare with results of other studies, plot- and stand-wise estimates for hemlock mortality between 0% and 95% have been estimated (Orwig and Foster 1998, Elliott and Vose 2011, Krapfl et al. 2011).

Shadows were omitted from the area of forest cover classification. This may have induced error to the results. Topographic corrections for high-resolution data are often problematic. Especially in case of very complex topography. During the preliminary examination of the data, topographic corrections methods, such as band ratios and Minnaert correction were tested. The corrections did not substantially reduce the shades. Further, the spectral resolution was compensated. With correct timing of data acquisition, shadowed areas would be less pronounced.

Most dead trees were assumed hemlocks since HWA was the only major mortality agent at the time. The area was infested by the southern pine beetle in the early 2000's (Knebel and Wentworth 2007). Other plausible causes for tree mortality included abiotic factors and mild infestations by other species. Dead trees may also include broadleaved species. Secondary pests could have also contributed to weakening of trees and further, tree mortality. An assessment of a high-resolution aerial image time-series in the Linville River Gorge revealed a time span of five or more years that dead trees remain visible in the canopy cover surface (Kantola et al., unpublished data). Thus, HWA herbivory may have resulted in mortality of about 5% of the overstory conifers, present in the summer of 2012. It has been suggested that HWA-induced mortality may be higher for suppressed understory hemlocks than those of dominated trees (Orwig and Foster 1998; Krapfl et al. 2011). Although the tree mortality in the suppressed canopy cover layers could not be detected, the results give a good insight of the scale and distribution of hemlock decline within the size-classes comprising most of the biomass. A major portion of the study area was overlapping with that of the sub-study III. The results of dead tree coverage were similar with both approaches. The spatial pattern of classified dead trees was also similar to the other sub-study. Other studies have shown that topography influence microclimate and soil properties further affecting HWA infestations (Hodkinson 2005; Narayanaraj et al. 2010).

A substantial portion of the area occupied by conifers was assumed hemlocks (Newell and Peet 1998; Knebel and Wentworth 2007). Other possible conifers included four pine species (*Pinus* spp.) (Newell and Peet 1998; Elliot et al. 2013). Distinguishing hemlocks from pines is challenging and susceptible to errors (Royle and Lathrop 1997; Orwig et al. 2002; Koch et al. 2005). The lack of field data inhibited testing of species recognition. Hemlock could not be separated from pines by naked eye with good accuracy. Hemlock dominated stands have been detected with accuracies of 69% from ASTER (Koch et al. 2005), 72% combining ASTER and Landsat data (Kong et al. 2008), and 83% utilizing AVIRIS hyperspectral images (Airborne Visible/Infrared Imaging Spectrometer) (Pontius et al. 2005). Using auxiliary information on suitable conditions for species, such as soil and topographic information may increase the accuracy of species separation. These variables could also be used in approximation of infestation probability.

7.3. Mapping defoliation in Fennoscandia (V)

The novel method for detecting forest damage utilized z-scores and ROC curves. The sub-study pointed out both the potential and disadvantages in using low spatial resolution remote sensing in monitoring forest disturbance. The z-score thresholds are land cover specific rather than site-specific and may applicable for similar land cover classes over an extensive area. Evaluation of the z-score method was conducted in two different regions of Fennoscandia. The results were moderate, at the best, in highly fragmented landscapes of eastern Finland. However, the z-score method could be also applied to a higher spatial resolution data to increase accuracy in this kind of environments. However, often increase in spatial resolution decrease the temporal resolution leading to a higher probability of cloudy data. The method was more successful on in more homogenous forest area in northern Sweden. The observed relatively high detection accuracy showed a potential of the method in certain forest areas. The results were unsatisfactory in Ilomantsi, were the long history of an insect outbreak most likely affected the detection (see Sulla-Menashe et al. 2014). The prolonged gradation phase of the common pine sawfly prevented establishment of the reference conditions. This shows the importance of available years of remote sensing data preceding the outbreak. This period facilitates sufficient identification of the reference conditions. It is also possible that Scots pine canopy does not fully recover between insect outbreaks affecting establishment of the reference conditions affecting detection.

The main contributing factor for the poor performance within fragmented landscapes is likely the low spatial resolution of MODIS data resulting in mixed pixels. Typical landscapes within populated regions in Fennoscandia are fragmented and the matrix consist of urban areas, agricultural fields, water, and forest. MODIS or other low spatial resolution data may be inadequate as a sole sensor for forest health monitoring within similar landscapes. Ilvesniemi (2009) reached a classification accuracy of 85.9% for two defoliation classes using Landsat images in Palokangas. Her results were only slightly better with aerial photography. Karjalainen et al. (2010) used multi-temporal ERS-2 and Envisat satellite SAR based backscattering intensities for 400 m × 400 m grid cells to assess defoliation. They obtained an accuracy of 67.8% for two defoliation classes in the Palokangas area. The accuracies obtained in the sub-study V were generally lower than in studies on MODIS in homogeneous forest landscapes (Kharuk et al. 2007; de Beurs and Townsend 2008). This method may perform better in deciduous forests or in areas under frequent infestations. Although a recovery period after on outbreak by a defoliator may be long for both conifers and broadleaved species (Tenow 1996; Lyytikäinen-Saarenmaa and Tomppo 2002), broadleaved tree species may be able to establish sufficient levels of foliage even the next year for reference conditions between the outbreaks. Severity of defoliation influences the monitoring success. An overall intensity in eastern Finland was lower than in Abisko, but also fluctuating annually. Further, timing of defoliation may be a factor affecting detection accuracy. The needle consumption occurred in both Outokumpu and Abisko during early summer (Kantola, personal observations; Tenow et al. 2007). The common pine sawfly feeds later in the season, in July-September in Ilomantsi area, i.e., well after the season max. Late season low solar elevation angles affect reflectance, and further vegetation indices. Furthermore, the sampling sites in Abisko were either highly defoliated of close to healthy. In the eastern Finland, higher heterogeneity among the stand-level defoliation may have affected the results as well. It can also be assumed that the method could work well in detection of drastic changes in forest health status, such as in case of wider bark beetle outbreaks.

High level of landscape fragmentation is quite common in many countries, especially in Europe. Use of MODIS data within areas with similar condition, i.e., level of landscape fragmentation may lead to underestimation of disturbed area. Higher spatial resolution data should be preferred if a sufficient cloud free data during the season is available. However, at northern latitudes, such as Fennoscandia, reasonable short growing season limits the number of data acquisitions. For example, in 2013, only small fractions of Abisko outbreak area were visible in Landsat images.

7.4. Potential distribution of hemlock woolly adelgid in North America (VI)

7.4.1. Feature selection for the MaxEnt niche models

Soil features were the most powerful variables in the MaxEnt niche models for HWA, calibrated within the introduced range, followed by climate and topographic variables. The soil features influencing HWA distribution, including proportion of silt in top soil (0-5 cm) and Ochrepts soils in the Inceptisols, most likely reflect the importance for the HWA host species in the eastern North America. Former studies on niche modeling of the eastern hemlock suggested importance of climate, land cover, and soil property in defining hemlock habitats (Iverson et al. 2008; Prasad et al. 2004). Soil properties potentially important for eastern hemlock included soil productivity and soil texture, which is related to the silt percentage found as an important predictor in the MaxEnt models. Furthermore, according to Prasad et al. (2008) Inceptisols soil order is important in hemlock niche models corresponding with the importance of Ochrepts and Udepts soils of the Inceptisols (Table 2).

In the eastern hemlock models, the most important climate variables included mean July temperature and annual precipitation (Prasad et al. 2008). In the HWA MaxEnt model, mean January and February precipitation were observed as important predictors. In previous HWA studies, minimum winter temperatures have been identified as a major limiting factor for HWA distribution (Paradis et al. 2008; McAvoy et al. 2017; Tobin et al. 2017). However, only the mean minimum October temperature was found among the used 27 climatic variables in the final models and it was not an important predictor. In contrast, the used RSFSA feature selection method ranked mean November PET and mean February maximum temperature as the top climatic variables. Often, only the 19 Bioclim climatic indices are utilized in niche models. In this study, other climate features, such as monthly AET/PET and temperature/precipitation indices were much more important that the Bioclim features.

Of the topographic features, slope was identified as the most important predictor. It was the second top ranked features for all the used ones. Deeper slopes can be most likely associated with suitable hemlock habitats. High resolution topographic features of 30 m, including elevation and distance to stream, have been found to affect the landscape-level spatial pattern and performance of both HWA and eastern hemlock (Narayanaraj et al. 2010; Kantola et al. 2014). However, in a study by Trotter and Shields (2009), elevation explained only 2% of the variation in HWA survival in the eastern USA.

7.4.2. MaxEnt niche models for the introduced range of the hemlock woolly adelgid

The MaxEnt FSE projection for HWA range covers most of the eastern hemlock range in the introduced eastern North America, including minor areas in southern Canada, such as southern Nova Scotia (Figure 12). The projection extends further north along the Atlantic coast area than inlands. The northernmost part of the eastern hemlock range (> 45° N) may be unsuitable for HWA under contemporary climate. The mid-continental hemlock range, excluding southwestern Michigan, in the coastal Lake Michigan may remain unsuitable for HWA. This can be related to more maritime climate corresponding better to the native range of the species in Japan.

Although some observations suggest that HWA tolerates quite cold temperatures and lengths of cold periods, rapid changes in temperature changes and the frequency of extreme cold temperatures, especially later in the season effect the HWA populations (Paradis et al. 2008; Skinner et al. 2003). Adelgids may die after exposure of a mean winter temperature of −5°C or for a period of 93 days of daily minimum temperature below −10°C (Paradis et al. 2008). The MaxEnt models in the introduced range covered areas with minimum temperature and mean temperature of the coldest quarter of -15.80°C and -7.97°C, respectively. These values agreed well with those from the HWA occurrence observations (-15.00°C and -7.20°C, respectively). According to Skinner et al. (2003), only about 14% of the most northern HWA survived from cold exposure to -15 °C in March, in eastern North America. Tobin et al. (2017) reported high mortality to HWA from the cold exposure below -15 °C, as well. Accordingly, the HWA distribution may already be close to the northern limit under contemporary climates in the eastern North America. However, HWA may be able to develop greater tolerance for cold weather facilitating future expansion farther to the north (Skinner et al. 2003). In addition, the historical climate data represents the years 1950-2000 (Hijmans et al. 2005). Temperatures have already been elevating since then (Dukes et al. 2009; IPCC 2014), and the potential range of HWA may have already started to shift northwards. According to Parmesan (2006), various species have already responded to this rather mild change in climate.

The maximum temperature of the warmest month in the MaxEnt projection for HWA was slightly higher than that of found for HWA occurrence observations (34.24°C vs. 32.00°C). The projected range extends south of the native eastern hemlock distribution, which already is defining the southern rage of HWA. Effect of heat exposure on HWA is not much studied. Mech (2015) investigated cumulative effect of temperature on HWA mortality. Hundred % mortality was reached at temperatures above +30 °C, supporting the projected southern HWA range.

7.4.3. MaxEnt projections to the native ranges of the hemlock woolly adelgid

Under optimal conditions, MaxEnt models would have been calibrated based upon species occurrence observations in the native range, in East Asia. Menke et al. (2009) also calibrated niche models for an invasive insect species using data from the invaded range. They suggested that inconsistencies in sampling and regional climatic variation may induce errors to models when projected outside of the already occupied area in the new environments. Despite the inadequate information on HWA range in Asia, the reverse-casted MaxEnt FSE projection was in accordance with the known information on the Asian range, particularly in the Asian islands (Figure 12B). All the final MaxEnt models projected suitability in the HWA origin, the Japanese islands. There is no available hemlock or HWA observations from the most northern Hokkaido Island and it also was projected mostly as unsuitable. High suitability was also projected for other known HWA populations, such as Taiwan and Ulleung Island of Republic of Korea (Havill et al. 2016). The generally successful projection to Asia may indicate that HWA is at or at least close to equilibrium in the eastern North America. Furthermore, the lower sensitivity of the model projections to continental Asia and western North America support the assumption of HWA in the eastern North America is originating from the Asian islands.

Extensive information on HWA distribution in the western North America was not available. However, the projected FSE model was in general in accordance with the HWA occurrence observations in the region, especially along the Cascade Mountains (Figure 12C). This projected range covers much of the western portions of the native ranges of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) and mountain hemlock (*Tsuga mertensiana* [Bong.] Carrière) from northern California to the southernmost British Columbia, Canada. However, all the models did not project suitability for HWA occurrences in Idaho to the East.

The reverse-casted MaxEnt projections suggest that Japan and the Cascade Mountains of Washington and Oregon would match environmentally best with the invasive HWA range. These areas also correspond with the native ranges of the primary introduced HWA predators in the eastern North America. These include *Laricobius nigrinus* (Coleoptera: Derodontidae) from the western North America and Sasajiscymnus tsugae (Coleoptera: Coccinelidae), and *L. osakensis* from Japan (Havill et al. 2014). The MaxEnt projections could be used for refining source locations for biocontrol agents. For example, more cold tolerant strains of *L. nigrinus* from more interior western USA could establish more successfully into New

England (Havill et al. 2014; Mausel et al. 2011) if the conditions are more closely matching those of in the eastern North America.

7.4.4. Future MaxEnt projections under changing climate

The future MaxEnt projections predicted an HWA range shift of 221-468 km to the north and 110-164 km to the east. The FSE projection under high emission scenario for 2070 (2070he85) indicates HWA suitability throughout most of the current eastern hemlock range (~46° N; Figure 13A-D). Minor isolated areas may remain uninfested. Paradis et al. (2008) estimated the future HWA suitability in the northern range with a threshold value of -5 °C of mean winter temperature. By the end of the century, all the northeastern states in the USA could be suitable for the species (Paradis et al. 2008). The Maxent future projections in the sub-study similarly projected northern boundary to roughly correspond to the US/Canadian border in the northeast and following roughly 35° N. This range also includes large areas of southern Canada. Ellison et al. (2018) projected HWA spread to north until 2050. Their projections extended further north of Lake Ontario (~46° N), similar to the 2070he85 projections. Moreover, no HWA habitat suitability was projected to Nova Scotia by Ellison et al. (2010). HWA have been already able to spread into Nova Scotia, which was projected by the current and future climate models in the sub-study. McAvoy et al. (2017) suggested, based on winter temperatures that HWA may almost reach the northern eastern hemlock range extending to ca. 46.5°-48° N. They also suggested that HWA may increase winter survival at the northern latitudes intensifying the impacts.

In general, warming climate increases insect metabolism and reduces the risk of winter mortality (Bale et al. 2000). However, declined fitness due to elevated temperatures may limit HWA range in the south, when temperatures beyond optimal are encountered (Lemoine and Burkepile 2012). Too high summer temperatures may shift the southern HWA range to northwards and upwards along the Southern Appalachians (Figure 13A-D). However, the future MaxEnt models did not project evident upward shift. There are indications, however, that HWA may adapt to temperature extremes (Skinner et al. 2003; Parmesan 2006; Sussky and Elkinton 2015).

Niche model projections may not reveal much of the potential of species for crossing new geographical barriers. Future projections are more suitable for estimating the potential range than probability or timing of establishment (Fitzpatrick et al. 2012). However, taken the high HWA dispersal potential into account, the species may be able to invade the whole ecological niche (Trotter and Shields 2009). Furthermore, species dispersal ability may advance at the range extremes as a response to the climate change (Parmesan 2006). Adaptation of invasive species may be very fast during the range expansion (Butin et al. 2005). Climate change influence the host species as well, especially the hemlock species (Hastings et al. 2017). Combined effects of climate change and HWA infestations may further increase to risk of extinction of the eastern hemlock species (Hastings et. al. 2017). Adaptation of eastern and Carolina hemlock is concerning due to their slow growth rate, restricted environmental preferences, and weak seed dispersal (Hastings et al. 2017). HWA may benefit from sub-optimal conditions for the host species (Niemelä et al. 1987; McClure 1997; Morin et al. 2009).

7.4.4. Impacts and interactions of the hemlock woolly adelgid

Other factors than used in the sub-study, including dispersal, competition, species interactions, and landscape change with various human impacts influence distributions. However, many of these factors are important only at higher spatial resolutions. The MaxEnt models for HWA may not be equivalent with to the conditions where the species can survive and persist. According to Parmesan (2006), effects of genetic constraints and asymmetric gene flow are more pronounced close to the borders of distributions leading to lower survival. On the northern HWA range, lower survival may induce isolated local HWA populations with much lower impacts on eastern hemlock.

Management of HWA to mitigate negative impacts is challenging. Trotter and Shields (2009) outlined four reasons behind the rapid rate of spreading and the high negative impacts of HWA within the introduced range: (1) HWA has bivoltine and parthenogenic life cycle allowing rapid reproduction and reducing the Allee effect because populations are not dependent on sexual reproduction; (2) HWA is lacking natural enemies, despite major biocontrol efforts; (3) HWA uses many vectors increasing the dispersal potential; and (4) eastern and Carolina hemlocks have very low resistance against the species. Climate change may not have high negative impacts on HWA, even though originating from a single genotype (Havill et al. 2016), the introduced population appears to have a high spreading potential and rapid adaptation ability (Parmesan 2006). The impacts on eastern hemlock communities can be magnified in the future due to slow adaptation ability of the host.

Extent of the impacts of invasive alien species are difficult to predict and they may be highly variable within the introduced regions (Kulhanek et al. 2011). In general, effects are expected to be milder close to the rages of habitat suitability. Conversely, lower suitability for the host species may increase the risk of high impacts. High species abundance correlates more strongly with the high risk than species presence. Abundance data is rarely collected for invasive species (Bradley et al. 2012). This is also the case with HWA. Additional information is required on factors affecting HWA abundance at high spatial scale to estimate the risk of high impacts, including impacts of anthropogenic factors or interrelation between different trophy levels, and habitat suitability of the host species. For example, higher HWA densities were observed in Japanese ornamental hemlocks than in forests due to less optimal conditions better control by natural enemies in forests (McClure (1997). Host tree abundance was observed as major factor supporting HWA dispersal (Morin et al. 2009). Host tree quality may also influence HWA invasions. For example, hemlocks growing on mountainous areas are often stressed by climate, and thus maybe more susceptible for invasion (Niemelä et al. 1987).

7.5. Outlook for the future

7.5.1. Next generation forest health monitoring systems

World’s forests are encountering massive outbreaks of both native and invasive insect pests. Infestations by these pests are increasing the demand of forest health monitoring. Sufficient information for reliable risk assessment, integrated with forest management planning have to be obtained from wide areas. Sometimes even highly detailed information on disturbance is needed. An optimal solution to deliver for the high demand of accurate, efficient, and cost-effective methods for forest health monitoring is to include these methods into comprehensive wall-to-wall forest monitoring systems. These systems should be applied across political and geographical boarders and over spatial and temporal scales. This includes monitoring over a variety of different forest ecosystems, including varying climate zones, forest structures, and management practices. The needed information is complex, up-to-date, and required to acquire in timely manner. These systems should provide timely disturbance detection, and assessment of intensity and spatial scale, as well as information on disturbance trends and projections. Ideally, these systems would also be able to identify the damage agent, however, this is in many cases a very difficult task. Modern modeling techniques to evaluate range shifts, impacts, and risk related to insect pests should also be included to the systems. Often, evaluating the future risks and magnitude of impacts is the only way leading to mitigations of future disturbance events. The information would enhance IPM, forest health management, and support risk assessment, and decision-making under increasing levels of uncertainty. These systems should support flexible use of varying resolution data and auxiliary information. Although low-resolution data is often enough for the demands of large-area monitoring, sometimes more detailed information is needed; such is case of ephemeral or scattered disturbance. At the best, these systems should be automated with only low level of human involvement. Accordingly, these systems are of a major challenge. In order to accomplish such elegant and complex systems, extensive future research is needed. This has to include, in addition to development of remote sensing methodology, substantial level improvement of standardized terminology, and data collection across the political boundaries.

7.5.2. Main challenges

There are several significant issues hindering accurate continental to global scale assessments of forest disturbance (Frolking et al. 2009). (1) Cloud coverage interfere remote sensing at all spatial scales, especially in case of humid tropical and temperate forests (Zhao et al. 2005; Sano et al. 2007). (2) Problems induced from varying definitions and assessment data and methodology (Grainger 2008; Houghton and Goetz 2008). Further, (3) development of robust and general algorithms with high transferability for finer spatial scales is difficult (Woodcock et al. 2001; Foody et al. 2003). In addition, (4) small-scale disturbance are difficult to detect. Collectively, these small-scale disturbances are important also at the global scale (e.g., Asner et al. 2002).

Predicting effects of climate change on insect pests is a complex due to various reasons (Bradshaw and Holzapfel 2006; Parmesan 2006). In case of species habitat suitability, four different types of uncertainty can be associated with future projection (Dukes et al. 2009). These include uncertainties related to internal ecosystem processes, climate change projections, forthcoming human actions, as well as the uncertainties due to lack of data on the species in question. Unfortunately, the first three types are very difficult to avoid (Dukes et al. 2009). In addition to climate change, biological invasions and range shifts are causing great uncertainty in forest health management (Liang et al. 2014; Dukes et al. 2009). According to Dukes et al. (2009), the approach of studying species-specific responses to climatic factors, despite the usefulness to forest managers, is too slow and limited to add needed information on the responses of complex forest ecosystems to the climate change. Comprehensive modeling systems are needed to evaluate host–pathogen, host–pest, and invasive plants interactions in a context of a forest ecosystem (Dukes et al. 2009). This kind of approach would deliver a range of expected responses of the complex systems. However, increased understanding of these forest ecosystems is needed to enable successful use of these kinds of modeling systems (Dukes et al. 2009). Responses of forest insect pests will never be precise. However, well-targeted research in the near future could lead to better quantitative and geographically relevant projections (Dukes et al. 2009). Usually there are other disturbance agent present with insect pests at the same time. Further, there may be more than one insect pest present at the time of monitoring. It would be important to distinguish damage by an insect pest from those of other agents in order to evaluate the impacts of the species in question (Senf et al. 2017b). However, this topic is less studied or discussed (Senf et al. 2017b). It is usually assumed that the study species is the only damaging agent within the area, or a mask is applied to rule out unlike areas to be affected by the species (as in the sub-study IV). These approaches may lead to overestimation of accuracy (Senf et al. 2017b). Insect disturbance have been separated from significantly different disturbance, as fire or forest management (e.g., Goodwin et al. 2008; Meigs et al. 2015; Senf et al. 2015). Further, methods for disturbance identification are developed (e.g., Kennedy et al. 2015; Hermosilla et al. 2016). However, distinction between subsequent damage, such as wind throws − bark beetles, or drought – defoliation, is highly challenging (Seidl and Rammer 2017; Senf et al. 2016). Future research should include methodology for improved discrimination of disturbance by various agents. Although, it should be also acknowledged that insect pests are often interacting with other species and disturbance agents and the impacts may not always be separable (Senf et al. 2017b).

Early stage insect infestations are often difficult to detect with remote sensing. That applies for both bark beetles and defoliators. The typical initial phase of a bark beetle infestation is called green attack. Mild changes are already present in the foliage but those are much harder classified than the later stages of red and grey attack. Research on detecting the green attack with remote sensing is scarce (Lausch et al. 2013). Forest health management practices are mainly based on high spatial resolution remote sensing and the red attack phase. At this point, efficient preventative measures are often too late. These remote sensing operations, however, are used to target field surveys for detecting green attack and related actions for mitigation (Lausch et al. 2013). Mild defoliation, as well as severity of defoliation is difficult to assess accurately form remote sensing data (Dennison et al. 2009; Zhang et al. 2010; Rullan-Silva et. al 2013). Visual assessment of defoliation level is widely used due to lack of accurate automated methods. Unfortunately, this method is prone to errors. Observers should be able to take into account, e.g., variation in foliage biomass between years, within season, and between site types. In addition, other factors induce error to the assessment. Leaf area index by itself, although correlated with defoliation cannot be used as it is in classification of defoliation. Relative defoliation is largely related to the stand characteristics, such as soil fertility. For example, a healthy Scots pine growing on poor soil has less needles than another one growing on more fertile site type (Innes 1993). A new automatic system to assess severity of defoliation is needed. That could also utilize LAI. The method would need an extensive library with calibrated LAI measurements under varying forest conditions and levels of defoliation.

Current knowledge on ecosystem resilience and sustainability decreases as the scale increases from the level of habitat management to landscape management and design (Landis 2017). The new implementations of remote sensing and modeling techniques may be used to increase wide-scale understanding of the complex interactions of forest health. Most of the studies on remote sensing of insect outbreaks are focused on quite restricted areas (Senf et al. 2017b). More research is needed, in which large areas over a gradient of climate and other conditions are covered (Senf et al. 2017b). Large-scale assessments would give valuable insight of insect disturbance patterns over landscapes and regions (Hicke et al. 2012; Kautz et al. 2016; Trumbore et al. 2015). With remote sensing and increasing computational power these kinds of large-scale assessments would be achievable (Hermosilla et al. 2016; Senf et al. 2017b). Senf et al. (2017b) suggest the main limiting factor for regional assessment is the method transferability as most of them are for specific occasions.

In addition to the problems related to detection or identification of insect pest disturbance, there are uncertainties and challenges related to other characteristics affecting the accuracy of insect disturbance monitoring. For example, tree species recognition and thus delineation of host pattern and distributions effect the disturbance detection. For instance, tree species identification between confers is challenging (Orwig et al. 2002; Koch et al. 2005). In case of insect pests, information on the pattern and distribution of the host trees, as well as the tree species composition is often limited. Improved methods for these tasks will improve disturbance monitoring as well, e.g., providing information on the extent and impacts of the infestation and on delineating the number of possible disturbance agents.

7.5.3. Developing remote sensing in insect disturbance monitoring

Despite the decreased need of field data resulting from development of modern monitoring methods, it is still widely used and needed as a reference. Senf et al. (2017b) found that *in situ* data collected in the field was the most utilized reference data in modeling insect disturbance. The amount of fieldwork, although the data is valuable, is desired to decrease due high costs, consumed time, and limiting spatial extent. Further, availability and quality of inventory data highly varies among the countries (Levers et al. 2014; Gschwantner et al. 2016; Neumann et al. 2016; Senf et al. 2017b). Large area remote sensing applications are often hindered by difficulties to match varying data, such as plot size, and spatial resolution of remote sensing data (Senf et al. 2017b). Senf et al. (2017b) suggested that researchers should publish the field data with spatial information used for the research. At the time of planning new inventories, fusion of data sources should be considered. For example, interpretation of very-high spatial resolution imagery is regarded as an important source of reference data in monitoring bark beetle infestations that can be utilized for wide areas with reasonable costs (Meddens et al. 2011; Olofsson et al. 2014; Senf et al. 2017b). Further, high-resolution remote sensing data can be utilized in scaling down field data for lower spatial resolution data (Wulder et al. 2004). One recent method for creating reference data is Landsat spectral trajectories. The method utilizing dense Landsat time series and corresponding image chips have already been used in disturbance detection (Cohen et al. 2010; Kennedy et al. 2012; Hermosilla et al. 2015; Meigs et al. 2015; Potapov et al. 2015). The method allows plot-level assessment of disturbance over a range of spatial extents (Senf et al. 2017b). However, detection of often more subtle damage by insects can be difficult, compared to, e.g., forest fires (Senf et al. 2017b).

Remote sensing is one of the most rapidly developing field of technology. The advancement is driven by development of sensors and increasing performance of the information infrastructure (Toth and Józ'ków 2016). New platforms, especially the introduction of UAVs and other remotely piloted aircrafts are contributing to the development (e.g., Pajeres 2015). High spectral resolution hyperspectral sensors, often carried by UAVs, can also contribute to more efficient detection of insect disturbances in the future. Increasingly available very high spatial remote sensing data may significantly improve monitoring of insect disturbance (Senf et al. 2017b). Used in detection, mapping and classifying of disturbance, but also as good quality reference data. However, this data should be accessible to researchers at reasonable costs (Senf et al. 2017b). Citizen science data is already utilized in ecology (e.g., Tracy et al. 2019). A new platform of crowd sensed data, including imagery and video data, is also becoming increasingly available (Toth and Józ'ków 2016). Crowd sensing refers to a large group of individuals collectively sharing mobile sensed data. Crowd sensing have already been used in, e.g., monitoring air quality (Liu et al. 2018) and assessing road conditions (Piao and Aihara 2017). These methods could be also utilized, at least to some extent, in recording anomalies in forest environments, especially in areas of high human population density, such as urban forests.

A major leap in remote sensing applications can still be expected (Wulder and Coops 2014). Quite recently, large remote sensing data sets and entire space missions, such as Landsat archive or Sentinel Missions of the European Space Agency (ESA), have been opened to public giving a new advantage for the development of remote sensing technologies and applications (Wulder et al. 2012; Wulder and Coops 2014; Majasalmi et al. 2016). Further, open source tools for processing remote sensing data are continuously developed (Wegmann et al. 2016). This current advancement in remote sensing will improve forest health monitoring techniques as well. High intra-annual remote sensing data seem to improve detection and impact evaluation of damage by defoliating insects, especially of broadleaved species (Senf et al. 2017b). However, currently only low-resolution data, such as MODIS can deliver such dense data. Unfortunately, these data have unsatisfying spatial resolution for detecting disturbance within fragmented landscapes (sub-study V). Remote sensing of defoliating insect will most likely improve with modern medium to high-resolution satellite data with increasing intra-annual data, such as with quite recent launches of Sentinel-2 satellites (Senf et al. 2017b). The two satellite provide up to 10 m spatial resolution with a ten-day revisit time each (5-days combined). One increasing trend is to blend remote sensing data with a high temporal resolution with higher spatial resolution data. The temporal scale of the high spatial resolution data is increased with blending auxiliary spatial and temporal characteristics of high temporal resolution data. The goal is to generate synthetic observations at high spatial and temporal resolutions (Lunetta et al. 1998; Hilker et al. 2009). Use of full waveform LiDAR in disturbance monitoring should also be investigated further. Instead of single wavelength LiDAR, multiple wavelengths can also be acquired. For example, a four-band LiDAR system was tested in distinction of green and dry leaves. (Wei et al. 2012). They obtained point clouds on four separate wavelengths and calculated vegetation indices, including LiDAR NDVI, that were used in the detection. This kind of technology may open new opportunities in disturbance mapping, as structural and spectral changes could be assessed simultaneously.

Remote sensing archives already offer information over past several decades. This long-term data could add new information to the quite poorly documented history of insect outbreaks (Assal et al. 2014). Although Landsat time-series of approximately 30 years are used for historical assessments of insect disturbances, their full potential has not been used much (Pflugmacher et al. 2012; Assal et al. 2014). The Landsat time-series could be extended to over 40 years if the older Landsat MSS data were integrated (Senf et al. 2017b). This extended timeline could provide information on, e.g., insect population dynamics and cover several outbreak cycles, as well as enable testing current hypotheses on the underlining drivers (Senf et al. 2016). Historical data can also be used to predict future impacts, climatic change related changes in outbreak patterns, or range expansions of invasive damage agents.

Spaceborne satellite technology provide often a convenient approach for development of future monitoring methods for insect-induced disturbance. Computation capacity have been increased to the needed level to analyze high-resolution data, but the availability and cost of the data are still included to limiting concerns (Frolking et al. 2009). Satellite data can be obtained without remote sensing campaigns at reasonable costs. New methods are facilitating improved and timely monitoring. However, to enable efficient and flexible forest health monitoring systems, satellite-based applications need to be developed further. Standardized and transferable workflows are needed to improve the quality of comparable information and the operational level implementations (Pause et al. 2016). Current problems hindering development of standardized processes, over the political boundaries, results in from *in situ* data quality and quantity, such as those related to quality of methodology or availability of data (Pause et al. 2016). In addition, political and commercial restrictions can affect data availability (Pause et al. 2016). The issues related to local policies needs to be addressed in order to reach the next level in the system development (Nabuurs et al. 2015). New lower spatial resolution satellite-based hyperspectral, polarimetric, RADAR, and LiDAR sensors are developed or already been launched (Lausch et al. 2016a). These new sensors can contribute substantially to wide scale forest health monitoring (Lausch et al. 2016a).

Single satellite systems are improving spatial and spectral resolutions. Sensor agile configuration enabling in-track and cross-track stereo data acquisition are developed (Poli and Toutin 2012). Further satellite-based systems are in transition from single sensor systems to a co-operative remote sensing approach (Toth and Józ'ków 2016). Certain satellite sensors operate flying in tandem (Krieger et al. 2007), such as Sentinel-2 and -3. Data constellations of several sensors, although having the spatial resolution based on the coarsest one, allow shorter revisit times (Murthy et al. 2014). Constellation refers to satellite operating synchronized under shared control, overlapping in coverage. These techniques enable observation of a certain location even several times a day (Murthy et al. 2014). These constellations are gradually developed based upon satellite 'families' (Toth and Józ'ków 2016). Constellation of Landsat, SPOT and GeoEye/WorldView families were pioneering this technique (Toth and Józ'ków 2016). For example, RapidEye system is a constellation of five identical satellites on the same orbit reducing the revisit time and providing unique measurement capabilities (Tyc et al. 2005; Toth and Józ'ków 2016). While constellations of multispectral sensors is the most common, the systems can include other sensors, such as a SAR sensor in the Kompsat constellation (Lee 2010). European Space Agency have plans to include other sensors to the Sentinel family satellites (Copernicus program) (Toth and Józ'ków 2016). Recent advancements include flocks of nano- or microsatellites sharing the same orbit, and thus allowing frequent observations (Toth and Józ'ków 2016).

7.5.4. Near real-time insect disturbance monitoring

Early and accurate detection of outbreaks is a requirement of efficient remote sensing based forest health monitoring systems. Adequate early warning systems are desirable as they would facilitate effective controlling and mitigation efforts (Lange and Solberg 2008; Kharuk et al. 2009). These methods include continuous detection of ephemeral forest disturbance episodes across large spatial scales (Rullan-Silva et al. 2013). With effective real-time or near real-time applications, systems of early detection, i.e., early warning would be achievable. For such systems, temporal composite images are aggregated in the way that wall-to-wall cloud-free coverage are enabled (Prados et al. 2006). In addition, improvement in quality of time-series and algorithms are needed (Cohen et al. 2010; Rullan-Silva et al. 2013).

Satellite-based technology can provide for the real-time disturbance detection (Verbesselt et al. 2012). Remote sensing can be employed in early warning of large-scale insect outbreaks emerging from local epicenters (Simard et al. 2012; Seidl et al. 2015; Senf et al. 2017b). At the best, the high impacts of these outbreaks could be mitigated (Foster et al. 2017). So far, there are not many studies on use of remote sensing in context of near real-time monitoring of insect-induced disturbances. Further, operational level applications, such as the Forwarn system (https://forwarn.forestthreats.org/), are rare. Main reasons for low utilization of remote sensing in real-time monitoring may include complex prepossessing and processing of remote sensing data, lack of ground-truth data, and the low availability of remote sensing data with sufficient spatial and spectral resolutions (Wulder et al. 2009). Further, high costs and biological and logistical aspects to be considered, hinder the development (Wulder et al. 2009). Currently, near real-time applications are developed for MODIS data due to the ready-to-use products that are available soon after the data acquisition (Senf et al. 2017b). Applications with higher resolution data should be developed in the near future along with the increased development of ready-to-use medium resolution products, data streams combining several medium-resolution sensors, cloud-based processing environments with standard disturbance detection algorithms, such as the Google Earth Engine (Wulder et al. 2015; Senf et al. 2017b). The development of UAV methods provides another suitable platform for rapid assessments of insect-induced disturbances (Senf et al. 2017b). So far, the applications for monitoring insect-induced disturbance are scarce (Näsi et al. 2015, 2018). Although methods for early detection of insect disturbance need substantial development, some research exists (e.g., Wulder et al. 2009; Foster et al. 2016). Remote sensing has also been utilized in assessing ecosystem vulnerability to insect infestations. The information can be used in management operations to control large-scale outbreaks (Senf et al. 2017b). Research include hyper-spectral detection of changes in chlorophyll absorption (Lausch et al. 2013) and detection of stand level stress from Landsat time-series as an indicator of susceptibility to bark beetle infestations (Hais et al. 2016).

8. CONCLUDING REMARKS

Frequency and intensity of insect induced forest disturbances are increasing. The main factors contributing this pattern include climate change and related extreme weather events, and invasions by non-native insect pests due to human actions, such as trade and traffic. Insect outbreaks and infestations of both native and alien species pose a greater threat to resiliency of forest ecosystems as well as to human welfare than earlier in the recorded history. Efficient and affordable methods for predicting and monitoring these events are needed in order to prevent, control, and mitigate the various negative impacts of pest insects, as well as to support decision-making.

Pattern, frequency, spatial extent, and intensity of forest disturbances vary between different damaging agents. In addition to the insect pests, factors contributing to the scale and realized impacts of a disturbance are multitude. These factors include various biotic, abiotic, and anthropogenic factors, such as weather patterns, tree- and stand characteristics, natural enemies, or landscape topology and fragmentation, just to name few. The factors have, often unpredictable, interactions affecting insect pest insect and the induced damage. A multitude of uncertainties are present in evaluating impacts of insect infestations. For example, it is difficult to predict timing, location, intensity, or scale of an insect outbreak. Furthermore, other natural disturbances may trigger insect outbreaks and vice versa. These uncertainties bring about a high complexity into development of efficient monitoring systems, compared to traditional forest inventory tasks.

Remote sensing can provide spatially contiguous data with options of reuse the data and revisit the areas of interest even at a high temporal resolution. A wide selection of sensors with varying resolutions, sampling schemes, combined with methods of spatial modeling to map and monitor insect induced damage gives advantage to remote sensing technology over *in situ* measurements in the field. However, at least in the near future, field inventories are needed to improve accuracy of remote sensing applications.

Data and methods, including the remote sensing sensor, as well as suitable scale and resolutions should be chosen based on the disturbance and situation in question. For instance, high-resolution information may be suitable, if the damage is small scale or tree-level information is needed. Further, high spatial resolution is needed, if the pattern of infestation is scattered and small-scale, or symptoms cannot be detected with lower resolution data. Typically, the costs increase along with the resolution. However, acquisition of high-resolution data from a relative smaller area can usually be organized promptly with moderate cost by using, e.g., UAV or small aircraft as a platform. Combining different resolution remote sensing may often enhance monitoring. Lower resolution data may be more suitable to estimate large-scale impacts or detect damage with more intense detectable symptoms. Auxiliary information, such as forest inventory data, disturbance history, topography, etc., may improve evaluation accuracy in many cases. It has to be kept in mind that, e.g., forest policies and practices differ between countries and continents. Available road-network, rugged topography, and level of landscape fragmentation give more restrictions to method selection, as well as to spatial resolution.

Timing of data acquisition is crucial in context of damage detection. Quite often, early detection and timely management operations are the only way to mitigate an already initiated insect outbreak. In the best case, open access remote sensing archives with high temporal resolution could facilitate continuous monitoring of wide forest areas. Continuously improving satellite technology may respond to these needs. Concurrently with the time-series and continuous monitoring, one-time data acquisitions are still needed. This may be necessary, e.g., in order to evaluate initial infestation of high mortality agents or areas of high value. Traditionally, spatial resolution of the data affects the temporal resolution as well. For example, lower spatial resolution satellite sensors acquire data form the same location more often than higher resolution sensors.

Equivalent to remote sensing, in case of spatial modeling approaches for assessing insect-induced damage or species distributions, scale and resolution of an insect damage has to be taken into account. The insect pest in question and geographic location, including the specific characteristics for the region, affect the needed information and relevant environmental factors. The sale of investigation employing spatial models can range from small areas to global approximations. However, often spatial modeling techniques are very useful in projecting large scale impacts or making future predictions. Often, these approaches of remote sensing and spatial modeling should be combined instead of being contrasted. Various factors may inhibit acquisition of remote sensing or collection of filed reference. Particularly in these cases, spatial models can facilitate the impact evaluation. The feasibility of modeling methods is emphasized when predicting and projecting future events, including simulation of various forest management operations, especially those connected with the climate change related changes in insect population dynamics. An explicit category of spatial modeling, ENM has increased in popularity. Unfortunately nick modeling methods are not used often enough, especially in case of invasive species. Information on species ranges and habitat suitability, particularly under the changing climate can direct monitoring and mitigation efforts within most probable areas of new infestations. Information from the niche models help, e.g., planning of forest health management operation. Coupled with dispersal models they also provide an estimate on the time-table for operations and plausible arrival time of the species.

Modern disturbance monitoring systems should employ both remote sensing and modeling methods. In many cases, a combination of different data sources and methodology can enhance forest health monitoring and management efforts. Monitoring systems should be flexible and transformable in order to respond various needs in the field of forest health monitoring. Plenty of valuable research on remote sensing and modeling of insect induced damage has been conducted, especially during last few decades. Results of this work has already been partly adapted at the operational level in different countries. However, considerably more research is still needed before comprehensive disturbance monitoring systems are developed and are able to facilitate automatic wall-to-wall applications at the managing level. Rapidly developing remote sensing and modeling techniques, as well as improving computing power and data base systems will permit continual improved forest health monitoring and management.

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