Dissertationes Forestales 363

Interactions between forest pest outbreaks and environmental characteristics in boreal forests – implications for forest management

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Academic dissertation

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ABSTRACT

Boreal forests have faced increasingly severe disturbances caused by insect pests. These disturbances are primarily due to human-induced loss in structural and functional diversity, forest heterogeneity, and changes in temperature and precipitation caused by climate change. In Finland, the intensity of forest insect outbreaks has increased, and many pest insect species have spread further north. More information is needed to understand the specific factors that make forest stands more vulnerable to pest outbreaks. This thesis aims to explore the challenges of forest pest dynamics by examining the interactions between biotic and abiotic factors and their ecological and economic impacts. It focuses on two key pest species: the common pine sawfly (*Diprion pini* L.) and the European spruce bark beetle (*Ips typographus* L.), investigating the triggers of pest outbreaks and their effects on forest ecosystems.

The first study examined the long-term effect of natural enemies on the mortality of *D. pini* during the cocoon stage, finding that forest characteristics, especially nutrient-poor sites, can reduce the effectiveness of natural enemies. The second study identified soil and topographic factors that increase the severity of defoliation by *D. pini*, with more severe damage occurring on flatter, more fertile sites. In the third study, the cumulative effects of prolonged *D. pini* outbreak on Scots pine (*Pinus sylvestris* L.) radial growth and associated economic losses were quantified, showing significant effects based on defoliation severity. Furthermore, the trees that suffered severe defoliation did not recover to the pre-outbreak increment level during the 10-year study period. The fourth study focused on environmental factors predisposing Norway spruce (*Picea abies* (L.) Karst.) forests to *I. typographus*. The highest probabilities of severe infestation were linked to eastern aspects, moderately steep slopes, and rich soil fertility.

Overall, these studies show that natural enemy regulation depends on specific stand factors, benefiting the performance of enemy species. Further, certain types of factor combinations could predispose stands to insect-induced disturbances. The key findings of my thesis will help to increase knowledge of factors that can regulate or predispose forest stands to insect-induced forest disturbance. These main outcomes should be considered for future forest management planning.

Keywords: defoliation, economic loss, growth loss, insect outbreak, forest stand factors, natural enemy complex, site fertility, stand susceptibility

Blomqvist M (2025) Interactions between forest pest outbreaks and environmental characteristics in boreal forests – implications for forest management. [Metsien hyönteistuhojen ja ympäristötekijöiden väliset vuorovaikutukset boreaalisissa metsissä – suositukset metsänhoitoon]. 53 p. Dissertationes Forestales 363. https://doi.org/10.14214/df.363.

TIIVISTELMÄ

Tuhohyönteisten aiheuttamat häiriöt ovat lisääntyneet boreaalisissa metsissä viime vuosina. Nämä häiriöt johtuvat ensisijaisesti ihmisen aiheuttamasta monimuotoisuuden vähenemisestä, metsien heterogeenisyydestä sekä ilmastonmuutoksen aiheuttamista lämpötilan ja sademäärien muutoksista. Suomessa metsätuhohyönteisten esiintymistiheys on lisääntynyt ja tuhohyönteislajit ovat levinneet yhä pohjoisemmaksi. Lisätietoa tarvitaan, jotta voidaan ymmärtää mitkä tekijät altistavat metsiköt hyönteistuhoille.

Tämän väitöskirjan tavoitteena oli tutkia metsätuholaisten dynamiikkaa tarkastelemalla bioottisten ja abioottisten tekijöiden välisiä vuorovaikutuksia sekä niiden ekologisia ja taloudellisia vaikutuksia. Väitöskirjassa keskityttiin kahteen taloudellisesti merkittävään hyönteistuholaislajiin: pilkkumäntypistiäiseen (*Diprion pini* L.) ja kirjanpainajaan (*Ips typographus* L.). Tavoitteena oli tutkia ympäristötekijöitä, jotka altistavat metsiä hyönteisten aiheuttamille häiriöille sekä eri bioottisten ja abioottisten tekijöiden välisiä vuorovaikutuksia.

Ensimmäisessä tutkimuksessa selvitettiin miten luontaiset viholliset vaikuttavat pilkkumäntypistiäisen kotelokoppakuolemiin pitkittyneen massaesiintymän aikana. Metsän ominaisuudet, erityisesti kasvupaikan niukkaravinteisuus, näyttävät heikentävän luonnollisten vihollisten tehokkuutta. Toisessa tutkimuksessa selvitettiin mitkä puusto- ja maaperä- sekä metsikön topografiaa kuvaavat tekijät selittävät pilkkumäntypistiäisen aiheuttaman männyn (*Pinus sylvestris* L.) neulaskadon voimakkuutta. Vakavimmat tuhot esiintyvät maanpinnanmuodoiltaan tasaisimmilla ja maaperätekijöiltään korkeampaan ravinteikkuuteen viittaavilla kasvupaikoilla. Kolmannessa tutkimuksessa mitattiin pilkkumäntypistiäisen massaesiintymän vaikutukset männyn läpimitan kasvuun ja arvioitiin siihen liittyvät taloudelliset menetykset. Selvisi, että pitkittynyt neulaskato aiheuttaa merkittäviäkin kasvutappioita ja tappiot kasvavat neulaskadon voimistuessa. Lisäksi vakavasta neulaskadosta kärsineet puut eivät toipuneet 10 vuoden tutkimusjakson aikana. Neljäs tutkimus keskittyi ympäristötekijöihin, jotka altistavat kuusikot (*Picea abies* (L.) Karst.) kirjanpainajalle. Suurimmat todennäköisyydet voimakkaille kirjanpainajan aiheuttamille puusto-oireille löytyvät kasvupaikoiltaan ravinteikkailta itään päin avautuvilta ja kohtalaisen jyrkiltä rinteiltä, ohuen maakerroksen tai maaperän korkean hiili/typpi -suhteen omaavilta alueilta.

Metsän eri abioottiset ja bioottiset tekijät säätelevät tuholaisten dynamiikkaa ja lisäävät alttiutta tuhohyönteisten aiheuttamille häiriöille metsässä. Väitöskirjani keskeiset havainnot tulisi ottaa huomioon metsänhoitokäytännöissä, jotta tilanteeseen voidaan sopeutua sekä hillitä hyönteisten aiheuttamien häiriöiden vaikutuksia tulevaisuudessa.

Avainsanat: harsuuntuminen, hyönteistuhot, kasvutappiot, taloudelliset tappiot, metsikön kasvupaikkatekijät, luontaiset viholliset, kasvupaikan ravinteikkuus, metsikön alttius

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This has been a very long journey. In 2010, I had already been collecting data for my PhD thesis, but I did not know that yet. In 2012, I was part of my supervisor's project in Lahti. She told me this would be part of your PhD thesis. I did not believe her, and I was like, 'Well, we will see. I do not know if this is my plan.' Well, it was—forest entomological research.

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II. Kosunen M, Kantola T, Starr M, Blomqvist M, Talvitie M, Lyytikäinen-Saarenmaa P (2016). Influence of soil and topography on defoliation intensity at an extended outbreak of the common pine sawfly (*Diprion pini* L.). iForest - Biogeosciences and Forestry, 10, 164–171. https://doi.org/10.3832/ifor2069-009

III. Blomqvist M, Lyytikäinen-Saarenmaa P, Kosunen M, Kantola T, Holopainen, M (2022). Defoliation-induced growth reduction of *Pinus sylvestris* L. after a prolonged outbreak of *Diprion pini* L.—a case study from eastern Finland. Forests 13, 12 p. https://doi.org/10.3390/f13060839

IV. Blomqvist M, Kosunen M, Starr M, Kantola T, Holopainen M, Lyytikäinen-Saarenmaa T (2018). Modelling the predisposition of Norway spruce to *Ips typographus* L. infestation by means of environmental factors in southern Finland. European Journal of Forest Research 137, 675–691. https://doi.org/10.1007/s10342-018-1133-0

AUTHOR’S CONTRIBUTION

Minna Blomqvist (MB) wrote the summary of the dissertation. MB is the main author of papers **I**, **III**, and IV, where she was responsible for preparing and analyzing the data, statistical methods, and writing the paper. MB also contributed to the study design of paper **IV**, but the study designs and studies included in papers **I**, **II,** and **III** were established before MB started her PhD. MB has participated in the data collection for all papers. In paper **II**, Maiju Kosunen (MK) is the corresponding author, and MB participated in carrying out parts of the fieldwork, assisted in statistical tests, and contributed to the manuscript's writing. Papers **II** and **III** have been a part of MK's thesis. Paper **II** has been added to this dissertation with the permission of co-authors. Detailed statements:

Study **I**: MB wrote the first draft of the manuscript; she is responsible for preparing and analyzing the data with statistical methods. She collected the data in the field and analyzed collected cocoon data from the last study year. Data from earlier years were collected and analyzed in the laboratory before her contributions by Päivi Lyytikäinen-Saarenmaa (PL-S). PL-S designed the study and was responsible for data collection and analysis before 2010. Tuula Kantola (TK), Mervi Talvitie (MT), and MK took part in the data collection. All authors contributed to the manuscript writing.

Study **II**: MK was the principal author of the manuscript and was in response to the data curation and analyses. MB participated in carrying out parts of the fieldwork by measuring tree-wise data, such as tree diameter and height, visually assessed defoliation percentages of trees, assisted in statistical tests, and wrote and revised manuscript drafts. Mike Starr (MS), PL-S, and TK planned and supervised the study and contributed to the writing of the original manuscript.

Study **III**: MB wrote the original draft of the manuscript. She took part in the study design, fieldwork and analyzed the data. TK supervised the analysis and took part in writing the manuscript. MK and Markus Holopainen (MH) wrote and commented on the manuscript. PL-S planned and supervised the study and contributed to writing the original draft of the manuscript.

Study **IV**: MB wrote the original draft of the manuscript. MB did the fieldwork, participated in the study design, and was responsible for the methodology and statistical tests. MK was responsible for soil sampling and analyzing methods and wrote parts of the manuscript. MS supervised the soil-related data and analysis. PL-S and TK planned and supervised the study. All authors contributed to the writing of the original manuscript.

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1 INTRODUCTION

1.1 Insect disturbances and their ecological, economic, and social impact

Forests have increasingly become more susceptible to biotic and abiotic disturbances promoted by a hotter and drier climate (Forzieri et al. 2020; Patacca et al. 2023). For example, storms, drought, insect pest, and pathogen outbreaks have become more frequent, and at the same time, the resilience of the forests to the disturbances has been decreasing (Jaime et al. 2024; Senf et al. 2018). While these disturbances are a natural part of the forest's function, their impact can be severe. The increasing frequency and intensity of insect outbreaks have significantly impacted the forests' ecological, economic, and social values. For example, the European spruce bark beetle, *Ips typographus* L. (Coleoptera: Curculionidae, Scolytinae), caused extreme tree deaths in the 19th century in Europe (Hlásny et al. 2021). In the Czech Republic, it damaged over 30 million m^3 of wood in 2019 (Fernandez-Carrillo et al. 2020) and in Germany, the economic loss due to the species was estimated at 260 million euros in 2018–2019 (Hlásny et al. 2021). Furthermore, large-scale disturbances can significantly impact ecosystem services, such as carbon sequestration, biodiversity, natural resources, and recreational use of forests.

There has also been a remarkable increase in insect disturbances in northern latitudes, and the insect pest outbreaks are still shifting northwards (Klapwijk et al. 2012; Romashkin et al. 2020). Climate warming is predicted to impact high latitudes, such as in northern Europe, which can lead to increasing problems with insect pest outbreaks. For example, *I. typographus* has caused severe damage in Estonia and Sweden (López-Andújar Fustel et al. 2024; Schroeder & Kärvemo 2022). In Finland, the magnitude and frequency of insect outbreaks have also been increasing (Blomqvist et al. 2016; Blomqvist et al. 2018; Neuvonen & Viiri 2017; Junttila et al. 2024). *I. typographus* has become a major threat to Finnish spruce forests in recent years, and the disturbances have multiplied. According to the Finnish Forest Centre, Finland's highest number of forest cuttings due to *I. typographus* was carried out in 2022 (Terhonen & Melin 2023). In addition, National Forest Inventory (NFI) data showed that damage caused by *I. typographus* has increased by over 200 % from 2022 to 2023 (Ylioja & Sutela 2024). Junttila et al. (2024) found that tree mortality, predominantly caused by bark beetles, such as *I. typographus*, has increased tenfold from 2017 to 2023. Defoliating insects have also caused intensifying damage to Finnish forests in recent decades. A large outbreak caused by a common pine sawfly (*Diprion pini* L.) belted through Finland during 1997–2001, influencing over 500 000 ha of forested areas, and in 2022–2023, a widespread outbreak caused by European pine sawfly (*Neodiprion sertifer* Geoff.) was causing remarkable defoliation of pines in different locations (Långström et al. 2001; Lyytikäinen-Saarenmaa & Tomppo 2002; Terhonen & Melin 2023).

Climate change directly and indirectly affects insects' survival, reproduction, dispersal, and ability to induce disturbances (Filazzola et al. 2021). For example, global warming directly affects insect phenology. An indirect effect comes from a change between different species; for example, through host tree defense or affecting the natural enemies (Kolb et al. 2019). Regulation of pest populations is divided into top-down (e.g., predators, parasites, pathogens) or bottom-up (resource limitations) factors (Vidal & Murphy 2018). For example, bark beetle epidemics are often promoted by windstorms or drought and heat periods; thus, the resources could be unlimited. Insects are poikilothermic, and they can have a great magnitude of phenotypic plasticity in the expression of their life history and behavioral traits

(Bentz et al. 2019). Therefore, changes in mean temperatures are expected to have a strong impact on their fitness and development, and they can adapt to changes in their environment relatively quickly (Bentz et al. 2022). For instance, previously univoltine species developing one generation in a year can be transferred to multivoltine due to longer and warmer summer periods (Möller et al. 2017). This can increase the damage caused by the species. Without regulation factors, the population would theoretically grow exponentially (Speight et al. 2008).

In addition to these, various predisposing environmental factors affect population growth. Forestry and soil properties, among others, have been shown to influence the performance of insect pests (Hilszczahski et al. 2006; De Somviele et al. 2007; Zolubas et al. 2009; Blomqvist et al. 2018). For example, soil properties can affect tree vitality, and suboptimal growing habitats can make them more vulnerable to insect pests. For example, a tree's defense mechanism can change during a prolonged drought (Kolb et al. 2019).

1.2 Role of natural enemies in regulating insect populations

Natural enemies, i.e., predators and parasitoids, can effectively regulate the density of pest populations (Hanski & Parviainen 1985; Herz & Heitland 2003). However, interactions between different trophic levels, such as between a prey or a host and its natural enemies, are complex (Jactel et al. 2019; Speight et al. 2008). Climate change can alter the interaction of the prey/host and natural enemies by mismatching their phenology (Damien & Tougeron 2019; Forrest 2016; Möller et al. 2017; Netherer & Schopf 2010; Pureswaran et al. 2015). This can have a massive influence on tropic levels. The effect of the natural enemies is considered delayed compared to the population density of the host organism, driven by multiple factors (Jactel et al. 2019). These factors are, for example, the life cycle of the pest, the life cycle of natural enemies, requirements of habitat, and resources (Bellone et al. 2017; Bellone et al. 2020; Herz & Heitland 2003; Kollberg et al. 2014; Kouki et al. 1998; Nordkvist et al. 2022).

Responses of natural enemies to the increase in pest insects' population size depend also on the pest species' occurrence and population density. Parasitoids are usually specialized to a host and can adapt their life cycle to match the host population (Kaltz & Shykoff 2002). Their impact is typically most pronounced when the host population densities are high or intermediate. Parasitoids, including wasps from the Ichneumonidae (Hymenoptera) and the Chalcidoidea (Hymenoptera) families and flies from the Tachinidae family, are regarded as the major cocoon parasites of the *D. pini* (Viitasaari & Varama 1987; Geri 1988; De Somviele et al. 2007; Blomqvist et al. 2016). For example, parasitoids can be an effective mortality factor of *D. pini* in the cocoon stage (De Somviele et al. 2007).

Predators, usually generalists, possess significant potential for reducing the severity of sawfly outbreaks (Bellone et al. 2020; De Somviele et al. 2007; Hanski & Parviainen 1985). Small mammals, such as shrews (Soricidae) and voles (Arvicolinae), and birds, tits (Paridae) for example, can exert a substantial impact on prey insects when their populations are at endemic levels, due to their dispersal capabilities and capacity to learn (Barbaro & Battisti 2011; Berryman 1986; Berryman et al. 1987; Crawford & Jennings 1989). However, their influence tends to be less pronounced at epidemic levels due to their lower reproductive rates, as noted by Berryman et al. (1987). Additionally, beetles like elaterids (Elateridae) and carabids (Carabidae) also contribute to the destruction of sawfly cocoons, as documented by Hanski and Parviainen (1985).

In addition, the effect of natural enemies on the pest population is related to environmental characteristics and the site's microclimate (Bellone et al., 2020). Stands with higher biodiversity are considered more optimal environments for natural enemies (Bellone et al. 2017; Nordkvist et al. 2023). Such habitats offer diverse food resources for natural enemies; thus, the overall natural enemy complex can be higher (Staab & Schuldt 2020). However, studies with sawflies have also found that sawfly parasitism could be more effective than predation in pure pine forests compared to more heterogeneous forests (Herz & Heitland 2003). For example, cocoon parasitoids of *D. pini* can benefit from the thin humus layer of pine forests because the cocoons are more exposed. On the other hand, fertile sites can hold bigger predator pressure than sites with poor vegetation cover, as denser understory also provides shelter for small mammals (Kollberg et al. 2014).

1.3 Role of environmental factors regulating insect populations

The functioning of forest insect pests is also influenced by different forest stand, soil, and site characteristics (Blomqvist et al. 2016; Blomqvist et al. 2018; De Somviele et al. 2007; Kosunen et al. 2017; Zolubas et al. 2009). These environmental factors are considered density-independent factors. Environmental factors can affect pest insects differently depending on the insect's life history traits. Forest development class, tree density, and tree species composition have varying effects on pest populations depending on the pest (Baier et al. 2002; De Somviele et al, 2007; Mezei et al. 2014). Tree and stand characteristics can directly impact pest insect populations and their performance. For example, *I. typographus* infests rather mature spruce trees than younger trees with thin bark (Netherer & Nopp-Mayr 2005). Host tree resistance and defense compounds also play a crucial role in the regulation of insect population, and environmental characteristics also influence those (Christiansen & Bakke 1988; Ryan et al. 2015).

Topographic features, such as elevation, slope, and aspect, can play a crucial role in influencing insect outbreaks and performance (Kantola et al. 2014; Martin et al. 2013; Niemelä et al. 1987). The impact of elevation on insect populations is predominantly indirect, altering microclimates, affecting foliage chemistry, and influencing the distribution of host species (Hodkinson 2005; Lausch et al. 2011; Netherer & Nopp-Mayr 2005). Topographic features usually influence insects in combination with other environmental features rather than as a single factor. Steep slopes, especially those facing south to west, may induce heat stress in host trees and potentially create more favorable local climates and habitats for both defoliators and bark beetles (Kaiser et al. 2013; Kharuk et al. 2007; Morse & Kulman 1986). Such environments generally contribute to drier and warmer conditions and are more nutrient-deficient than gentle slopes and other aspects. On the contrary, there are different results on how, for example, the aspect affects the presence of insects. Damage caused by a defoliator, Siberian silkmoth (*Dendrolimus superans sibiricus* Tschetw.), has also been observed to be higher on flat areas as opposed to steeper slopes (Kharuk et al. 2007). The preferences can depend, among other things, on the order of insects. For example, sapsucking insects have demonstrated a preference for north-northwest-facing slopes in the Appalachian Mountains (Kantola et al. 2014). The potential for excessive direct solar radiation may limit infestation due to elevated thermal conditions under the bark and dryness of the phloem

(Bartos & Amman 1989). Thus, northeast-facing slopes can also pose a risk for bark beetle infestation (Huo et al. 2024; Jurc et al. 2006).

Soil fertility also has a significant influence on tree growth and vitality, impacting the defense mechanisms of host trees (Baier 1996). Trees growing in areas with greater soil fertility demonstrate enhanced resilience, attributed to increased nutrient abundance and improved access to water resources, in contrast to trees growing in poorer environments. These trees possess the ability to allocate higher amounts of carbon (C) and nutrients toward the production of secondary metabolites, including defense compounds (Raffa et al. 2015). Poor soil fertility, which is related to dry sites, thin soil, and coarse soil texture, has been associated with more severe defoliator performance (Mayfield et al. 2007; Nevalainen et al. 2015). On the other hand, Kosunen et al. (2017) found that D. pini defoliation was more significant in more fertile sites in the study area with limited variability of site types. Growth, performance, and, e.g., immune defense of herbivorous insects is nitrogen-limited (Lee et al. 2008; Lindstedt et al. 2020). Soil nitrogen (N) availability, which has been linked to needle N content and concentration of N in the phloem (Björkman et al. 1991), can benefit insects by boosting their reproduction and performance due to an optimized nutritional status (Goodsman et al. 2012; Lyytikäinen 1994). However, the effects of specific nutrients on tree health and vulnerability to defoliators or bark beetle infestations can be complex and depend on several issues (Baier 1996; Blomqvist et al. 2018; Kosunen et al. 2017).

1.4 Growth and economic losses due to defoliation

Defoliation caused by insects can significantly hamper tree growth since it reduces the photosynthetically important parts of the tree crown, such as leaves or needles. The relationship between defoliation intensity and growth loss can be either linear or non-linear, with the latter occurring especially when growth stabilizes after a certain defoliation threshold (Jacquet et al. 2012). The impact of defoliation on tree growth is influenced by various factors, including needle age, tree age, infestation timing and intensity, consumption period length, and a defoliation history of the stand (Austarå et al. 1987; De Somviele et al. 2004).

The carbon reserves in needles and relative needle nitrogen content may be altered by defoliation. When defoliation occurs, the carbon sink diminishes, which affects the relative N content (Jacquet et al. 2014; Lyytikäinen-Saarenmaa 1999). Biochemical changes in remaining needles further influence tree growth responses. Long-term defoliation can alter tree height and radial growth, as well as needle biomass or shoot length (Lyytikäinen-Saarenmaa & Tomppo 2002; Nordkvist et al. 2020). Radial growth is more affected by defoliation intensity compared to shoot length (Nordkvist et al. 2020). For instance, radial growth decreased significantly due to needle consumption by *D. pini*: defoliation intensities of 50% and 90% diminished radial growth by 86% and 94%, respectively (Lyytikäinen-Saarenmaa and Tomppo 2002).

Generally, defoliation caused by insects is not noted as severe as tree mortality by insects, for example, by the forest owners. However, the influence of defoliation can be remarkable, leading to a significant impact on economic returns through growth losses. For example, the economic impact of outbreaks of *N. sertifer* in Norway ranged from 321 NOK to 11,757 NOK (32 to 1188 € reverted to corresponding monetary value in 2022) per hectare in a nine-year period, depending on stand age and site index class (Austarå et al. 1987). The outbreak of *D. pini* caused an economic loss of about 288 € per hectare after a one-year outbreak in western Finland (Lyytikäinen-Saarenmaa and Tomppo 2002). The cumulative economic impact of *D. pini* over a nine-year recovery period, involving growth losses and tree mortality, ranged from 365 € to 1,218 € per hectare, depending on defoliation intensity (Lyytikäinen-Saarenmaa et al. 2006).

1.5 Aims and objectives of the dissertation

As mentioned before, the damage caused by insect pests can be remarkable, and many aspects affect insect population dynamics and the vulnerability of forests to insect outbreaks. The main aim of the dissertation was to study how different biotic and abiotic regulating factors influence the level of disturbances caused by pest insects. More specifically, my thesis analyzes how environmental characteristics impact natural enemies' control over the pest population, the intensity of damage, and factors that make trees more vulnerable to insect-induced damage. Additionally, it examines the consequences of long-term insect disturbance on tree growth and economic losses. My study species were *D. pini* and *I. typographus*. The main study objectives were:

i) To examine the long-term impact of natural enemies on *D. pini* mortality during the cocoon stage and to investigate the relationship between stand characteristics and the influence of natural enemies on *D. pini* cocoon mortality (study I).
ii) To investigate the most important soil and topographic factors that explain the defoliation intensity caused by *D. pini* (study II).
iii) To estimate the quantitative effect of prolonged outbreak of *D. pini* on the growth and economic losses of Scots pine (*Pinus sylvestris* L.)
iv) To identify the environmental characteristics that predisposed stands to *I. typographus* infestation.

2 MATERIALS AND METHODS

2.1 Study areas and sampling plots

Studies **I, II,** and **III** were carried out in Palokangas, Ilomantsi, in eastern Finland (62°52'N, 30°56'E) from 2002 to 2010 (Figure 1, Table 1). The research area (34.5 square kilometers) is mainly dry pine forests (*Pinus sylvestris* L.) consisting mainly of *Vaccinium* and *Calluna* forest types (according to Cajander's forest type classification, 1926) with a thin humus layer. The population of *D. pini* has been at an epidemic level, and the damage has been chronic since 1999, slowly showing a decreasing trend towards 2010. Forest stand development classes of the study area are relatively heterogeneous and fragmented due to forest management practices (Olsson et al. 2016). Eleven circular plots (r = 8.5–13 m) were established in 2002 (**I**, **II** & **III**) and 17 in 2007 (**II & III**). The sampling plots were chosen subjectively to cover a wide range of defoliation levels. The center of each study plot was located with a Trimble Pro XH GPS device (Trimble Navigation Ltd., Sunnyvale, CA, USA). All trees were located by measuring azimuths and distances to the plot centers. Tree-wise measurements were carried out during the establishment years and in 2010. Diameter-at-breast-height (dbh) of all trees over a dbh threshold of 5.6 cm was measured. Mean height and age were estimated to be seven to eight trees per plot covering various diameter classes. In addition, basal area (m2/ha) and stand tree density (n/ha) were calculated.

Study **IV** was carried out in the urban forest in the city of Lahti, in southern Finland (60°59′N, 25°39′E) during the years 2012–2014 (Figure 1, Table 1). Summer 2010 was warm and stormy in Finland (Neuvonen & Viiri 2017), which led to the outbreak of *I. typographus* in 2011 in the study area. Forest stands are dominated by mature and over-mature Norway spruce, growing mainly on fertile *Myrtillus*, *Myrtillus-Oxalis,* and *Oxalis-Maianthemum* site types. Stand age, Norway spruce dominance, and root rot infestations (*Heterobasidon* spp.) have been promoting the outbreak vulnerability. The Salpausselkä I terminal moraine crosses the study area (Rainio et al. 1995; Tschudi et al. 2000), which gives soils their characteristic form. The tops of terminal moraine are formed of till and bedrock with or without shallow topsoil, while flanking slopes are formed of sorted silt and clay deposits. The forests of the study area are in intensive recreational use by the citizens. For that reason, only selective forest thinning had been carried out in the area.

Circular sampling plots (r = 10) were established in 2012 and 2013. The study plots (n=48) were established for monitoring the infestation level of *I. typographus* (in 2012) or as reference data for remote sensing of the infestation (in 2013) (Näsi et al. 2015, 2018). In 2014, all the plots were reassessed for **IV**. Field inventories included basic tree- and stand-level measurements: dbh of all trees on the plot, tree height of median tree on the plot and from every seventh tree, stand-wise tree density (n/ha), basal area (m^2/ha), proportion of spruce trees (%) and proportion of dead spruce trees (%). All trees were positioned by measuring azimuths and distances to the plot centers. The center of each plot was located with a Trimble GPS device (Trimble Navigation Ltd., Sunnyvale, CA, USA).

The average diameter at breast height (dbh) of the spruce trees (n=461) across all plots was 31.7 cm, accompanied by an average height of 24.9 m. Within the plots, the average basal area of the spruce trees was 28.6 m^2/ha. Tree density per plot ranged from 159 to 955 trees/ha. The mean proportion of Norway spruce trees in the study plots was 78% (varying from 31 to 100% across individual plots). Additionally, the average proportion of dead spruces per plot was 13.5%, with variability from 0 to 100%.

Figure 1. Location of the study areas: Ilomantsi (**I**-**III**) and Lahti (**IV**) in eastern and southern Finland, respectively. Google Maps provided the background map.

Table 1. Summary of information and measured variables from study areas and sampling plots. Site type classification: CT =*Calluna* type, VT = *Vaccinium* type, MT = *Myrtillus* type, OMT = *Oxalis* type, OMaT = *Oxalis-acetosella* type or other herb-rich type. C = carbon, N = nitrogen.

	Ilomantsi	**Lahti**
Studies of the thesis	I, II, III	IV
Location (WGS84)	62°52’ N, 30°56’ E	60°59’ N, 25°39’ E
Study years	2002–2010	2012–2014
Size of the study area	34,5 km^2	135 km^2
Mean annual temperature and annual precipitation sum	2–3 C^o and 650–700 mm	4–5 C^o and 600–650 mm
Forest site types	VT, CT	MT, OMT, OMaT
Dominant tree species	Scots pine *Pinus sylvestris*	Norway spruce *Picea abies*
The mean basal area on study plots	17.5	29
Stand development category	Advanced thinning and mature	Mature and over-mature
Description of forests	Commercial forests fragmented due to forest management operations	Urban forest areas, fragmented due to urbanization
Dominant forest pest insect	Common pine sawfly *Diprion pini*	European spruce bark beetle *Ips typographus*
Studied environmental factors	Elevation, slope, forest floor vegetation, soil factors (C, N, pH), site type, tree factors	Elevation, slope, aspect, soil factors (C, N, soil stoniness, soil type), site type, tree factors
Explanatory variable	Cocoon mortality, defoliation, tree growth	Infestation level

2.2 Target species

2.2.1 *Diprion pini*

D. pini is a native species in Finnish forests with eruptive population dynamics (Geri 1988; De Somviele et al. 2007). The species mainly occur in even-aged mature Scots pine stands growing on dry soils. *D. pini* belongs to foliage-feeders by defoliating needles of pines.

During the last two decades, *D. pini* has become a more severe pest in Finland (De Somviele et al. 2007; Blomqvist et al. 2016; Blomqvist et al. 2018). In Palokangas, Ilomantsi, the population of *D. pini* remained at the epidemic phase for over ten years, contradicting the typical gradation pattern. However, the population density decreased slowly towards a postgradition phase (Blomqvist et al. 2016). Still, in 2016, the defoliation caused by *D. pini* was recognizable in Palokangas.

In Finland, adults of *D. pini* hatch from cocoons between May and July in several waves, and the life cycle of the species is univoltine (Viitasaari and Varama 1987; Geri 1988). In Central Europe, *D. pini* can be bivoltine. Adults lay eggs on needles. Larvae hatch after 3–4 weeks and consume needles from older and current years during late summer (Geri 1998). With the bivoltine cycle, the first generation develops in the tree crown, and the second generation spins the cocoon for overwintering in the litter or humus layer at the end of the summer or early fall. The cocoon stage is immobile and exposed to natural enemies. Therefore, the mortality during the cocoon stage is expected to be an important factor that regulates population sizes (Herz & Heitland 2003; Blomqvist et al. 2016). Compared to the other harmful pine sawfly species, *Neodiprion sertifer* (Geoffr.), in Finland, *D. pini* can cause more extreme defoliation and even tree deaths by consuming all needle year-classes from pines.

2.2.2 Ips typographus

I. typographus is economically the most harmful forest pest species in Finland and Europe, yet it belongs to Finnish native species. The species has eruptive population dynamics, which are controlled and driven, e.g., by seasonal temperatures, drought, the number of windthrows, intraspecific competition and natural enemies (Wermelinger & Seifert 1999; Wermelinger 2004; Biedermann et al. 2019). *I. typographus* attack mainly weakened mature and over-mature Norway spruces (Zolubas et al. 2009). Storms can simultaneously offer considerable amounts of optimal breeding material as windthrown trees, leading to populations developing to epidemic levels (Eriksson et al. 2005). Furthermore, if the weather and environmental conditions are optimal, the population density can increase rapidly, spreading to vital trees (Kärvemo et al. 2014; Lausch et al. 2011).

In spring, the adults swarm when the air temperature is above app. 18 ºC, thus the optimum flight temperature is above 22 ºC (Wermelinger 2004; Öhrn et al. 2014). When the optimal air temperature is reached, *I. typographus* attacks spruce trees for reproduction. The species uses aggregation pheromones to colonize a spruce (Schlyter et al. 1987). Females lay eggs under the bark along the maternal gallery, and the immature stage of the beetle starts to consume the phloem. Larval feeding disturbs the nutrition and water flows of the tree, resulting in discoloration and defoliation of the crown and, eventually, death of the tree. The beetle is a vector of blue stain fungus, which accelerates tree death (Paljakka et al. 2020). *I. typographus* hibernates in the bark or the litter next to the tree trunk (Weslien 1992). In Finland, the species hibernates mainly in the soil (Annila 1969).

In 2010, storms, exceptionally high temperatures, and drought led to a wider reproduction of *I. typographus* in Finland (Neuvonen & Viiri 2017). This was seen as cumulated tree deaths during the following years until the population densities decreased. For example, in southern Finland, the population peaked in 2011–2012, according to the tree deaths in the Lahti area (Blomqvist et al. 2018). In 2012, the population was still high, according to the pheromone trap data, but decreased in 2013 (Blomqvist et al. unpublished data). The year 2010 was also the first year when individuals from the second generation were found in Finland (Neuvonen

& Viiri 2017). In addition, living individuals from the presumably second generation were found in October 2012 in the Lahti study area (Blomqvist, personal observation). The second generation of young adults probably cannot survive the winter in Finland. In the early 2020s, populations have risen again (Junttila et al. 2024). Increasing disturbances have occurred during the study period of six years between 2017–2023.

2.3 Assessment of damage caused by the species

2.3.1 Defoliation by D. pini

D. pini larvae cause varying degrees of defoliation depending on the number of larvae (population level) by eating needles (Figure 2). When eating continues for several years, that can cause tree dieback. The defoliation caused by *D. pini* was visually assessed during May and early June between 2002 and 2010, excluding 2003. The assessment was done in spring before the elongation of new needles; thus, the situation represented the status from the previous year. Tree-wise defoliation was classified using a precision of 10%. Defoliation was assessed from the upper two-thirds of the crown, and 0% of defoliation described a healthy tree, and 100% described a tree without any needles, i.e., a dead tree. The mean defoliation of a plot (in studies **I & II**) was calculated without trees from the suppressed canopy layer because those can be influenced by other stress factors. In study **II**, plot-wise defoliation was classified as ‘mild’ (<20%, n= 21) or ‘moderate to severe’ (>20%, n=7). This threshold was used because defoliation intensity over 20% has been studied to affect tree growth substantially (Lyytikäinen-Saarenmaa and Tomppo 2002).

In study **III**, we classified trees based on defoliation (n=197) into four groups: low (0–10%), mild (20–40%), moderate (50–60%) and high (70–100%) based on defoliation intensity in 2007 (see study III).

2.3.2 Estimating growth and economic losses

We took tree ring samples (n=184) in 2010 to study the effect of defoliation intensity on radial growth using an increment borer. The increment core samples were taken at breast height from the median trees of plots and every third tree across the plots. The samples were prepared in the laboratory for measurements, glued to wooden chutes, and then polished with sandpaper. Annual radial growths were measured inwards from the bark to the core using a stereomicroscope attached with a linear scale encoder (ENC-150) (Accurite, Jamestown, NY, USA). Data were saved using the MeasureJ2X program (VoorTech Consulting, NH, USA).

The dissimilarities in the radial growths between the four defoliation classes were investigated by developing an index. The index was calculated using annual radial growths. For the index, the annual radial growth was divided by the average growth of the tree from the period before the initial sawfly outbreak (1994–1998; 1998 was the last healthy year) and then multiplied by 100. The annual radial growth of each defoliation class was computed as the mean of the tree-wise indices. Those annual radial growths were compared to the index baseline, which was computed as a mean of radial growths from the years 1994–1998.

Figure 2. Larvae of *D. pini* (up left), a landscape with heavily defoliated and dead Scots pines surrounded by final cutting (down left), and Scots pines with different levels of defoliation in a study plot (right). Photos: Päivi Lyytikäinen-Saarenmaa and Minna Blomqvist.

Tree heights were modeled using Näslund's equation for tree height (Näslund 1937) because we did not measure heights from all the trees with defoliation information. To estimate growth losses, we modeled each sample tree volume for three different years: 1989, 1998, and 2009. Tree volumes were modeled based on dbh measurements from the increment cores and tree heights using a variable regression model for Scots pine volume (Laasasenaho 1982). The average yearly increase in volume for individual trees was determined. We then compared the mean annual volume growth, categorized by tree defoliation classes, over an 11-year interval encompassing the gradation and post-gradation phases of *D. pini* (1999–2009) with the average growth rate during a 10-year baseline period preceding the outbreak (1989–1998). To derive estimates per hectare, we multiplied these tree volumes by their corresponding mean stem density.

2.3.3 Classification of symptoms caused by I. typographus and the infestation index class

A tree-wise visible symptom classification was developed to investigate the attack level of *I. typographus* (Figure 3). In 2014, the symptoms were assessed from each spruce tree on the study plots during the late growing season, i.e., in August. This classification described the health status of the tree. The assessed symptoms were visible on the tree trunk and in the crown: holes (entrance and exit) in the lowest 2 m from the trunk, condition of the bark (healthy, chipping/minor damage or part of the bark already pealed), the number of resin flows, crown color, and defoliation (Figure 3). The crown symptoms were evaluated at a distance corresponding to approximate tree height from different directions. The holes, bark condition, and resin flow were classified into three classes, and the defoliation and crown color were classified into four classes based on the severity of the symptom. The crown color was classified as green as a healthy tree, yellow as a moderate attack, red as a severe attack, and gray as a dead tree (Figure 4). For more details on classification, see (Blomqvist et al. 2018).

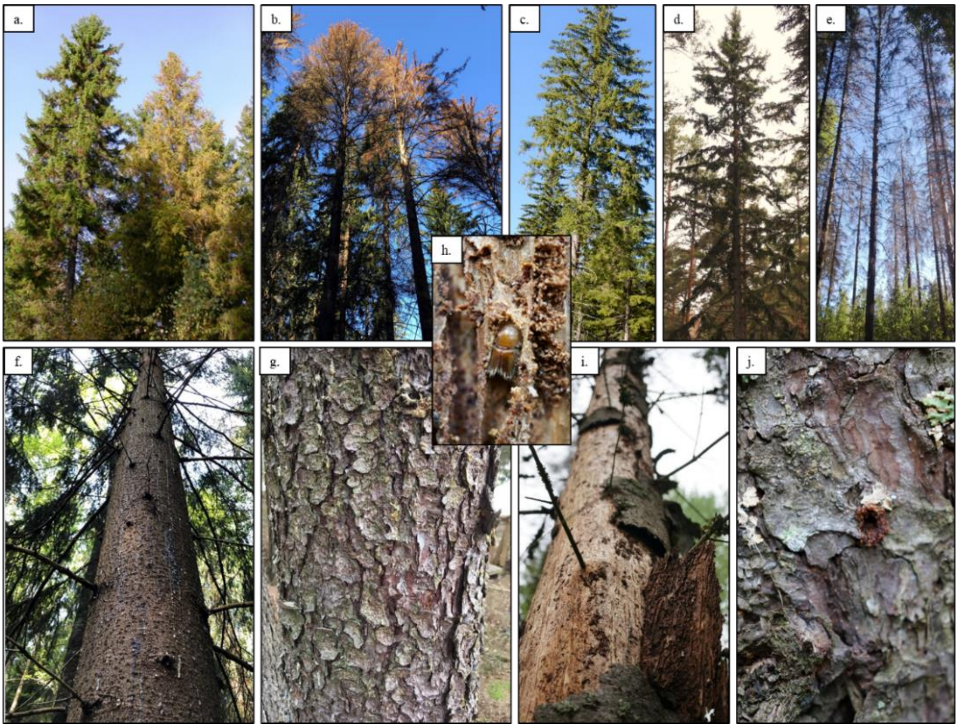

Figure 3. Examples of classification of visible symptoms caused by *I. typographus.* Spruces with green and yellowish crowns (a), spruces with reddish crowns (b), a spruce tree with defoliation of 26–50% (c), a spruce tree with defoliation of 51–75% (d), dead spruces with defoliation of 75–100% (e), a tree trunk with > 30 resin spots (f), minor bark damage (g), a young adult of I. typographus in mother gallery (h), major bark damage with I. typographus feeding galleries (i) and a boring hole with resin and sawdust in it (j). Photos: Päivi Lyytikäinen-Saarenmaa and Minna Blomqvist.

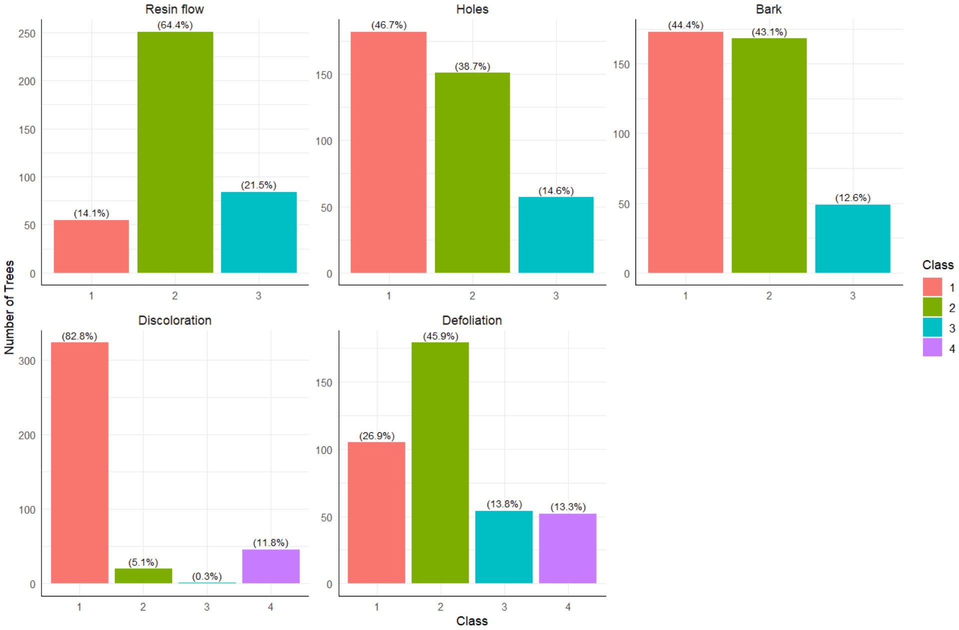

Figure 4. Classification of symptoms caused by *I. typographus* into three categories for trunk symptoms and four categories for crown symptoms, along with the number (y-axis) and percentage (in parentheses) of spruces classified under each category in the Lahti study area in 2014. The classification criteria are as follows: Resin flow: 1 = 0 spots, 2 = 1–30 spots, 3 = >30 spots; Holes: 1 = No infestation (0), 2 = Mild infestation (1–30), 3 = Severe infestation (>30); Bark: 1 = Healthy, 2 = Minor damage, 3 = Major damage; Discoloration: 1 = Healthy/green, 2 = Yellowish, 3 = Reddish, 4 = Dead/grey; Defoliation: 1 = 0–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%.

We summed the classes of symptoms of resin flow, crown color, and defoliation to get a tree-wise bark beetle attack level score. For example, if all three symptoms were in the healthy class (1), the attack level score was three, and if the symptoms were in the most severe class (resin flow = 3, crown color = 4, and defoliation = 4), the attack level score was 11. Hence, the attack level score ranged between three and 11.

Trees smaller than dbh of 20 cm were excluded from the classification due to other stress factors, such as light competition. In addition, the bark condition and the holes were excluded from the attack level score due to difficulties in observing holes, thick bark, and other factors (see more justification from study **IV**). We classified the attack level scores into *infestation index classes* based on the severity of the infestation: *no infestation* (attack level score 3–4, n=116), *moderate infestation* (attack level score 5–7, n=223), and *severe infestation* (attack level score 8–11, n=51). The *infestation index class* describes the severity of *I. typographus* infestation. The *moderate infestation class* was included in the infestation index class because I observed that not all the infested spruces die right after beetle infestation. In addition, it was important to detect early and mild infestation for control efforts.

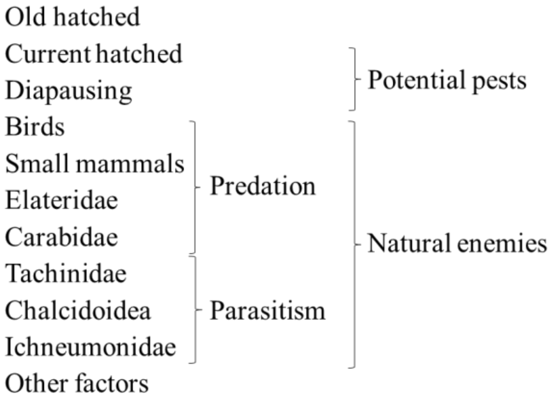

Figure 5. Classification of D. pini cocoons. Current hatched and diapausing individuals form the group of potential pests, and predators and parasitoids are natural enemies.

2.4 Assessment of natural enemies

The impact of natural enemies on defoliation caused by *D. pini* was studied between 2005–2010 in Palokangas, Ilomantsi, by collecting cocoon samples from the litter and humus layer (**I**). The assessment was carried out in May before the hatching of *D. pini*. Consequently, the samples corresponded to the situation of the previous fall. Frames of 0.5 m x 0.5 m were placed next to every fifth tree trunk. The place of the frames moved clockwise every year to the next tree trunk. The number of the transferred cocoons in and out from our study plots was assumed to be even.

Classification of cocoons was made into groups by different mortality factors. Identification of mortality factors was classified from cocoons visually into insect families Ichneumonidae (wasps), Chalcidoidea (wasps), and Tachinidae (flies) (together parasitism) and small mammals, birds, and the insect families Carabidae (ground beetles) and Elateridae (click beetles) (Hertz 1933; Viitasaari & Varama 1987) (together predation) (Fig 5). Parasitoids and predators together represent the natural enemy complex. In addition, diapausing individuals (unbroken cocoons), both current and old hatched, were identified. The current hatched and diapausing individuals were combined and called '*potential pests'* because those can affect defoliation intensity via their offspring. We used relative proportions of cocoons in each class.

2.5 Environmental factors

*2.5.1 Topography (**II** and **IV**)*

A digital elevation model (DEM) with a resolution of 1 m was used to extract elevation above sea level (m a.s.l.) in studies **II** and **IV**. DEM was acquired from a high pulse density LiDAR (Light Detection and Ranging) data set for study **II**. For study **IV**, the DEM was downloaded from the open data source of the National Land Survey of Finland (NLS Topographic Database 11/2016). Elevation for each plot was calculated as a mean of pixel values within study plots. Plot-wise slope (**II**, **IV**) and aspect (**IV**) were derived from the elevation data utilizing ArcMap® (ArcGis ESRI, Redlands, CA). The slope was calculated as a mean pixel of each plot. In study **IV,** the mean slope (%) of the plots was classified into five classes: very gently sloping, gently sloping, sloping, strongly sloping, and moderately steep sloping. The aspect was calculated as the majority of pixels (the value that occurred most often in pixels within the zone) within each study plot, and it was classified into eight classes by cardinal and semi-cardinal directions (see the classification from study **IV**).

*2.5.2 Forest floor, soil sampling, and laboratory analysis **(I, II, & IV)***

In study **I,** forest floor vegetation assessment was done within a 1m x 1m frame in each plot in 2010. The assessment was done with a precision of 5% from five points: from the center of a plot and 5.3m from the center towards each cardinal direction. The coverages (%) of blueberry (*Vaccinium myrtillus* L.), lingonberry (*Vaccinium vitis-idea* L.), lichen (*Lichenes*), moss (*Bryobionta)*, heather (*Calluna vulgaris* L.), and other minor plant species were estimated. The depth of the humus layer was measured from vegetation frames.

From Palokangas (**II**), soil samples were collected from the center of a plot, and each cardinal direction was at a distance of 5.3 m from the center of a plot in 2010. The soil samples were taken with a steel auger (diameter 58mm) from a depth of 0.5 m or until the bedrock. The surface litter layer (Ol) was removed, and the thickness of the humus layer (Of+Oh), (Ah+)E, B, and C-horizons was measured with a precision of 0.1 cm. The layers were separated into plastic bags and kept at 5 °C until laboratory analysis. Only the humus layer and B-horizon samples were analyzed because the other layers were not always adequate. The five samples from a plot were combined. Dried humus layer samples were milled and filtered through a 2mm sieve. A 25 ml subsamples of B-horizon samples were filtered through a 2 mm sieve. The weight of >2 mm and <2mm fractions were recorded. The particle size distribution of <2 mm B-horizon sample was determined utilizing laser fractionation (Coulter LS230®, Beckman Coulter Inc., Brea, CA, USA). We utilized the following texture classification: clay (< 0.002 mm), fine silt (0.002–0.006 mm), medium silt (0.006–0.02 mm), coarse silt (0.02–0.06 mm), fine sand (0.06–0.2 mm), medium sand (0.2–0.6 mm) and coarse sand (0.6–2 mm). A VarioMax CN device (Elementar Analysensysteme GmbH, Hanau, Germany) was used to determine total organic C and N contents from the humus layer and <2 mm B-horizon samples. The soil C/N ratio was calculated from the contents of C and N. To determine soil pH, we used a glass electrode for milled humus layer samples and 0.1 M calcium chloride solution (1:2).

In Lahti (**IV**), soil cores were collected with a steel auger (diameter 35 mm, length 30 cm) from the center of each study plot and at a four-meter distance from the center towards the south and north in 2014. First, green vegetation and the litter layer (Ol) were removed from the samples, then the thickness of the remaining organic surface layer (Of+Oh) was recorded at a precision of 0.1cm. In most samples (65%), the organic material and mineral soil were mixed in the topsoil. Thus, only a minor of the samples had a clear humus layer. The mineral soil was divided into layers of 0–5 cm, 5–10 cm, and 10–20 cm. The separated layers were placed into plastic bags and stored at –18°C until laboratory analysis. The samples were dried and then weighed. The mineral soil samples were filtered through a 2 mm sieve and the fractions > 2 mm and < 2 mm were weighted. The humus layer samples were milled. We used only the samples from the humus layer and 0–5 cm mineral soil because of the fine roots in those layers. Fine roots are important for tree nutrient acquisition (Helmisaari et al. 2007). A VarioMax CN device (Elementar Analysensysteme GmbH, Hanau, Germany) was used to determine total organic C and N contents from the humus layer and <2 mm B-horizon samples. We used ArcGIS for a digital map available from the Hakku open database maintained by the Geological Survey of Finland (https://hakku.gtk.fi/) to derive the type and texture of quaternary superficial deposit in which the soil had formed. The soil texture classes for sorted deposits in the study area were classified as follows: clay (<0.002 mm), fine silt (0.002–0.006 mm), medium silt (0.006–0.02 mm), coarse silt (0.02–0.06 mm) and sand (0.06–2 mm) (Haavisto-Hyvärinen & Kutvonen 2007). In addition, the following two classes of glacial moraine deposits, sandy till and shallow till (soil depth <1 m over the bedrock, subsequently referred to as shallow till), were found.

The soil stone content (**IV**) was estimated using a rod penetration method by Viro (1951). A steel rod (d =10 mm) was pushed into the soil to measure the depth of the soil layer at a precision of 1 cm. The stone contents were measured from each study plot from the plot center and at 1 m intervals outwards along the cardinal directions until 10 m (the radius of a plot). A total of 44 stone content measurements were taken per plot. A mean soil penetration for each plot was used for the equation by Tamminen and Starr (1994) to transform the values into volumetric stone content.

2.6 Statistical analyses

This chapter describes the main statistical analyses of the studies. Before the tests mentioned below, other statistical tests were utilized, e.g., to find out data distribution and significant differences between variables and/or classes; nevertheless, those are not described here. A detailed description of the method can be found in the original articles. In all statistical tests, p-values less than 0.05 were considered statistically significant. R statistical software (The R Project 2014) was employed in all the statistical analyses.

2.6.1 Random Forest (I)

A non-parametric Random Forest (RF) algorithm (Breiman 2001) was utilized in investigating the importance of environmental characteristics and defoliation for explaining plot-wise parasitism and predation of *D. pini* cocoons (**I**). The RF method was chosen due to the small sample size. It can be utilized to study a nonlinear phenomenon that does not meet the normal distribution criteria. RF applies the nearest neighbor (NN) search and is suitable for variable selection in addition to classification (Cutler et al. 2007). For more details, see, e.g. Falkowski et al. (2010) and Crookston and Finley (2012). In investigating the importance of natural enemies to *D. pini*, we classified the study plots using 10% intervals as a threshold of parasitism (five classes) and predation (three classes). Parasitism and predation were separately used as dependent variables, and environmental characteristics (see from **I**) were used as predictors. In the modeling, we used data from 2010. The estimation was repeated 2000 times, i.e., the number of regression trees was set as 2000 in both studies. Parameter k was set (numbers of NNs) as three, which have been used to gain robust results (e.g., Kantola et al. 2013).

*2.6.2 Logistic and linear regressions (**II** & **III**)*

To assess the ability of topographical and soil variables to predict a plot's affiliation with the mild (<20 % defoliation, n=21) and moderate to severe defoliation (>20 % defoliation, n=7) classes in study **II**, logistic regression was employed. Logistic regression was chosen because of the non-parametric characteristics of the data and its usability when predicted variables are regarded as dichotomous. To maintain model simplicity and prevent overfitting (limited to three predictors), variables strongly correlated with each other were not simultaneously included. The logistic regression analysis was carried out using various combinations of predictor variables.

In study **III**, a simple linear regression was used to study the relationship between defoliation and radial growth in the following year. This relationship was studied separately for each study year. The regression models were evaluated based only on p-values (**II**, **III**) or, in addition to those, overall classification accuracies and Cohen's Kappa-values.

*2.6.3 Cumulative link model (**IV**)*

The cumulative link model (CLM), which is also known as an ordered logit model or a proportional odds model (Christensen 2015b), was utilized to estimate the probability of infestation caused by *I. typographus*. CLM can be used when data is multinominal, and the dependent variable is ordered. We used tree-wise *I. typographus infestation index class* as the ordered dependent variable (no infestation < moderate infestation < severe infestation) and the tree and environmental characteristics (see from **IV**) as predictor variables. Subgroups (tree variables, topography, and soil factors) of variables were used to find the significant predictors to the predictor variable selection for the final models. Box plots were utilized to show the significant differences between the infestation index classes. Model convergences and parameter accuracies were studied, and variable dropping off from the model was tested to find how this affects model accuracy. The maximum absolute gradient and the condition number of the Hessian matrix were studied to evaluate the convergence of the models, and the accuracy of parameter estimates was controlled (Christensen 2015a). AIC (Akaike information criterion), ΔAICs, and Akaike weights were used to test the relative goodness of the final models (Akaike 1987; Burnham et al. 2011).

3 RESULTS AND DISCUSSION

3.1 The effect of natural enemies on pest population (I)

3.1.1 The overall impact of the natural enemy complex on D. pini cocoon mortality

The natural enemy complex can regulate pest insect populations (Herz & Heitland 2003; Alalouni et al. 2013; Blomqvist et al. 2016). The impact of natural enemies, having a functional response, may intensify more rapidly during the population gradation phase, then accelerate before the peak of gradation. During our six-year study period from 2005 to 2010 in Palokangas, we observed consistently high cocoon mortality rates, with the impact of the natural enemy complex remaining relatively stable. Overall, cocoon mortality increased by approximately 20% when comparing 2001 and 2010. The impact of the natural enemy complex was highest in 2010 (79.9%). The peak proportion of newly hatched and diapausing nymph (=potential pests) was in 2005 (23.5%) (Figure 6). De Somviele et al. (2007) found 40.4% overall cocoon mortality two years after the initial *D. pini* outbreak in 2001 in the same Palokangas area (Figure 6). After four years, we observed a 63% higher overall cocoon mortality (65.7%). Our results, while not directly comparable to those of De Somviele et al. (2007), suggest potential saturation of natural enemies in the Palokangas area. The outbreak of *D. pini* began in 1999, with high population densities persisting for several years before our 2005 cocoon sampling. Unusually, the population density remained high for over a decade by 2010, contrary to the typical two to four-year duration of *D. pini* outbreaks in Finland (Viitasaari & Varama 1987). The effect of pathogens or other mortality factors was not separated, so their effect remains unclear.

The results suggest that populations of *D. pini* cannot be entirely controlled by natural enemies despite over a decade-long outbreak and a slowly increasing proportion of the natural enemy complex. At the epidemic level of a pest population, natural enemies alone may not be able to control the outbreak, as abiotic factors and habitat-induced variations in the feeding preferences and behavior of natural enemies can play a critical role (Kollberg et al. 2014). The population density of eruptive forest pests may stay at endemic densities but erupt rapidly into epidemic level if environmental factors or weather anomalies are predisposing forests to population growth at a high level (Berryman et al. 1987). This might have been the case in the early outbreak phase of *D. pini* in Finland (De Somviele et al. 2007).

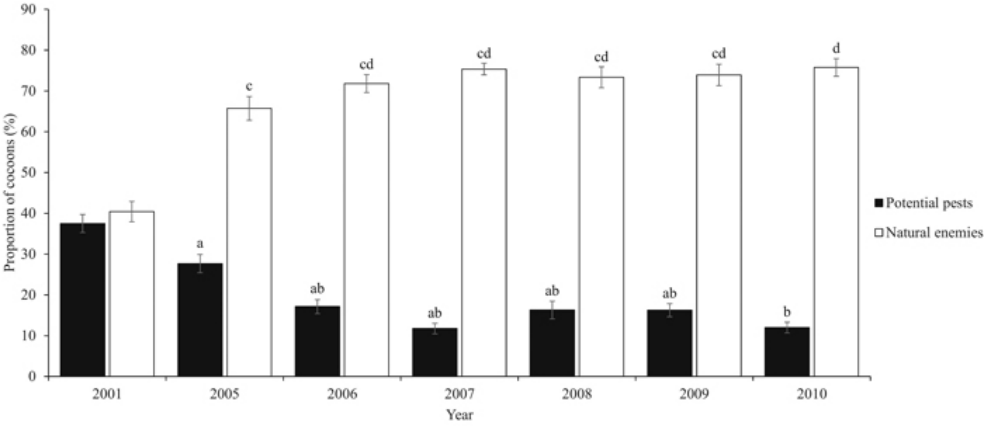

Figure 6. Proportion (%, ±SE) of the potential pests (2001 hatched and intact cocoons and 2005–2010 new hatched and diapausing cocoons) and natural enemy complex (parasitoids and predators). Our study period covers the years 2005–2010. Data from 2001 are from De Somviele et al. (2007). Letters indicate statistical differences ($p < 0.05$) separately for both series (year 2001 not included in statistical tests). Figure adapted from study I (Blomqvist et al. 2016).

3.1.2 The impact of parasitism

Parasitism is considered a crucial factor regulating the sawfly populations. The effect of parasitism is typically density-dependent and delayed, as confirmed in our study. In Palokangas, we revealed a relatively high rate of cocoon parasitism, with a slight amplifying over time. The effect of parasitism at the endemic phase of *D. pini* is approximately 20 % (De Somviele et al. 2007; Herz & Heitland 2003; Simsek & Kondur 2017). The Ichneumonidae family was one of the main natural enemy factors affecting cocoon mortality (**I**: Figure 2). It was also the major parasitoid group with an increasing proportion of cocoons destroyed by Ichneumonidae during the study period (from 19.9% to 31.6%). Already in 2005, Ichneumonidae species represented over half of the cocoon parasitism. The families of Tachinidae and Chalcidoidea do not have that significant role in cocoon parasitism. The effects of those were rather stable and low. For example, the cocoon morality of Tachinidae has been studied to be more effective during other life stages of sawflies (Knerer 1993) or only in a minor role (Simsek & Kondur 2017). Examples of *D. pini* cocoon parasitoids are species such as *Pleolophus basizonus* (Grav.) and *Exenterus oriolus* (Htg.) from the Ichneumonidae family (Simsek & Kondur 2017). In our study, the species composition was not studied.

Parasitoid populations can thrive and peak during prolonged outbreak periods (Berryman 1986; Pschorn-Walcher 1987). The rate of cocoon parasitism is influenced by the parasitoid complex's ability to synchronize with the host's population dynamics and environmental factors like stand characteristics (Kidd & Jervis 1997; Turchin et al. 2003). The composition of the parasitoid complex may change during the pest population’s gradation phases (Alalouni et al. 2013; Eveleigh et al. 2007).

3.1.3 The impact of predation

Usually, cocoon predation of *D. pini* does not reach the same level as parasitism (Herz & Heitland, 2003). Pure pine forests do not necessarily provide potential alternative food resources or shelters for predators. Vegetation in our study sites was less diverse, however, we found that cocoon predation was similar to cocoon parasitism. Cocoon predation included small mammals (voles, mice, shrews), birds, Elateridae and Carabidae. The mean cocoon mortality by small mammals was approximately 19.6%, and the mean cocoon mortality by birds was 14.7%. Therefore, small mammals and birds covered the highest proportion of predation events, whereas mortality due to invertebrate predators (Elateridae and Carabidae beetles) was lower (2%).

Previous studies have shown that in pine forests, sawfly cocoon predation by small mammals exceeds 12.6% at the beginning of the gradation phase, 48.9% at the gradation peak, and 30.0% at the postgradation phase (Orbtel et al. 1978, Hanski & Parviainen 1985, De Somviele et al. 2007). Our study identified the peak of cocoon predation in 2006 (28.7%) (**I**: Figure 2), which correlated with the pine sawfly cocoon density peak in 2005. This suggests that a higher abundance of cocoons in 2005 may have helped small mammals to reproduce more effectively and increased the predation pressure on cocoons in 2006. However, our data collection period does not cover the start of the outbreak and levels of mammal predation in earlier years. This difference between our and other studies may indicate that the effect of small mammals had already been at a higher level before our study started. Bird predation had the lowest impact in 2005 (2.8%) and its peak in 2006 (25%). In the study by De Somviele et al. (2007), the predation caused by birds was only 2.9% at the beginning of pest population gradation. The increase in bird predation in our study could be due to the behavior of birds; birds can return to habitats that can provide optimal food resources (Morris et al. 1958). The number of parasitized cocoons was low during high bird predation, which suggests that birds might also utilize cocoons with parasitoids.

To study the effect of natural enemies in the most natural circumstances possible for *D. pini* pupation into litter and soil, we intentionally avoided altering the environment with experimental planting, marking cocoons, or using plastic underlays or gauzes. Cocoons, whether in diapause or as empty because of predation or parasitism, can persist for many years, potentially causing cumulative effects in our study plots. To mitigate this, we employed relative proportions instead of densities or absolute numbers of cocoons. However, uncertainties arose from the assumed balanced input and output of predated cocoons in the study plots. The duration of cocoons in detritus until decomposition remains unresolved, posing methodological challenges that future studies should address to improve accuracy and reliability.

3.2 The impact of environmental characteristics on insect disturbance (I, II & IV)

3.2.1 The impact of stand characteristics on the natural enemies

Generally, natural enemies are more likely to be present in forests with high biodiversity, such as in forests with a high diversity of species and a high volume of dead wood (Klapwijk & Björkman 2018; Langellotto & Denno 2004). There is also evidence that the increase in dead wood does not correlate strictly with natural enemy pressure, which may also depend on other factors (Nordkvist et al., 2022). Thus, tree and stand characteristics are also likely to affect the species numbers and abundance of potential predators and parasitoids. In study **I**, which investigated the importance of environmental predictors for cocoon mortality of *D. pini* by natural enemies, we found that the most important factors explaining parasitism were basal area (m^2/ha) and coverages (%) of lingonberry and lichen. With these predictors, we achieved a high overall classification accuracy of 82% with a Kappa value of 0.694 (p=0.002) by utilizing random forest analysis. Furthermore, basal area (m^2/ha), plot-wise defoliation (%), and lichen coverage (%) were the most significant predictors of predators (i.e., small mammals, invertebrate predators, and birds). The accuracy of this classification was 82%, with a Kappa value of 0.741 (P=0.000). The correlation between the proportion of predated cocoons with the mean defoliation intensity and with lingonberry coverage was negative, -0.73 and -0.74, respectively.

Basal area and stem density impact the stand's microclimate, which again can impact the occurrence of parasitoids and predators, as these organisms are sensitive to temperature and humidity (Hance et al., 2007). Different plant species found on the forest floor serve as indicators of the nutrient status and hydrology of a site (Salemaa et al. 2008). For instance, higher coverage of lichen and lingonberry suggests lower soil fertility and reduced diversity in forest floor vegetation. In Palokangas, the understory vegetation is rather poor, with site types dominated by lingonberry. Habitats with higher vegetation diversity may offer alternative food resources and shelters to natural enemies (Hanski & Parviainen 1985; Herz & Heitland 2003; Langellotto & Denno 2004). For example, Herz and Heitland (2003) found that the parasitism rate remains under 24 % in poor soils in pine forests. In study **I**, we found that parasitism was over 30 % in prolonged outbreaks. The habitat could also affect generalist and specialist natural enemies differently (Bellone et al. 2020). For instance, generalist enemies may succeed in habitats with higher biodiversity, causing higher enemy pressure. In pure pine forests, this may be limited. However, according to Kouki et al. (1998) the prey species' population cycle has a more substantial impact on predation risk rather than the fertility of the forest or its stand characteristics. For example, the local vole population cycle could have affected the predation rate. Furthermore, Nordkvist et al. (2022) found that an increase in biodiversity did not affect the predation rate. They stated that an increase in dead wood can still be a key factor for pest control, but the influence may increase only with certain factors.

3.2.2 Effect of stand factors on sawfly defoliation

Topography features can have a significant role in predisposing forest sites to insect disturbances. Elevation, slope, and aspect have been studied to impact disturbances caused by defoliators (Kharuk et al. 2007; Niemelä et al. 1987). However, research on the effect of topography on insect outbreaks has focused on mountainous terrain; even smaller variations in key topographic characteristics may also enhance insect outbreak severity. In study **II**, we found that slope showed a negative correlation with defoliation caused by the sawfly. Elevation did not significantly affect the defoliation severity caused by *D. pini*. The defoliation was higher in sites with less steep slopes. Notably, the study area was rather flat, having an elevation from 165 to 200 m a.s.l. and a mean slope of a plot from 1 to 14°. Other studies have found that elevation could influence the defoliator's performance (Kantola et al. 2014; Niemelä et al. 1987; Paritsis et al. 2011). For example, *N. sertifer* has been shown to cause more severe defoliation in higher elevations than in lower areas (Niemelä et al. 1987). They found that the results could be due to an increase in the nutritional quality of the needles for the larvae as the nitrogen content of the needles increased with increasing elevation.

Accordingly, the mean defoliation was significantly more severe in more fertile areas. More specifically, the greater fertility was associated with high N content of the humus layer and lower C/N ratios of the humus layer but also high contents of fine soil textures (<0.02 mm = medium silt and finer) in B-horizon (Spearman's correlation coefficients (ρ) = 0.45, -0.68 and 0.44, respectively, with p-values <0.05). We also found that defoliation was more pronounced with thicker soil in the (Ah+)E-horizon layer (**II**, table 4, Fig 2). However, the thickness of the humus layer did not correlate between defoliation classes. Among the soil factors, the thickness of the (Ah+)E-horizon layer was the only one that correlated with topography – negatively with slope (Spearman's correlation coefficients (ρ) = -0.49). This means that the thickness of the (Ah+)E-horizon increases with a decreasing slope. Soil pH was relatively low, with a plot mean pH of 4.03, which means higher acidity. A low pH value decreases the availability of most nutrients, which can lead to limited tree vitality.

Interestingly, we also found that the thickness of the (Ah+)E-horizon showed the most accurate classification in predicting the likelihood of a plot experiencing *moderate to severe* (>20%) defoliation. With that predictor variable, we gained an accuracy of 88% with a Kappa-value of 0.65 (model 1). Other environmental variable combinations that predicted *moderate to severe* defoliation classes were: the C/N ratio and pH of the humus layer, with an accuracy of 86% and Kappa-value of 0.58 (model 2), C/N ratio of B-horizon and slope, with accuracy of 85% and Kappa-value of 0.57 (model 3), and N concentration and pH of humus layer, with accuracy of 82% and Kappa-value of 0.5 (model 4) (**II**, Table 5).

The relationship between soil nitrogen content and insect damage is complex and context-dependent. High nitrogen levels may promote the performance of certain herbivores, but they can also affect plant defenses that deter or affect insect performance negatively. For example, nitrogen is a limiting nutrient for herbivorous insects (Lee et al. 2008; Mattson 1980) and therefore, likely to be an important part of the sawflies' diet (Lyytikäinen 1994). Furthermore, nitrogen also impacts the secondary chemistry of tree (e.g. Björkman et al. 1991). An input of N increases the palatability of the needles but, at the same time, changes the C/N ratio (Li et al., 2016). It has been assumed that sawfly defoliation is more severe in sites with relatively poor soil fertility (i.e., low N, high C/N ratio). For example, Larsson and Tenow (1984) found that an outbreak of *N. sertifer* was more common at sites without N fertilization. *D. pini* outbreaks have also been found to be more severe in sites with low fertility (Nevalainen et al. 2015). The range in fertility was relatively limited (mostly CT site type) in our study sites, which could have been affected by these partly contradictory results of fertility interactions and defoliation severity. Notably, the outbreak was prolonged and continued over a long period, which could have affected the results. Insect herbivores can also alter soil factors, for example, by adding nutrients through frass (Frost & Hunter 2007; Kaukonen et al. 2013). However, we did find a strong correlation between the nitrogen content of the humus layer and fine soil particle proportion in B-horizon, which indicates rather long-term nutrient status of the site than being a consequence of *D. pini* defoliation.

3.2.3 The impact of environmental characteristics on the bark beetle damage

Generally, it is assumed that *I. typographus* infests large trees more than smaller ones (e.g., Zolubas et al. 2009). Sproull et al. (2015) and Jakuš et al. (2011) found that smaller trees were more likely to be infested. Differences between the results could be due to the outbreak phase of *I. typographus* or the thickness of the spruce bark in large tree trunks. For example, differences can be found in whether the infested tree is a windfall or standing tree. In the endemic phase of *I. typographus*, tree size may be more important than other factors, unlike in the epidemic phase when population pressure diminishes the significance of host selection based on size, i.e., age (Hlásny et al. 2021; Junttila et al. 2024). Junttila et al. (2024) found that tree mortality, presumably by *I. typographus,* in younger trees had increased from latent phase to outbreak. Between the *I. typographus infestation index classes*, tree density and proportion of spruces were not significantly different (**IV**: Figure 2). Tree dbh in the *severe infestation class* was lower compared to the *no infestation class*. However, this could be because the diameter of the largest trees was over 60 cm within the study plots; the bark of that large tree is not optimal for *I. typographus* reproduction. Varying results have been shown in terms of tree size and infestations.

The tree species composition did not clearly affect the *I. typographus* infestation in our study. However, the tree species composition was more mixed in the *no infestation* and *moderate infestation classes*. Birch and aspen were found in the study area as admixture tree species. However, other studies have found (Hilszczanski et al. 2006; Huo et al. 2024; Kärvemo et al. 2016) conflicting results about the effects of mixed trees on *I. typographus*. It is generally thought that multiple tree species composition reduces the risk of *I. typographus*, for example by creating a more pronounced generalist predation pressure (Kozhoridze et al. 2024), but Huo et al. (2024) found that the deciduous trees exposed spruces to *I. typographus*. Presumably, this is because they used a pheromone attractant, which has resulted in greater pressure on individuals in the area and forced those in the spruces within the stand. Studies, such as ours, have often been carried out in areas where the share of spruce trees has already been significant, thus providing the bark beetle a favorable environment for breeding.

The variations of the plot elevations were 86 and 151 m a.s.l, and the slope was 2.6 and 44.5%. The *severe infestation class* significantly differed from other classes in terms of aspect. Sandy moraine deposit (n=21) was the main soil texture among the plots, but there were also plots with shallow till (n=10), sandy soil (n=6), and finer textured soil (n=6). Soil texture in the *severe infestation index class* significantly differed from other classes (p=0.000). The plots displayed varying soil volumetric stone content ranging from 0.5% to 63.5%. Humus layer thickness varied significantly (p=0.015) between *moderate* and *severe infestation index classes* and ranged from 0.1 to 13.3 cm based on soil samples. Mineral soil C/N ratios varied between 13.7 and 21.4%.

In CLM, *model 1,* with aspect, site type, and slope, showed that *severe infestation class* was most likely to occur on eastern aspects with moderately steep slopes and OMT or OMaT site types (Figure 7). In steeper slopes, the cumulative probability for *moderate infestation* was also relatively high on south-facing aspects. Otherwise, the probability for *severe infestation* was relatively low in such aspects. Plots with a southern aspect, very gently slope, and MT site type had the lowest probability for *I. typographus* infestation. *Model 2,* with aspect, site type, and soil texture, indicated that the sites most vulnerable to severe infestation were those with an eastern aspect, OMaT site type, and shallow till soil texture (Figure 8). In southwest-facing slopes, the probability of *severe infestation* was very low, but the probability of *moderate infestation* was relatively high. *Severe infestation* was less than 0.1 for most other sites, with a slight increase in *moderate* and *severe infestation* for shallow soils.

We also studied how the topsoil C/N ratio acts when it is applied to the model with other important environmental factors (*Model 3* AIC=711.8, ΔAIC=18.77) despite there being no significant differences between the three infestation index classes (**IV**: Table 4) and with the aspect, site type, and mineral soil C/N ratio implied that a higher mineral soil C/N ratio increased the probability of *severe infestation* (**IV**: Figure 5). The maximum probability was gained in the east-facing sites with OMaT site type. The lowest probability for *severe infestation* was found in plots with south-facing aspects and MT site type. However, with the same input, the probability of *moderate infestation* increased with a higher C/N ratio. Our results with the increasing C/N ratio seem to benefit bark beetles. This was a contradiction to assumptions that high soil C/N ratios indicate low soil N availability, leading to lower soil fertility (Stevenson and Cole 1999) and, thus, probably, lower reproduction of bark beetles (Goodsman et al. 2012). This difference may be due to the combined effects of the aspect. Low soil C/N ratios indicate higher soil N availability, leading to greater soil fertility. Bark beetles can benefit from this due to the optimal nutritional value of the phloem. In addition, soil C/N ratio influences tree c-based defense compounds (Raffa et al. 2015). Since there was no significant difference in soil C and N concentrations or the C/N ratio (**IV**: Figure 2), interpreting the relationship between these variables and infestation remains speculative.

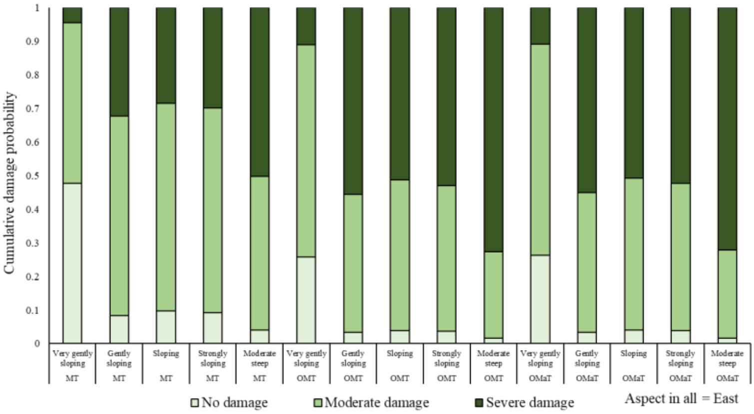

Figure 7. Cumulative infestation probabilities are based on model 1, with explanatory factors as aspect class + slope + site type and aspect class set to east (67.5°–112.5°). Order from left to right of site types reflects its relative fertility (from less fertile to more fertile; MT = mesic, relatively fertile, OMT = herb-rich, and OMaT = fertile groves) and slope from gently to steeper sloping sites. Figure adapted from study IV (Blomqvist et al. 2018).

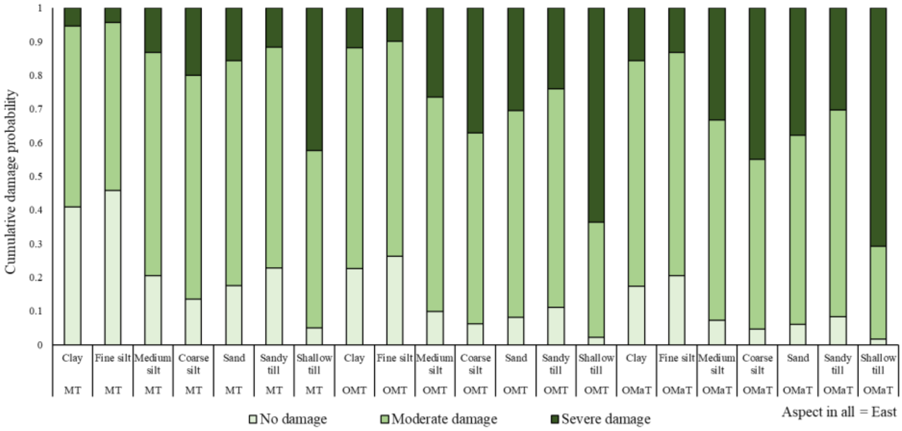

Figure 8. According to *model 2*, cumulative infestation probabilities with explanatory factors as aspect class + site type + soil type for slopes having east aspect (67.5°–112.5). Order from left to right of site types reflects its relative fertility (from less fertile to more fertile; MT = mesic, relatively fertile, OMT = herb-rich, and OMaT = fertile grove) and soil texture class from finer to coarser soil. Figure adapted from study **IV** (Blomqvist et al. 2018).

When comparing the three models mentioned, we found that *model 1* was the most accurate (AIC weight=0.999). After all, *models 2* and *3* were found to be relatively poorly supported in the pair-wise comparison of all three models (IV: Table 6). However, they were all significant, and the convergence criteria were fulfilled (**IV**: Table 5).

Overall, the results showed that the severity of the infestation could be explained by the environmental factors studied. Combining the most important variables, we gained high cumulative probabilities for different infestation levels. Over 70% of the *moderately* or *severely infested* trees were in eastern aspects, and almost 80% on shallow till. The results were promising and showed that the sites with severe infestation are the most vulnerable sites for *I. typographus*. Aspect and site type were given high probabilities in CLM modeling when one of them was included in the model; thus, those were included in all model variations. Our results showed that more fertile site types were most predisposed to *severe infestation*. Other studies from Finland found that tree mortality or forest management operations due to *I. typographus* occurred most in forests with mesic heath (correspond to OMT, *Oxalis-Myrtillus* -type) or herb-rich heath (correspond to MT, *Myrtillus-type*) forests (Junttila et al. 2024, Pulgarin et al. 2024). In addition, Pulgarin et al. (2024) found that stands with *I. typographus* damage were growing on semi-coarse or coarse heath forest soils.

However, it has been shown that host tree preferences may vary with the outbreak phase (Mezei et al., 2014). More severe infestations have also been found in thin soils (Worrel 1983). Thinner soils have limited water availability, resulting in more stressed trees. Water stress diminishes trees' resistance towards bark beetles by reducing defense compounds, such as resin (Kolb et al. 2019). Eastern and northeastern aspects were more prone to severe infestations. In contrast, southern and southwestern aspects have lower probabilities of severe infestation. However, they can experience moderate infestations, particularly when combined with specific site characteristics like OMaT site types on shallow till. One explanation could be that beetles may avoid slopes with excessive insolation, such as some southern and southwestern aspects, where temperatures can become lethal for them (Powell 1967). The species may also prefer more shady sites with more Norway spruce (Christiansen & Bakke 1988), such as those that might be in our study area. Higher pheromone trap catches on eastern and northeastern aspects are also found (Jurc et al., 2006). In Sweden, Huo et al. (2024) found similar results to ours; the north and east aspects were more infested than other aspects. Furthermore, the slope was an important variable in stand predisposition for *I. typographus*. Slope steepness also influences microclimate but has a less pronounced effect on infestation intensity than aspect. Although steeper slopes had a higher probability of severe infestation, this factor did not significantly vary between infestation levels in our study.

There may have been factors that affected the results. We did not know the initial damage timing nor what has been the infestation pattern before our study period because the outbreak had already begun a few years before; thus, we do not know the exact pattern and predisposition of stands. Infestations and the severity of *I. typographus* damage can be affected by the outbreak phase. Thus, different factors can be important depending on whether it is a latent, pre-outbreak, outbreak, or post-outbreak phase (Mezei et al. 2014; Wermelinger 2004). There have also been tree cuttings from the study plots that may have had an influence first on the trees that have been removed but also on the plot-wise results; the number of stumps was not considered. Thus, we do not know the exact situation before infestations. It also could have been realistic to classify the trees only into two categories. However, we could have missed information about the spruce trees that suffered, not only the infestation itself but also other stressors that can lead to future infestations of *I. typographus*.

3.3 Defoliation caused by D. pini and growth and economic losses (I, II, III)

3.3.1 Defoliation as a symptom of D. pini outbreak

In all three studies concerning *D. pini*, we utilized defoliation of the pine trees from the study plots to describe the population level of the sawfly. In **I**, we used plot-wise mean defoliation. In **II**, defoliation was classified as *mild* and *moderate to severe,* and in **III** *low*, *mild*, *moderate* and *high*. In **II**, mean defoliation in the *mild* defoliation class was 10% (n=21), and in the *moderate to severe* defoliation class, 54% (n=7) (**II**: Table 1). Defoliation varied considerably between the plots in **I** (Figure 9). Seven of eleven plots recovered shortly after the initial outbreak to the level before the outbreak. However, the outbreak continued in four plots and peaked in 2004 (assessed in May 2005, as seen in Figure 9).

While defoliation reduces the important photosynthetic parts of trees, it is a visible symptom that can be used to assess the overall health of a tree (Jacquet et al. 2012). By classifying the health of the tree or the occurrence of insects, it is possible to determine the intensity of defoliation on a tree-by-tree basis. The severity and timing of defoliation depend on the feeding period of the insect. For example, the *D. pini* feeds on later summer and consumes all needle age classes, causing significant damage at outbreak densities. Although extended outbreaks can lead to tree death, this is still uncommon (Långström et al. 2001). In Palokangas, tree deaths were rare, but they were found especially in study plots near clear-cutting areas. This suggests that other stressors could have impacted tree health. The sawfly-

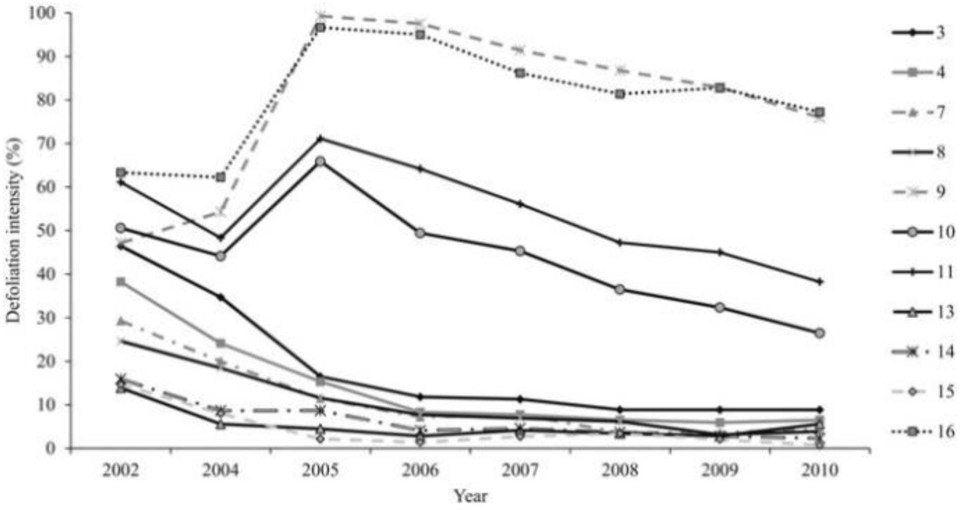

Figure 9. The mean defoliation intensity of 11 sampling plots from study **I** (figure adopted from Blomqvist et al. 2016).

induced defoliation changed over time, indicating that the population of sawflies fluctuated or changed spatially.

The assessment of defoliation into classes with ten percentage intervals could be challenging. However, the assessment was based on an imaginary health tree growing in such an area. Experts calibrated their eyes to match, and at least two sides of the tree assessed every individual tree.

3.3.2 Growth and economic losses

Tree-ring analysis was used to investigate the growth and economic losses during the outbreak of *D. pini*. In **III**, we found that radial growth was influenced by the previous season's defoliation almost every study year (Figure 10, **III**: Table 2), indicating that tree growth decreased when defoliation intensity increased. The annual growth indices significantly differed between at least two defoliation classes almost every study year. The growth indices of low and high defoliation classes were significantly different.

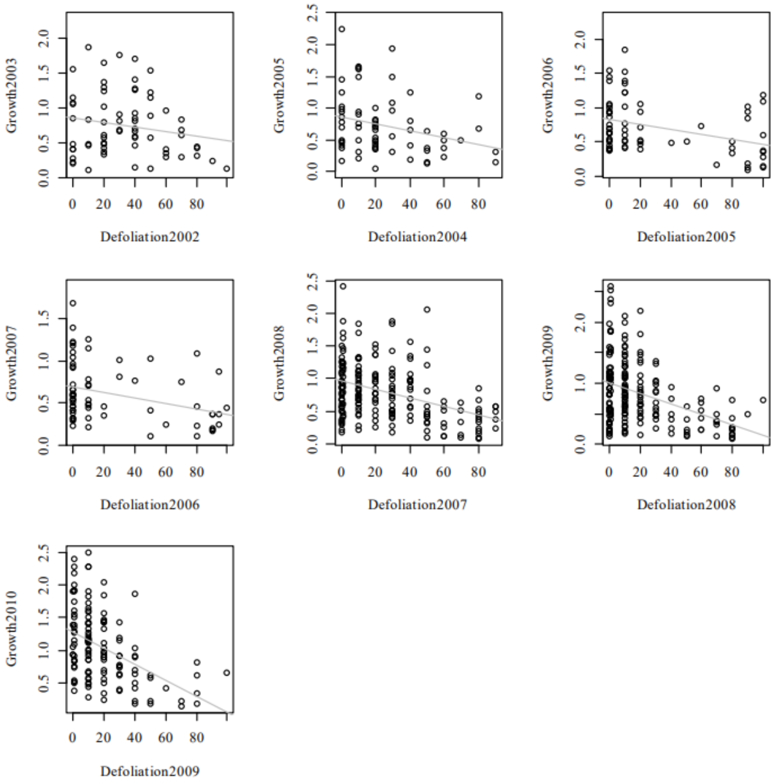

Figure 10. The relationships between radial growth (n+1, mm) and defoliation (n, %) of the study trees (black circles) in scatter plots. Gray lines represent regression lines (figure adopted from Blomqvist et al. 2022 Supplementary materials).

Growth reductions were observed across the mild, moderate, and high defoliation classes (**III**: Table 3). Trees categorized in the healthiest class experienced a slightly increased volume compared to the baseline period of 1989–1998. However, the other three defoliation classes experienced losses of 4.2%, 20.8 and 40.4%, and the cumulative economic impact of defoliation for the 11-year outbreak was estimated at 51 €, 272 €, and 734 € per hectare for the mild, moderate, and high defoliation classes, respectively.

We observed how different levels of defoliation affected the growth of *P. sylvestris* trees. Low defoliation showed minor changes in growth, while mild and moderate defoliation led to a typical V-shaped growth pattern (Långström et al. 2001), with mild defoliation, almost fully recovered by the end of the study. However, trees with moderate to high defoliation did not fully recover during the study period. Complete recovery from severe defoliation may take up to a decade due to various factors such as declined carbohydrate reserves (Lyytikäinen-Saarenmaa et al. 2006). This was observable in Palokangas too.

Several factors contributed to the impact of insect outbreaks on tree growth and economic losses. First, prolonged outbreaks causing severe defoliation can result in missing annual growth rings, making the detection challenging (Lyytikäinen-Saarenmaa et al. 2006). In addition, economic loss estimation could be hindered by a lack of data on tree mortality and forest management expenses. The financial consequences of cumulative defoliation for the whole outbreak and the whole study area (34.5 km^2, (Kantola et al. 2013), even with the mild defoliation, could be 178 500 € for the 11-year outbreak. This does not include all forest management operations carried out due to the outbreak: sanitation felling and forest regeneration. Also, *D. pini* spread to the surrounding sampling stands from the clear-cut area. If the overall effects on the area (10,000 ha, Kantola et al. 2013) where *D. pini* has caused needle loss during the outbreak are estimated, we are discussing considerable totals.

The subsequent attacks by pine shoot beetles (*Tomicus* sp.) might have reduced tree growth further by cutting off shoots and affecting tree water balance. In Palokangas, some areas had suffered their influence, intensifying the effect of D. pini; thus, these species attacked especially trees with severe defoliation. In addition, growth calculations were based on a ten-year reference period before the initial outbreak, assuming stability in tree functions. Fluctuations in defoliation from year to year introduced potential errors.

Cumulative defoliation as an explanatory factor could have been an option for investigating the effect of defoliation on tree growth. However, it can be hard to interpret due to the possible high sum that is not unambiguous. Therefore, these broader classes could be more straightforward to understand. We investigated the tree-wise variation between the years and excluded trees with considerable variation within defoliation during the study period.

It would be interesting to study the overall interplay between defoliation level, natural enemies, tree growth, and stand factors from studies **I-III** in future studies. It has been noted that climatic factors affect *D. pini* performance more than many other biotic and abiotic factors (Hentschel et al. 2018)Thus, it would be feasible to add climatic variables to study the mutual effects of these factors. We should also research how different forest management practices, such as continuous cover forestry, rotation length, and stand development class composition, can influence intensity and dispersal.

3.4 Implications for forest management

In Finland, we have not yet experienced large outbreaks caused by insect pests as much as in Central Europe and Southern Sweden. However, we are shifting along a similar trajectory, and there is potential for intensive outbreaks in the future in Finland (Venäläinen et al. 2020). More extensive forest disturbances have been avoided in Finland because the cooler climate has been a limiting factor (Aalto & Venäläinen 2021). Forests in Finland have traditionally been managed by doing one or two thinning with a clear-cutting at the end of the rotation period. Forest hygiene with monocultures and marginal dead wood has been a part of forestry. Previously, such forest management was also assumed to limit insect disturbances. With the current forest management practices and the existing forest structure, it may not be possible to avoid widespread disturbances in the future. Intensive forest management has disadvantages in forest resilience towards insect-induced disturbances. For example, it is known that low biodiversity directly affects natural enemies, reducing their number, especially the number of specialists, affecting the regulation of the insect population.

The methods used to prevent the spread of insect pests are currently sanitation felling and salvage logging (Weslien et al. 2024). Sanitation logging minimizes bark beetle spread from infested trees, and salvage logging is operated to save timber value (Stadelmann et al. 2013; Pietzsch et al. 2021). The latter usually means clear-cutting. It can be an effective solution for dealing with bark beetles in commercial forests to ensure income (Kulakowski 2016). Implementing the management operations at the right time in important; for example, felling during the wintertime does not produce the desired result with bark beetles (Weslien et al. 2024). It has been studied that winter felling diminishes the potential natural enemy complex more than cutting the bark beetle population (Weslien et al. 2024). However, salvage logging can also increase the presence of pests, such as sawflies, by driving hatching insects to forest edge areas and seedling stands, which was the situation in Palokangas.

Specific forest stand and landscape characteristics and management strategies could reduce the risk of insect-induced disturbances (Jactel et al. 2009; Marini et al. 2022). Now, it seems the solution to mitigate insect damage would be to make forests more resilient and resistant to large-scale insect damage. A diverse range of tree species in the forest can minimize financial losses caused by disturbances to monocultures. To mitigate the *D. pini* outbreaks, the heterogeneity of the forest should be increased. This could be implemented by increasing the diversity of tree species (especially adding more deciduous trees), diversity in age structure, and stand characteristics (Marini et al. 2022). All above also increases the resources for natural enemies (Nordkvist et al. 2022). Mainly the same factors help forests to achieve better resilience to mitigate bark beetle outbreaks. In addition, a clear decrease in the planting of Norway spruce but also a shortening of the rotation period of spruce-dominated forests (i.e., reducing resources for *I. typographus*) is crucial for preventing large-scale outbreaks (López-Andújar Fustel et al. 2024).

Furthermore, the effectiveness of the Forest Damages Prevention Act (20.12.2013/1087) should be frequently and openly evaluated, and stricter legislation, such as in Sweden, may need to be considered in the most vulnerable areas. In most parts of Sweden, forest owners are allowed to leave under $5m^3$/ha of recently damaged coniferous wood in the forest, and in some parts, the amount is only $3m^3$/ha of recently dead wood in areas with high *I. typographus* populations. In Finland, the amount is 10 m^3/ha. Nevertheless, there is a need to understand and emphasize the possible trade-offs between strict legislation or selected forest management practices and nature conservation or biodiversity (Filazzola et al. 2021; Thom & Seidl 2016). The negative effects of large-scale insect disturbances have been studied to be primarily negative on different ecosystem services but mainly positive on biodiversity, but not all cases are straightforward (Thom & Seidl 2016). For example, extending the rotation period would be a solution to maintaining carbon sinks, but it could also create optimal breeding material for wood-boring insects. Furthermore, the possible presence of root rot of spruce (*Heterobasidion parviporum*) would further weaken the condition of trees in continuous cover forestry, exposing them to bark beetles.

Consequently, site-specific, and detailed forest management, including integrated pest management (IPM) and continuous use of modern tools like satellite imagery or drones to detect initial disturbances in time (e.g., Näsi et al. 2018 Junttila et al. 2024 López-Andújar Fustel et al. 2024) is essential for proactive risk management in forestry. To minimize large-scale insect disturbances in the future, we need a national strategy that includes cooperation between different actors, open communication, consistent policy, and shared operating methods. By considering these facts, we can prepare for and minimize future insect damage.

4 CONCLUSIONS

Changes in the population and outbreak vulnerability of insect pests are promoted or limited by changes in climate, such as increased periods of drought. In addition to the climate, very important driving factors are the forest stand and tree factors, the regulation of natural enemies, and human-caused changes in the forest, i.e., forest management methods. Studying the interactions between these topics is important to understand what kind of habitats are susceptible to insect pests.

My dissertation's results show that ecological and environmental characteristics influence the magnitude of disturbances caused by pest insects. We found that during six years of high sawfly population density, the influence of natural enemies on the cocoon stage was stabilized. The site fertility in the study area was relatively low, which probably affected the presence of natural enemies and their interaction within natural enemy groups and between pest/host species. The disturbance was severe and prolonged, especially in some stands; nevertheless, the natural enemy complex was relatively strong, decreasing the proportion of current hatched sawflies. The environment was relatively harsh in those stands, and some trees were growing in a patch surrounded by clearcuts. Defoliation yielded up to 40 % growth losses in the hotspot areas, leading to apparent economic losses. Although our study plots generally exhibited poor fertility and minimal topographical variation, we observed that *D. pini* defoliation of *P. sylvestris* trees was more severe on the more fertile and flatter sites than on the less fertile and steeper ones. The findings highlight that soil and terrain conditions significantly influence pine sawfly population dynamics and disturbance caused by the sawfly.

Lastly, we developed an infestation index to classify Norway spruces based on infestation intensity using crown and trunk symptoms. Using cumulative link modeling, we analyzed the predisposition of sites to *I. typographus* infestations in mature urban forests of southern Finland. We propose that factors affecting soil moisture and fertility, such as slope and soil texture, play a significant role in the risk of *I. typographus* attacks and tree resistance. Topographic features that moderate microclimatic conditions also influence bark beetle attraction. *Severe infestation* was associated with eastern aspects, moderately steep slopes, the most fertile site types, and shallow soil.

The dissertation dealt with two different insects that are classified as forest pests because they play a significant role in forestry in Finnish forests. Understanding the interplay between environmental factors, forest management practices, and pest dynamics is crucial for mitigating the negative impacts of insect-induced damage on forest ecosystems and their ecological and economic values. It is important to get more knowledge about the factors affecting forest insect pest performance, their interaction with host trees, and their association with other environmental factors and natural enemies to understand these population dynamics better. Furthermore, there should be an increasing understanding of the big picture dealing with large-scale insect disturbances and trade-offs with biodiversity.

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