

# The effect of Heterobasidion root rot on *Ips typographus* infestation risk on Norway spruce

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Faculty of Agriculture an	nd Forestry Depar	ry Department of Forest Sciences			
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Title					
The effect of Heterobasidion root rot on Ips typographus infestation risk on Norway spruce					
Subject					
Forest Ecology and Man	agement				
Level	Date – Month and	Number of pages			
Master's Thesis	year	62			
	January 2024				
Abstract					

Norway spruce (*Picea abies*) is one of the most economically important tree species in northern and central Europe. Root rot caused by *Heterobasidion annosum* s.l. and European spruce bark beetle (*Ips typographus*) are major disturbance agents of Norway spruce, and likely to have even greater impact on spruce-dominated forests as climate warms. This thesis investigated the direct interaction between Heterobasidion root rot and *I. typographus*. The aim was to examine if presence of root rot and the stress it poses to a tree increases the risk for subsequent bark beetle attack.

442 Norway spruce trees from nine different stands were measured and included in this study. Before the final felling, symptoms caused by *I. typographus* were evaluated from each tree based on visual assessments of crown and stem conditions. After the final felling, the sample plots were relocated from the clearcut areas, and the stumps of the sampled trees were re-assessed for Heterobasidion root rot. Exploratory analysis and binomial Generalized Linear Mixed Model (GLMM) were used to analyze relationships between different explanatory variables and their affect to *I. typographus* infestation.

The best predictors for *I. typographus* infestation were incidence of root rot and to a lesser extent, decreased 5-year diameter growth and larger diameter at breast height. 75% of root rot infected trees were also infested with *I. typographus*, and the amount of root rot was considerably higher within dead and severely infested trees compared to alive and moderately infested trees. Results suggest that root rot is one of the significant factors making trees susceptible to *I. typographus* infestation, especially when the population density of bark beetles is low and stable. Thus, protecting trees from root rot infection may help to protect trees from *I. typographus* infestation as well.

# Keywords

Heterobasidion root rot, Ips typographus, European spruce bark beetle, Norway spruce, forest disturbances, disturbance interactions

# Where deposited

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# Additional information

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Tiedekunta Laitos					
Maatalous-metsätieteellin	en tiedekunta Metsätieteiden laitos, metsätieteiden maisteriohjelma				
Tekijä					
Werna Wahlman					
<b>Työn nimi</b> Juurikäävän vaikutus kuusen kirjanpainajatuhoriskiin					
Oppiaine					
Metsien ekologia ja käyttö					
Työn laji Aika – Kuukausi ja vuosi Sivumäärä					
Maisterintutkielma	Tammikuu 20	024	62		
Tiivistelmä	<u> </u>				

# Tiivistelmä

Metsäkuusi (*Picea abies*) on yksi taloudellisesti merkittävimmistä puulajeista Pohjois- ja Keski-Euroopassa. Juurikääpä (*Heterobasidion annosum* s.l.) ja kirjanpainaja (*Ips typographus*) ovat merkittäviä metsäkuusen tuholaisia, ja niiden merkitys kuusivaltaisten metsien tuhonaiheuttajina odotetaan korostuvan ilmaston lämmetessä. Tässä maisterintutkielmassa tarkasteltiin juurikäävän ja kirjanpainajan välistä suoraa vuorovaikutusta. Tutkimuksen tarkoituksena oli selvittää, heikentääkö juurikääpä puita tehden niistä alttiimman kirjanpainajatuholle.

Tutkimuksessa mitattiin 442 kuusta yhdeksältä eri päätehakkuuleimikolta. Ennen päätehakkuuta jokaisesta puusta arvioitiin kirjanpainajan aiheuttamat oireet sekä latvuksesta ja rungosta. Päätehakkuun jälkeen samojen puiden kannoista arvioitiin puiden lahotilanne. Kuvailevaa analyysiä ja binomiaalista yleistettyä lineaarista sekamallia (GLMM) käytettiin analysoimaan erilaisten selittävien muuttujien välisiä suhteita ja niiden vaikutusta kirjanpainajatuhon esiintymiselle.

Parhaat ennustajat kuusen kirjanpainajatuholle olivat juurikäävän esiintyminen ja vähemmissä määrin heikentynyt viimeisen viiden vuoden läpimittakasvu sekä suurempi rinnankorkeusläpimitta. 75 % juurikäävän infektoimista puista oli myös kirjanpainajan vaivaamia. Lisäksi juurikäävän osuus oli huomattavasti suurempi kuolleissa ja vakavasti oireisissa kirjanpainajapuissa, verrattuna eläviin ja lievästi oireisiin kirjanpainajapuihin. Tulokset viittaavat siihen, että juurikääpä voi altistaa kuusia kirjanpainajatuholle etenkin silloin, kun kaarnakuoriaisten populaationtiheys on alhainen. Siksi puiden suojaaminen juurikäävältä voi välillisesti auttaa suojaamaan puita myös kirjanpainajatuhoilta.

# Avainsanat

juurikääpä, I. typographus, kirjanpainaja, metsätuhot

# Säilytyspaikka

Helsingin yliopiston kirjasto – Helda / E-thesis (opinnäytteet) ethesis.helsinki.fi

# Muita tietoja

Ohjaaja: Juha Honkaniemi. Avustavat ohjaajat: Risto Kasanen ja Lauri Lappalainen

# **ACKNOWLEDGEMENTS**

I want to thank Lallemand Finland Oy for providing an interesting research topic and for funding it.

Warm thanks to my supervisor Juha Honkaniemi for guidance, constructive criticism, and encouragement throughout the entire challenging thesis process. I have learnt a great deal about research form you, and with your help I have exceeded my goals regarding this thesis.

I want to thank my assistant supervisor Risto Kasanen, for suggesting me this topic and kick-starting this project, as well as helping me to get started with the fieldwork. I also much appreciate all the help and support Lauri Lappalainen has provided me on behalf of Lallemand Finland Oy.

Last but not least, I am thankful for my friends and family for their compassion and endless support they have provided me during this thesis process and throughout my studies.

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# **1 INTRODUCTION**

# 1.1 Background

# 1.1.1 Norway spruce

Norway spruce (*Picea abies*) is one of the most common and economically important tree species in Northern and Central Europe. In Finland, 25% (50 738 km<sup>2</sup>) of the productive forest land is Norway spruce-dominated and Norway spruce accounts 30% (740 M m3) of total volume of growing stock (Korhonen et al., 2021). In addition, Norway spruce is an economically significant tree species as in 2022 its share was 46% of the total stumpage income in Finland (Luke, 2023). The share of Norway spruce in forests has risen strongly over the past 20 years and it has been Finland's most cultivated tree species since 2005 (Ruotsalainen et al., 2022). Popularity of Norway spruce has risen especially in southern and central Finland, where its planting share has been more than 70% in several areas during the past few years (Ruotsalainen et al., 2022).

Norway spruce has been planted extensively throughout Europe because of its good growth performance and high timber qualities, as well as modest requirements regarding site quality (Hlásny et al., 2019). The current distribution of secondary Norway spruce forests in Europe extends far beyond its potential natural limits, as it has widely been planted to the sites naturally dominated by broadleaves and/or sites naturally preferred by other conifers (von Teuffel et al., 2004). According to von Teuffel et al. (2004), 5.7-7.3 million hectares pure Norway spruce forests are located either at the edge or outside of species' natural distribution area in Europe.

Norway spruce has expected to face many challenges under the climate change. Norway spruce has relatively shallow root system, which makes it more prone to drought stress (Lévesque et al., 2013; Pretzsch et al., 2013), as well as increases the risk of wind damages (Peltola et al., 1999). In general, dominance of one tree species in forestry may increase the risk of insect and pathogen outbreaks (Felton et al., 2016). This effect is highlighted, as the climate warms and extreme weather phenomena such as drought become more common (Patacca et al., 2023). European spruce bark beetle (*Ips typographus*) and root rot caused by *Heterobasidion* sp. are major biotic disturbance agents on Norway spruce, causing great economic losses (Hantula et al., 2023). Both of these agents are likely to have greater impact on spruce-dominated forests as the climate warms (Seidl et al., 2017).

# 1.1.2 Heterobasidion root rot

*Heterobasidion* sp. are considered to be the most harmful and economically significant root rot pathogen infecting coniferous forests in Europe (Asiegbu et al., 2005). In Europe, Heterobasidion root rot is caused by three species of the genus *Heterobasidion* with different host preferences (Niemelä & Korhonen, 1998). *H. annosum* s.s. colonizes mainly *Pinus* species, but it has a wide host range including many other conifer species and some broad-leaved trees such as *Betula* sp.. *H. parviporum* attacks mainly Norway spruce, causing mostly growth losses and decreasing the timber quality, but sometimes advanced decay also leads to mortality. In Central and Southern Europe, *H. abietinum* infects *Abies* species (Niemelä & Korhonen, 1998).

*Heterobasidion* sp. are common in intensively managed forests, especially if logging activities have been done during the warm season. Primary infection by *Heterobasidion* sp. occur, when basidiospores spread in the air and land on freshly exposed wood substrate such as freshly cut stumps or wounds in stem or roots (Redfern & Stenlid, 1998). After primary infection, fungus spreads to the neighboring uninjured trees through vegetative growth of the mycelium and root contacts (Garbelotto & Gonthier, 2013). This is the main pathway for infections to spread within the stand, and makes silvicultural control of the disease difficult (Garbelotto & Gonthier, 2013; Nevalainen & Piri, 2020). Pathogen may remain viable and infective in the stumps for decades and serve as inoculum source for the new tree generations (Piri et al., 2021). However, *Heterobasidion* sp. cannot freely grow and spread in the soil, so the infection risk is reduced when the roots and stumps infected by the root rot are decomposed (Garbelotto & Gonthier, 2013; Korhonen & Stenlid, 1998).

The optimal temperature for *Heterobasidion* sp. of the Northern Hemisphere ranges from 22°C to 28°C and the sporulation begins when the average daily temperature exceeds +5 °C (Korhonen & Stenlid, 1998; Piri et al., 2021). As the temperature optimum of *Heterobasidion* sp. is higher than the current average daily air and soil temperatures in boreal forests, increasing temperatures may increase not only infection rate but also the spread and decomposition activity of these fungi in forests (Müller et al., 2014). The risk of stump infection is linked to the temperature optimum of *Heterobasidion* sp. and is generally perceived to be zero when temperatures are below +5°C (Gonthier et al., 2005). In Fennoscandia, the sporulation is currently most abundant at the summertime and non-existent at winter, whereas in Central and Southern Europe presence of airborne spores has been recorded from February to October and sporulation peaks in the late summer and autumn (Gonthier et al., 2005).

The best way to protect northern European forests from the infection of *Heterobasidion* sp. is to schedule logging operations to the wintertime, when the temperature is below +5 °C (Nevalainen & Piri, 2020). However, due to warming climate a higher proportion of logging activities will take place during the warm season, which increases the infection risk through aerial spore spread of *Heterobasidion* sp. (Müller et al., 2014). If logging is done during the time of sporulation, stump surfaces should be treated immediately with chemical or biological control agent. Disodium octoborate tetrahydrate (DOT), urea, and the biological control fungus *Phlebiopsis gigantea* are all proven effective and can be used as a stump treatment (Garbelotto & Gonthier, 2013). Thor & Stenlid (2005) found that all three above mentioned stump treatments significantly reduced colonized stump area after thinning by 88-99% compared to the untreated stumps. The same effect was obtained when harvesting was done in the wintertime (Thor & Stenlid, 2005). The obvious downside of the stump treatment is that it cannot prevent the infections of injured standing trees.

If the forest stand is heavily infested, stump removal, including removal of all roots, is an effective control strategy against Heterobasidion root rot (Garbelotto & Gonthier, 2013). However, stump removal is expensive, time consuming and heavily invasive method, that may have adverse effects on biodiversity and carbon balance of the forest (Roberts et al., 2020). Therefore, it may not be suitable for all forest site types. Another option in heavily infested areas is to replace the main tree species to one that is not susceptible to *Heterobasidion* species in question (Nevalainen & Piri, 2020). For example, *P. sylvestris* and broadleaved trees are resistant to *H. parviporum*. However, it is difficult to find alternative tree species for pine growing sites infected with *H. annosum*, since it is able to infect many different conifers and broadleaved trees (Nevalainen & Piri, 2020) In addition, tree species that are normally resistant to root rot may be exposed to infection if for example the wrong origin is used or the tree species is not suitable for the site for other reasons.

# 1.1.3 Ips typographus

*Ips typographus* is one of the most significant insect pests in European spruce forest ecosystems, and its mass outbreaks have led to extensive mortality of Norway spruce across the Europe (Netherer & Hammerbacher, 2022). *I. typographus* is an eruptive bark beetle species, that colonize stressed and dying trees when their population density is low, but then mass-attack large numbers of healthy trees once environmental conditions (host availability, weather) have allowed the population to increase significantly (Hlásny et al., 2021). Outbreaks of *I. typographus* are usually linked to other disturbances or extreme weather conditions (Wermelinger, 2004). The insect population may increase dramatically especially after heavy windstorms, as newly windthrown trees are suitable for breeding (Komonen et al., 2011). Also, other disturbances such as snow breakage, severe drought or heat waves are known to trigger *I. typographus* outbreaks, since they weaken the trees and supply easily accessible breeding material for beetles (Wermelinger, 2004).

Successful colonization of living trees requires large numbers of invading beetles to overcome tree defense systems (Hlásny et al., 2019). When there is plenty of suitable breeding material available after windfall events, the population size may rise above the density threshold required to colonize and kill healthy trees (Christiansen & Bakke, 1988). Even though abiotic factors have an important role in triggering *I. typographus* outbreaks, there is also evidence for a negative density feedback regulating *I. typographus* populations (Marini et al., 2013). After large outbreaks, lack of suitable breeding material, such as weakened trees may strongly regulate *I. typographus* 

populations (Marini et al., 2017). Switching from wind-felled trees to standing trees poses a potential threat of colonization failure or reduced reproductive success for beetles. (Komonen et al., 2011). This intra-specific competition could serve as a natural mechanism leading to population decline, and thus increase the forests resilience at a regional scale (Marini et al., 2017).

The phenology and development rate of beetles change in response to changes in temperature (Jönsson et al., 2009). Warmer summer temperatures typically shorten the development period of bark beetles as well as enhance their overall performance and adaptability. As number of sister broods and generations per year increases with rising temperatures, so does the population impacts on forests (Jönsson et al., 2009; Öhrn et al., 2014). Also, drought induced transpiration deficits make trees more vulnerable to subsequent bark beetle attacks (Netherer & Hammerbacher, 2022). Warm summers with below average rainfall are in relation with greater timber loss due *I. typographus* (Marini et al., 2017).

In Finland, *I. typographus* damages have been relatively mild compared to Central Europe or even Sweden, where damages and economical losses after outbreak have been extensive (Hlásny et al., 2021; Komonen et al., 2011; Neuvonen & Viiri, 2017). One reason for this is that in large parts of the Europe there are two or more generations of *I. typographus* per year, but in Finland typically only one (Pouttu & Annila, 2011). However, summer 2010 in Finland was exceptionally hot and dry and thunderstorms caused damage in large areas of central and eastern Finland (Neuvonen & Viiri, 2017). This resulted in an outbreak of *I. typographus*, and the second generation of spruce bark beetle was observed for the first time in Finland (Pouttu & Annila, 2011). As average summer temperatures have increased in the 21<sup>st</sup> century, it is no longer uncommon for the temperature sum to accumulate to the point where *I. typographus* is able to develop two generations per year in the southernmost parts of Finland (Neuvonen & Viiri, 2017).

Pheromone traps can be efficiently used to monitor the flight activity and population density of bark beetles and guide management decisions on timing and intensity of control measures (Hlásny et al., 2019). Sanitation felling is one of the most common active control measure against bark beetle damages (Hlásny et al., 2019). It means removing infested trees and all potential breeding materials such as weakened trees, windthrows and logs before the offspring develops to pupae and adult beetles emerge (Fettig & Hilszczański, 2015). Sanitation felling may include a buffer zone, where uninfested trees are removed in order to halt the further outbreak expansion (Fettig & Hilszczański, 2015). If trees cannot be removed before the adult beetles emerge and exit, debarking and further bark chipping or burning are effective methods to prevent the beetles from leaving the trees and infesting the surrounding forest (Wermelinger, 2004).

In the long run, one of the most effective strategy is to reduce forests' susceptibility to *I. typographus* outbreaks through silvicultural management (Fettig & Hilszczański, 2015). Connectivity between host and beetle populations at landscape-level is one of the key factors affecting the bark beetle infestation risk (Seidl et al., 2016). Therefore, high risk areas characterized by mature Norway spruce forests should be separated from each other by buffer zones consisting of non-host trees, which have low habitat suitability for bark beetles (Honkaniemi et al., 2020). Another key factor is minimizing factors causing stress to Norway spruce, such as density dependent competition and drought stress, through adequate silvicultural measures and planting spruce only in suitable sites. Forest management should aim for landscape heterogeneity in terms of age, size, and species compositions (Fettig & Hilszczański, 2015). Heterogenous forests are less susceptible to large scale insect outbreaks and generally exhibit a higher survival rate as well as resilience under compounding disturbances compared to stands with homogeneous structure (Seidl et al., 2016; Hlásny et al., 2019).

# **1.2** Disturbance interactions in forests

#### 1.2.1 Concepts and theory

Disturbance is a sudden change in biomass, resource availability or ecological structure or functioning (Burton et al., 2020). Disturbance is a relatively discreet event in relation to the lifespan of ecosystems dominant organisms (Pickett & White, 1985). Natural disturbances, such as fire, wind, drought, diseases and insect outbreaks have an essential role in ecosystem functioning and composition (Canelles et al., 2021). Disturbances release nutrients and growing space which in turn promotes ecological succession (Jentsch & White, 2019). Succession and disturbances are opposite but complementary processes that are jointly responsible for vegetation dynamics in forest ecosystems (Burton et al., 2020).

Disturbances have long been studied under the field of ecology, but far less is known on how individual disturbance agents interact with each other (Burton et al., 2020; Seidl et al., 2017). Disturbances leave functional, structural and biological legacies into ecosystems, and these legacies may either facilitate or inhibit the next disturbance (Buma, 2015; Burton et al., 2020). Primary disturbance may drive an interaction in two different ways: either by altering the resistance or resilience of the system to subsequent disturbance (Buma, 2015). First of above-mentioned interaction type is often termed as a "linked disturbance" and the latter one a "compound disturbance" (Paine et al., 1998; Simard et al., 2011). Interaction is linked, when the initial disturbance affects the occurrence of the subsequent disturbance as well as its spatial extent, intensity or severity (Buma, 2015). However, typically disturbance interactions extend beyond single direct link, forming disturbance loops or disturbance cascades (Burton et al., 2020).

In disturbance loop, one disturbance leads to another, which is then responsible for initiating the first disturbance type again (Burton et al., 2020). The drivers of disturbance loops are often dependent on ecosystems internal composition and structure, creating relatively predictable disturbance regimes. Disturbance cascades occur when two or more disturbances are triggered in sequence by prior disturbance (Burton et al., 2020). Cascading effects typically occur when one disturbance type is affected by an external driver, such as anthropogenic pressure or climate change (Buma, 2015). Disturbance cascades are relatively unpredictable and may consist from multiple nonlinear links forming complex networks (Burton et al., 2020). Such disturbances create maximum departure form ecosystems' reference conditions and are more likely to expand beyond initial spatial scale (Burton et al., 2020).

Disturbance is compounded, when new type of disturbance is created from the individual disturbance events (Paine et al., 1998). Compound disturbance may reduce or enhance systems resilience for example by creating conditions outside the species tolerance and altering the capacity of resilience mechanisms to successfully recover (Buma, 2015). In conclusion, compound disturbance interaction makes recovery from the subsequent disturbance event more or less likely, or alters the speed of ecosystem recovery (Paine et al., 1998).

# 1.2.2 General trends in disturbance dynamics

In a global review, Seidl et al. (2017) found that the majority (71.0%) of recorded interaction effects in the literature were positive or primarily positive, meaning growing impact of disturbance as a result of interaction between the agents. Correspondingly, only 16.2% of the studies on disturbance interactions reported a negative or mainly negative (dampening) effect between interacting disturbance agents (Seidl et al., 2017). As almost all disturbances have the effect of reducing resources or the stress that facilitated the initial disturbance, dampening effect lowers the probability for subsequent disturbances by the same agent (Burton et al., 2020). However, links between abiotic (influencing agent) and biotic (influenced agent) disturbances have been found to been strong (Seidl et al., 2017).

Individual disturbance agents and interaction between them are being increasingly affected by climate change and growing anthropogenic pressures (Buma, 2015). Especially biotic agents may be susceptible to further intensification through the influence of other disturbance agents (Jactel et al., 2012). For example, severe or prolonged drought may increase forests susceptibility to insect attacks, as especially bark beetles' benefit from drought (Jactel et al., 2012). Under warmer and drier future conditions large majority of studies suggest increase in fire, drought and insect disturbance agents are expected to reduce (Seidl et al., 2017). Wetter conditions promote especially wind disturbance and pathogen activity, as most fungi require high humidity conditions for spore dispersal, germination and infection (Jactel et al., 2012; Seidl et al., 2017).

Disturbances are often studied either in isolation or as an interaction between two disturbances focusing on either linked disturbances or compound disturbances (Lucash et al., 2018). Modelling can be used to study complex interaction networks and effects of multiple interaction agents simultaneously. A simulation study conducted by Lucash et al. (2018) showed that tree mortality was lower in a scenario, where four disturbance agents occurred concurrently in the landscape compared to the sum of all single disturbances. Results suggest significant negative feedback and compensatory effects among disturbances, and this effect was even stronger after adding climate change into simulation (Lucash et al., 2018). Another simulation study found that bark beetle disturbances change forest structure and composition as well as host availability, and thus dampen the potential severity of subsequent insect attacks (Sommerfeld et al., 2021). Reduction of future disturbance activity was of up to -67%, but not able to fully compensate for the effect of climate change, as disturbances by I. typographus were increasing between 59% and 221% compared to reference climate (Sommerfeld et al., 2021). These results are contrary with the general view according to which interaction effects are mostly positive and climate change amplifies the effect of many disturbance agents (Buma, 2015; Burton et al., 2020; Seidl et al., 2017). These examples highlight the fact that knowledge about interaction between different disturbance agents is still fragmented and contains many uncertainties.

# 1.2.3 Root rot and bark beetle interactions

Bark beetles are typically associated with trees of low vigor and root pathogens are known to be important in making trees more susceptible to infestations by certain bark beetle species (Cobb, 1989; Goheen & Hansen, 1993; Hlásny et al., 2019). Interaction between root pathogens and bark beetles appears to be stronger when bark beetle population densities are low and stable (Alexander et al., 1980; Cobb, 1989; Goheen & Hansen, 1993). During bark beetle outbreaks the proportion of trees killed by bark beetles that are also root-diseased tend to be lower, as beetles can attack and kill also seemingly healthy trees (Alexander et al., 1980; Goheen & Hansen, 1993).

The reason why root diseased trees are predisposed to bark beetle attacks is not entirely clear. However, it is frequently suggested that root rot weakens the trees and reduces

their resistance against bark beetles through two possible mechanisms (Goheen & Hansen, 1993; Tkacz & Schmitz, 1985). First, the water uptake of the trees is disrupted as pathogen and decay progresses within the tree, which increases moisture pressure and reduces resin exudation pressure (Alexander et al., 1980; Tkacz & Schmitz, 1985). Therefore, stressed trees exhibit reduced capability to defend against beetle attacks by pitching out the beetles (Tkacz & Schmitz, 1985).

The second reason is linked to the tree's carbohydrate reserves and their allocation for different mechanisms. Reaction zones are necrotic regional barriers that trees form against fungal attack or injury (Shain, 1979). They are characterized by high pH which together with the high concentration of several lignans partly prevent the growth of the pathogen (Shain, 1979; Shain & Hillis, 1971). In the beginning of root rot infection fungus is limited to the heartwood and it is presumed that the fungus has only little impact on tree physiology at this stage (Lewis & Lindgren, 2002). However, reaction zone formation requires synthesis of secondary metabolites and re-allocation of resources to compartmentalization of decay (Oliva et al., 2010). Also, the amount of constitutive resin available at the time of bark beetle attack is dependent on energy in the form of carbohydrates (Christiansen et al., 1987). Therefore, defense against both root-rot and bark beetles are directly related to the tree's carbon balance (Christiansen et al., 1987). Hypothetically, if a tree has allocated resources to the formation of reaction zone, it may affect its ability to defend itself against bark beetle attack.

It has also been speculated that some beetles may be attracted to diseased trees by the chemicals that such trees release (Tkacz & Schmitz, 1985). There is some evidence that ponderosa pines with black-stain root diseases are attractive to certain species of *Dendroctonus* bark beetles (Goheen et al., 1985). Also, Gara et al. (1984) suggested that *D. ponderosae* is primarily attracted to lodgepole pines with root disease. However, Moeck et al. (1981) found no significant difference between landing rates of *D. brevicomis* and *D. ponderosae* on screened treated trees and screened control trees. The researchers concluded that there is no evidence that trees (Moeck et al., 1981).

Interaction between root pathogens and bark beetles has been studied especially in North-America and studies have focused mainly on genus *Dendroctonus* and pine trees. Lessard (1985) found significant associations between mountain pine beetle (*D*.

*ponderosae*) and *Armillaria* sp. Similarly, Tkacz and Schmitz (1985) concluded that mature lodgepole pines infected with *A. mellea* were attacked more frequently by mountain pine beetle compared to uninfected lodgepole pine. Hadfield et al. (1986) reported that pine trees infected with *H. annosum* s.s. were frequently attacked by the mountain pine beetles and western pine beetles (*D. brevicomis*). Alexander et al. (1980) found significant and consistent association between *H. annosum* s.s. and the southern pine beetle (*D. frontalis*) on loblolly pine. *H. annosum* s.s. was found to be a significant factor in increasing the susceptibility of trees to southern pine beetle attacks in thinned stands located at high risk Heterobasidion root rot sites (Alexander et al., 1980).

Less research has been done on spruce trees and their insect pests. Lewis and Lindgren (2002) studied the relationship between the root disease fungus *Inonotus tomentosus* and spruce beetle *D. rufipennis*. Results suggest that *I. tomentosus* infected trees are not more attractive to spruce beetle as such, but infected trees appear to have potential to maintain greater numbers of beetles at low populations compared to healthy trees (Lewis & Lindgren, 2002).

Disturbances caused by root rot and bark beetles have also indirect interaction through wind damages. *Heterobasidion* root rot predisposes Norway spruce to uprooting and windthrow by weakening their root system and thus their ability to anchor to the ground (Giordano et al., 2012). *I. typographus* then colonizes and breed on weakened windfallen trees (Komonen et al., 2011). There are also some indications in the literature, that root rot infestation by *Heterobasidion* sp. could make Norway spruce more vulnerable to the spruce bark beetle attack, at least together with another predisposing factors (e.g. Blomqvist et al., 2018; Melin et al., 2022).

# **1.3** Research problem

Effects of climate change on different abiotic and biotic disturbance agents have been increasingly studied on recent years. However, less is known about the interactions between different disturbance agents, especially between the biotic ones (Seidl et al., 2017). Indirect interaction between Heterobasidion root rot *I. typhographus* through wind disturbances is well-known and described (e.g., Honkaniemi et al., 2017).

However, direct interaction between *Heterobasidion* sp. and *I. typographus* has not been researched under field-studies.

Both *Heterobasidion* sp. and *I. typographus* are expected to benefit from global warming. Damages caused by *I. typhographus* are likely to increase as response to the hot and dry summers, and the sporulation time of *Heterobasidion* sp. extends as winters get warmer. If there is direct and consistent association between these two disturbance agents, Heterobasidion root rot and *I. typographus*, it may have significant impact on the health of Norway spruce dominated boreal forests in the future warming climate.

# 1.4 Aims and objectives

The aim of this thesis is to study the potential direct interaction between Heterobasidion root rot and *I. typographus* and their impacts on Norway spruce. Specifically, the aim is to analyze if decay in stem and the stress it poses to a tree increases the risk for bark beetle attack.

The research questions and the related hypothesis for the study are:

RQ1: Is there consistent association between the Heterobasidion root rot and *Ips typographus*? H1: Trees infested with bark beetles are consistently also infected with Heterobasidion root rot.

RQ2: Does the Heterobasidion root rot weaken the tree making it more susceptible to colonization of *Ips typographus*? H2: Advanced decay of root rot weakens the tree resistance and make it easier for bark beetles to colonize and kill the tree.

RQ3: Is interaction between Heterobasidion root rot and *I. typographus* stronger when bark beetle population density is low compared to outbreak phase? H3: When *I. typographus* population density is low, a higher proportion of trees infested with bark beetles are also infected with Heterobasidion root rot.

The research objectives are:

• Measure and quantify the impacts of bark beetles in Norway spruce stands in eastern Uusimaa and southern Pirkanmaa regions.

• After final felling, re-measure the plots and identify the decay status of trees as well as to evaluate their potential stress effects on trees.

# 2 MATERIALS AND METHODS

# 2.1 Collection of material

Collection of material was done in the southern Finland during the year 2023. In total, 10 Norway spruce stands with varying *I. typographus* infestation levels were measured (Figure 1). In order to reliably observe root rot incidence, stands were harvested, and measurements were done both before and after the final felling. Four of the stands were located in Urjala municipality, which is located in southern Pirkanmaa region. Five of the stands were located in the eastern Uusimaa region in Mäntsälä, Askola and Karkkila municipalities and one stand was located in Loppi municipality at Kanta-Häme region. All of the stands were Norway spruce-dominated stands located at mineral soil and stand area varied between 1.1 to 10.8 hectares, with an average of 3.3 hectares. 4 circular sample plots with an 8.92 m radius were measured from each stand. In total, 40 sample plots with varying bark beetle infestation levels were measured. This results in a total area of one hectare measured. The locations of the sample plots were chosen in situ, so that the four sample plots would comprehensively represent different degrees of bark beetle damages present within the forest stand.



Figure 1. Location of Norway spruce stands included in the study. Aerial maps from two of these stands, and the locations of sample plots within them.

Before the final felling, symptoms caused by *I. typographus* were assessed from each tree following the classification method first described by Blomqvist et al. (2018). The classification of symptoms was based on visual assessments of the tree's crown and stem. The stem symptoms include the number of entrance and exit holes (jointly 'holes') in the lowest 2 m, number of resin flow spots and general bark condition. Also crown defoliation and discoloration were evaluated. The stem symptoms were classified into three severity classes, and the crown symptoms into four classes (Table 1). Trees were then classified into three infestation index classes based on the symptoms assessed in the field. This was calculated as the sum of all the symptoms, thus forming a variable of infestation intensity. Three infestation index classes were: 'no infestation' (score 5 or 6), 'moderate infestation' (score 7–11), and 'severe infestation' (score 12–15).

Symptom	Class	Description
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, gray
Defoliation	1	0-25%
	2	26-50%
	3	51-75%
	4	76-100%

Table 1. Classification of symptoms caused by I. typographus.

Tree diameter at breast height (DBH), tree species, and distance of trees from the center of the sample plot were also determined before the felling. All trees with diameter of 10 cm or above were measured, and diameter was determined with caliper as the average of two perpendicular measurements. The center point for the sampling plot was recorded with GPS and the bases of the trees were marked with spray paint so that they could be found more easily after the final felling. The first pre-harvest measurements were done already in February in one stand located in Mäntsälä. The rest of the preharvest measurements were done in a two weeks period at the turn of the April/May.

After the final felling, the sample plots were relocated from the clearcut areas, and the stumps of the sampled trees were re-assessed for Heterobasidion root rot. All stumps were photographed with scale and the diameter of rot was measured in situ, from two directions. The degree of decay was defined by using a "knife test", which involved pressing a knife into a stump and measuring the depth of penetration. In addition, if feasible, the diameter growth of the 5 last years prior to the harvest was measured from

the stump surface. This was done by counting and measuring the width of the 5 last growth rings. However, some stumps were in poor condition and counting the growth rings from these stumps was not feasible (Figure 2).



Figure 2. The condition of the stumps varied a lot between and within the sample plots.

Time period between the final felling and the re-measurements following them varied between the stands. Some stands were re-measured a week after the final felling, whereas some stands were re-measured almost two months past the felling. The first re-measurements were done within one stand in February and all the rest was done between May and October. All the sample plots were found after the final felling, but all stumps within the sample plots could not be found and/or measured mainly for two reasons (Figure 3). Firstly, logging residue piles had been stacked onto some sample plots, covering one or more of the stumps. Secondly, the forest harvester had run over some of the stumps, making any analysis or measurements impossible. In addition, in some cases trees with smaller diameter were left standing.

In total, 493 Norway spruce trees were measured from 10 different stands. The final felling of the stand located in Karkkila was delayed and it had to be excluded from the study. Results from the first measurements were not used, because no root rot

observations were obtained. As a result, 442 Norway spruce trees form 9 different stands were included in this study.



Figure3. Left-side picture: a stump that has been run over with a forest machine. Right-side picture: a pile of logging residues on the sample plot.

# 2.2 Analysis of data

Data analysis was completed to test if there is a direct and consistent association between root rot and *I. typographus* infestation, as well as to examine what other factors besides root rot may have contributed to the *I. typographus* infestation. Exploratory analysis with cross-tabulation, boxplots, bar plots and other charting techniques was utilized to explore the structure and nature of the data along all steps of data analysis. All analyses were completed with RStudio, and all the graphs were drawn with RStudio as well.

Basal area of larger trees (BAL) was calculated for each tree within every sample plot. The BAL of a given subject tree is the sum of the basal area of all trees in a given area which are larger in DBH than the subject tree (Wykoff, 1990). When calculating the BAL value, the largest tree in the sample plot gets the value 0, and the smaller the tree, the higher the BAL value. Thus, BAL represents the competition status of a tree within a forest stand and provides an effective measure of tree dominance (Burkhart & Tomé, 2012). Formula for calculating BAL is:

$$BAL_{ij} = \sum_{j=1}^{n} BA_j$$
(1),

Where  $BA_j$  is the basal area (m<sup>2</sup>) of trees which are larger than the subject tree per ha in the plot.

The distance of the center of each sample plot from the nearest forest edge was calculated from the latest (2022 or 2023 depending on the stand location) orthophotographs provided by National Land Survey of Finland using QGIS desktop. Distance was calculated from each plots' center to the nearest forest edge located southward of the east-west axis. 5-year diameter growth (Growth) calculated from the growth rings, BAL value and sample plot distance from the nearest forest edge were used as explanatory variables for *I. typographus* infestation in further analysis.

Binomial Generalized Linear Model (GLM) and binomial Generalized Linear Mixed Model (GLMM) were used to analyze relationships between explanatory variables and their affect to *I. typographus* infestation. However, GLMM was chosen over GLM as it allows one to model both fixed effects (the relationships between predictors and the outcome) and random effects (variability within groups or clusters) simultaneously. Therefore, GLMM was used to predict tree infestation status based on the fixed predictors (DBH, Rot, BAL, Growth), considering nested random effects due to data grouping into sample plots within forest stands. Plot distance from the forest edge was considered, as Plot was included in the model as random effect. GLMM excludes all the observations that contain missing values (NA), meaning all the trees of which stump was not found were excluded from the model.

The selection of explanatory variables with significant effect on tree infestation status was made with the backward stepwise method. Akaike information criterion (AIC) and Schwarz's Bayesian Information Criterion (BIC) were used for model comparison, with lower values indicating a better fit. A Receiver Operating Characteristic (ROC) curve and its associated metric, the Area Under the Curve (AUC), were used to evaluate the model's performance. ROC curve is a graphical representation of a binary classification model's ability to distinguish between the two classes, in this case "Infestation" and "No infestation" (Fawcett, 2006). It plots the True Positive Rate (Sensitivity) on the y-axis against the False Positive Rate (1 - Specificity) on the x-axis. Sensitivity measures how well the model correctly identifies positive cases, while 1 - Specificity quantifies the rate of false alarms. AUC is a single numeric value that summarizes the ROC curve. It represents the overall performance of the model. AUC ranges from 0 to 1, with higher values indicating better model performance (Fawcett, 2006).

In addition, Q-Q plots and Residual vs. Fitted plots were drawn with DHARMa (Residual Diagnostics for HierArchical Models) package in R, and used to evaluate the goodness of fit of the models. DHARMa package provides alternative diagnostic tools that are specifically tailored for hierarchical models, including binary GLMMs. The package simulates residuals based on the fitted model and compares them to the observed residuals to assess model fit. The emphasis is on assessing the distribution and patterns of the residuals instead of assuming normality. Traditional Q-Q plots may not be as informative because the residuals from logistic regression are not normally distributed.

The final GLMM (Model 1) had DBH and Rot as fixed predictors and Stand and Plot as nested random effects. As growth was observed only from 6 stands and the number of observations was relatively small (n=207), it was included as explanatory variable to secondary GLMM (Model 2), together with the DBH and Rot.

The formula for Model 1 is:

$$P(\text{Infestation} = 1) = logit^{-1}(\beta_0 + \beta_1 \times DBH + \beta_2 \times Rot + v_{Stand/Plot})$$
(2)

And for Model 2:

 $P(\text{Infestation} = 1) = logit^{-1}(\beta_0 + \beta_1 \times DBH + \beta_2 \times Rot + \beta_3 \times Growth + v_{Stand/Plot})$ 

Where:

- P(Infestation=1) is the probability of infestation being 1.
- *logit<sup>-1</sup>* is the logistic function that transforms the linear combination of predictors to the probability scale.
- $\beta_0$  is the intercept.
- $\beta_1$  is the vector of coefficients for variable DBH.
- $\beta_2$  is the vector of coefficients for variable Rot.
- $\beta_3$  is the vector of coefficients for the variable Growth.
- U<sub>Stand/Plot</sub> represents the vector of random effects for the grouping structure Stand/Plot.

# **3 RESULTS**

#### **3.1 Exploratory analysis**

47 % of Norway spruce trees were infested with *I. typographus*, while 53 % had no signs of infestation. After the final felling, 87% of the stumps were found and identified, which means that 384 stumps were assessed in total. Root rot was observed from 8% of the assessed stumps. 75% of the stumps with root rot were ones from the trees infested with *I. typographus* and the rest 25% were from trees with no infestation. Of the stumps that could not be assessed (NA), 36% were from trees with *I. typographus* infestation and 64% were from trees without infestation. In a stand level, the number of stumps that were not assessed varied between 0 to 37%, with a median value of 10.7%. Figure 4a-b shows the distribution of *I. typographus* and root rot infested trees by stand.

(3),



Figure 4a-b. *I. typographus* infestation and root rot observations across different stands. a) represents the count and percentage of observations for *I. typographus* infestation status, while b) provides a similar breakdown for root rot observations. Legends indicate the categories under consideration. NA represents stumps that were not found and/or measured after final felling. n=442 Of *I. typographus* infested trees 50.7% of the trees were in class "Moderate infestation" while 49.3% where in class "Severe infestation". Correspondingly, 19% of all stumps where root rot was observed were in class "Moderate infestation" and 56% in class "Severe infestation". Thus, the proportion of stumps with root rot was highest within the infestation class "Severe infestation" (Figure 5). Trees within this class were either dead or severely affected by bark beetle infestation: 78% of trees within this class had defoliation of 76-100% and/or significant bark damage and 70% of trees had dead/gray needles. Trees within class "Moderate infestation" were generally in better condition, and bark beetle infestation had not progressed as far as in the class "Severe infestation". When *I. typographus* infested trees were further divided into the classes "Dead" and "Alive" based on their symptoms, amount on root rot infected trees was two-fold among the dead trees compared to living trees (Figure 6). Also, the relative proportion of root rot is considerably higher in dead trees compared to living trees. Within the class "Dead" degree of defoliation in the trees was 76-100%, and the needles were either brown or gray.



Figure 5. Distribution of observations based on the degree of infestation and the presence of rot. The x-axis represents different infestation classes, and the y-axis shows the percentage of observations, with each bar filled by the proportion of rot categories. n=442.



Figure 6. The distribution of *I. typographus*-infested trees based on their status ("Alive" or "Dead") and the presence of rot. Percentages represent the proportion of observations within each category, with counts indicated in parentheses. n=207

*I. typographus* incidence did not increase or decrease together with the root rot incidence. Stands with proportionally most stumps with root rot were Purola, Pölkinvuori and Lippuleuka, whereas least stumps with root rot were found from Vatilahti and Vaasankulma. Respectively, stands with proportionally most *I. typographus* infested trees were Venu, Vatilahti and Purola and least infested stands were Könnilä and Lippuleuka. Results suggest that the relationship between *I. typographus* and root rot is not linear, which can be observed from Figure 7 and Table 2. The rot proportion of *I. typographus* infested trees was generally higher within those stands, where the share of the infested trees was less than 50% from all the trees within the sample plots (Table 2). The exception to this trend was a stand located in Purola.



Figure 7. The relative proportion of trees infested with *I. typographus* (green line) and root rot (red line) in each stand. Each point represents the proportion of infestation within a stand. The y-axis indicates the proportion of infestation relative to all trees in percentage, while the x-axis represents different stands. n=442.

Table 2	The proportion of <i>I</i> .	typographus	infested t	rees, and	proportion	of rot in 1	trees
infested	with I. typographus	in each stand	•				

Stand	Proportion of <i>I. typograpus</i> infested trees	Rot proportion in <i>I.typographus</i> infested trees
Könnilä	16.1%	20%
Lippuleuka	32.3%	28.6%
Mieliö	34.1%	14.3%
Pölkinvuori	37.5%	33.3%
Vaasankulma	50%	5.6%
Leikkikangas	50.9%	7.1%
Purola	59.3%	28.6%
Vatilahti	71.4%	0%
Venu	83.7%	9.8%

Based on the exploratory analysis, BAL and sample plots' distance from the forest edge did not have clear effect on the tree infestation status (Figure 8 a-b). The lack of any discernible pattern in the scatter plot, along with the similar distribution of data points for both groups, suggests that there is no significant correlation between BAL and infestation status and distance from forest edge and infestation status. In Figure 8c, lower median in group "Infestation" indicates that, on average, growth is slower among infested trees compared to non-infested trees. However, outliers and lack of clear pattern can be observed in both groups. In Figure 8d, the slight upward trend visible in the scatter plot suggests a positive correlation between DBH and Infestation, which is further supported by the higher median in group "Infestation" in the boxplot.





Figure 8a-d. Influence of different factors on the *I. typographus* infestation status on a tree-level.

The diameter at breast height (DBH) ranged from 10 to 50 cm and above. *I. typographus* infested trees were found from all diameter classes, but relative proportion of *I. typographus* infested trees increased together with the growing diameter. In DBH classes from 30-34 and above, the proportion of *I. typographus* infested trees was greater than or equal to non-infested trees, whereas in smaller DBH classes proportion of trees without infestation was greater (Figure 9a). Root rot was observed in all DBH classes except trees with diameter of 50 cm or above. The number of stumps with root rot was greatest among the trees with diameter between 20-29 cm, but otherwise stumps with root rot were evenly distributed among the DBH classes (Figure 9b). Relative proportion of root rot was highest among the trees with diameter of 40-49 cm and smallest in diameter classes 15-19 cm and 30-34cm.





Figure 9a-b. Influence of DBH on *I. typographus* infestation and root rot presence in trees. a) shows the count and percentage of observations for *I. typographus* infestation across different DBH classes, while b) provides a similar breakdown for root rot observations. N=442

#### 3.2 Modelling

The selection of explanatory variables with significant effect on tree infestation status was made with the backward stepwise method, and the final GLMM (Model 1) had DBH and Rot as fixed predictors and Stand and Plot as nested random effects. The best predictor of infestation found by Model 1 was presence of Rot (P < 0.001), while DBH was not significant (P = 0.55) (Table 3). However, DBH was included into the model based on the results of exploratory analysis and since it decreased both the AIC and BIC values of the model.

Model 1: Infestation ~ DBH + Rot + (1   Stand/Plot)					
Fixed effects	Coefficient	Standard Error	Z-Value	Р	
(Intercept)	-0.98030	0.62882	-1.559	0.11901	
DBH	0.03330	0.01733	1.922	0.05464	
Rot [1]	1.28725	0.49749	2.588	< 0.001	

Table 3. Coefficient table for Model 1. n=384

Bold values are significant at P < 0.05.

The ROC curve of the Model 1 hugs the upper left corner of the plot, indicating it has a relatively high true positive rate and a low false positive rate (Figure 10). The AUC value of the Model 1 was 0.8249. AUC value of 0.8249 suggests that the model has a high probability of ranking a randomly chosen positive instance higher than a randomly chosen negative instance about 82 % of the time. This implies that the model is good at differentiating the cases into classes "Infestation" and "No Infestation." Moreover, in the Q-Q plot, points closely follow the diagonal line (Figure 11). There are no departures from linearity that would indicate model misspecification or outliers. In the Residual vs. Predicted plot, residuals are rather evenly distributed suggesting that on average the model's predictions are unbiased (Figure 11). In addition, the straightness of the lines in the plot indicates that the model is effectively capturing the underlying relationship between the predictors and the binary outcome.



Figure 10. ROC curve and AUC of Model 1. Rot and DBH as explanatory variables. Since GLMM excludes all the observations that contain missing values, n=384.



Figure 11. Q-Q plot and residuals of Model 1.

Model 2 had Growth, Rot and DBH as explanatory variables and Stand and Plot as nested random effects. The results of the Model 2 indicate that the variables Rot (P < 0.001) and Growth (P = 0.03) are statistically significant in predicting the infestation, while DBH (P = 0.23) does not appear to be statistically significant (Table 4). The negative coefficient for Growth suggests that an increase in growth is associated with a decrease in the probability of infestation, and vice versa.

Model 2: Infestation ~ DBH + Rot + Growth + $(1   Stand/Plot)$					
Fixed effects	Coefficient	Standard Error	Z-Value	Р	
(Intercept)	0.50927	1.09674	0.464	0.64240	
DBH	0.03135	0.02619	1.197	0.23127	
Rot [1]	3.23176	1.24347	2.599	< 0.001	
Growth	-0.15254	0.07031	-2.170	0.03004	

Table 4. Coefficient table for Model 2. n=207

Bold values are significant at P < 0.05.

The ROC curve of Model 2 is similar to Model 1 (Figure 12). The AUC value of Model 2 was 0.8776, suggesting that the Model 2 is effective in predicting infestation status based on the explanatory variables. In the Q-Q plot, points follow the diagonal line although not quite as closely as in the Model 1 (Figure 13). A subtle curve is observed in the middle of the diagonal, which may indicate potential issues with the model fit. In addition, curvature in the upper quantiles in the Residual vs. Predicted plot indicates problems with the model's ability to accurately predict higher probabilities (Figure 13). However, these problems are probably due to the small sample size.



Figure 12. ROC curve and AUC of Model 2. Rot, DBH and Growth as explanatory variables. n=207



Figure 13. Q-Q plot and residuals of Model 2.

Finally, it is good to consider that DBH distribution is different between the whole dataset and subsets used in the Model 1 and Model 2 (Figure 14a-c). GLMM excludes all the observations that contain missing values. Since it was not possible to measure rot and growth from all trees, GLMM excludes all the DBH observations from the trees that contain missing values of rot (Model 1) and growth (Model 2).







Figure 14. Comparison of *I. typographus* infestation across different DBH classes for three datasets: a) All trees i.e., whole dataset (n=442), b) Model 1 subset (n=384), and c) Model 2 subset (n=207). Each bar represents the percentage of *I. typographus* infestation observations in a DBH class.

# 4 DISCUSSION

# 4.1 Effect of root rot on I. typographus infestation

In this study, the best predictors for *I. typographus* infestation were presence of root rot and to a lesser extent, decreased 5-year diameter growth and larger diameter at breast height. Unlike hypothesized, trees infested with *I. typographus* were not consistently infected with root rot. Only 11.6 % of trees with *I. typographus* infestation also had root rot infection. However, the majority (75%) of root rot infected trees were also infested with *I. typographus*, supporting the second hypothesis that root rot may weaken the trees resistance and make it more susceptible to colonization of *I. typographus*. Trees with root rot are likely to be more suitable host for bark beetles compared to healthy, vigorous trees. In this study root rot was observed from 8% of the trees, which is slightly lower than the average in Southern Finland. Approximately 10% of the total amount of harvested wood has root rot in Southern Finland's Norway spruce stands (Piri et al., 2019).

Trees with root rot but without *I. typographus* infestation were found from three stands, where both proportional and absolute root rot incidence was highest. Given that root rot spreads within the stands to adjacent trees via root contacts, this result is not surprising. Propagation of decay from roots further to the stem base of the tree may take several years (Stenlid & Redfern, 1998). Therefore, it is possible that root rot is present in a part of the root system and weakens the tree, without causing any visual symptoms on the stump. This may at least partly explain *I. typographus* infestation of trees that are adjacent to the root rot infected trees. On the other hand, even though *I. typographus* has a dispersal range of 500 meters and above, new attacks typically occur in the near vicinity of old ones (Wermelinger, 2004). Especially during an outbreak, beetles fly shorter distances and attack neighboring trees of the just attacked one (Jakuš et al., 2011; Sproull et al., 2015). Thus, root rot weakened trees may attract *I. typographus* and once these trees with root rot may even serve as focal point for a new bark beetle infestation.

Results of this study support the third hypotheses and previous interaction studies presented in the introduction, suggesting that interaction between root pathogens and bark beetles is stronger when the beetle population density is at a low level (Alexander et al., 1980; Cobb, 1989; Goheen & Hansen, 1993; Lewis & Lindgren, 2002). In this study root rot incidence was highest among the trees that were in the infestation class "Severe infestation". A large proportion of trees within this class were either dead or severely damaged by bark beetle, in other words the infestation had progressed further compared to the trees within infestation class "Moderate infestation". When *I. typographus* infested trees were further divided into classes "Alive" and "Dead", relative proportion of root rot was considerably higher among dead trees compared to living trees. These results suggest that root rot has a bigger impact to the *I. typographus* infestation risk in the beginning of the outbreak, when population density of the bark beetle is relatively low. When the outbreak progresses, impact of root root weakens, as

bark beetles can attack and kill also vigorous trees. This theory is further supported by the fact that the proportion of trees which had both *I. typographus* infestation and root rot was generally higher within those stands, where the share of the bark beetle infested trees was less than 50% from all the trees within the stand. However, the exception to this trend was a stand located in Purola, where both the proportion of *I. typographus* infested trees within the stand and proportion of stumps with root rot and bark beetle infested infestation was among the three highest in this study.

# 4.2 Stand and tree characteristics

Even though root rot had the most significant effect on the *I. typographus* infestation among the studied variables, it certainly was not the only factor affecting the bark beetle incidence, as it was only observed from 11.6% of the *I. typographus* infested trees. Sproull et al. (2015) concluded that stand structure characteristics, especially diameter, best indicate the likelihood of *I. typographus* attack. Similarly, Zolubas et al. (2009) found that larger mean diameter, higher spruce basal area, and higher stand density index for spruce increase the *I. typographus* incidence compared to uninfested sites. Both Jakuš et al. (2011) and Korolyova et al. (2022) found that *I. typographus* infested trees were usually located in a stands with higher basal area compared to uninfested trees. Korolyova et al. (2022) concluded that higher stand density leads to resource limitations and increasing competition, which in turn may affect negatively on trees ability to allocate resources to the defense.

*I. typographus* is generally perceived as a pest of mature Norway spruce trees, as it preferably attacks trees with larger diameter (e.g., Jakuš et al., 2011; Korolyova et al., 2022; Sproull et al., 2015). Preference of *I. typographus* towards trees with larger diameter was also observed in this study, as the relative proportion of *I. typographus* infested trees was higher in the diameter classes of 30 cm and above compared to the smaller classes. The reason why DBH was not found to be statistically significant predictor to infestation status in the GLMM, was probably due to the technical restrictions of the model. GLMM excludes all the observations that contain missing values, meaning that all the trees which stump was not assessed after the felling were

excluded from the Model 1. Even more observations were excluded from the Model 2, as Growth was measured only from 207 trees.

When comparing distribution of infested and non-infested trees within DBH classes, differences between these three datasets can be observed. When comparing the dataset containing all the DBH observations to the dataset included in the Model 1, *I. typographus* infested trees' slight trend towards larger diameter narrows. When looking at the DBH distribution of infested trees included in the Model 2, no clear trend can be observed. Instead, all the trees in the smallest DBH class are infested with *I. typographus*. This may explain why DBH is not statistically significant predictor in the Model 1, and why its' significance further diminishes in the Model 2. However, the importance of tree diameter decreases as the population density of *I. typographus* increases, as beetles attack less selectively during the peak of the outbreak (Sproull et al., 2015). Also, Lausch et al. (2011) did not find DBH or the increment of trees to affect the preferences of *I. typographus*.

*I. typographus* is known to attack stressed trees with low vigor. Baier (1996) suggested that reduced growth could be a sign of reduced tree vigor, which in turn increases trees susceptibility to bark beetle infestation. Hilszczanski et al. (2006) found some decrease of annual radial increment in *I. typographus* infested plots compared to healthy plots, but the differences were not statistically significant. In this study, growth was on average slower among infested trees compared to non-infested trees, but there was also lot of variation between individual trees. According to the GLMM, reduced diameter growth was statistically significant predictor to *I. typographus* infestation, but the sample size was relatively small, which limits the predictive power of the model. It is also good to consider how growth was measured in the field. A substantial number of the stumps were in poor condition: consumed by weather or damaged during the felling. Also, abundant resin bleeding made counting the annual rings difficult.

While the growth of an individual tree is largely influenced by its vigor, it is also influenced by the competition with other trees for limited resources (Wykoff, 1990). In a study conducted by Jakuš et al. (2011), trees social status determined whether the tree was dead or survived from the *I. typographus* attack. Superior trees were mostly alive,

while majority of the dominant trees were dead. Korolyova et al. (2022) used stand density as simple proxy for competition and found that variation in stand density was the most important factor affecting the *I. typographus* infestation. Increment achieved by an individual tree is dependent on its competitive status relative to neighboring trees, and thus BAL can be used to measure competition status and relative dominance of trees (Wykoff, 1990). BAL was also evaluated in this study because competing for resources can cause stress for subordinate trees and thus predispose trees to attacks to *I. typographus*. However, BAL did not have an effect on the probability for *I. typographus* infestation. Contrary to expectations, BAL value had slightly lower median among the infested trees, suggesting that trees in a better competitive position were more frequently infested compared to subordinate trees. As trees with larger diameter have lower BAL value, this result may be due to the preference of *I. typographus* towards trees with larger diameter.

Another thing to consider is BAL-resolution and size variation of the trees within the sample plots. The plot size determines a specific BAL-resolution, defined as the variations in BAL among adjacent trees in the DBH distribution (Ledermann & Eckmüllner, 2004). The smaller the differences are in BAL, the bigger is the BAL-resolution and vice versa. When there is a small amount of tree records per sample plot with almost same DBH, this bias becomes large (Ledermann & Eckmüllner, 2004). In this study, the number of trees within the sample plot varied between 8 to 29 trees. Trees in Finnish commercial forests are typically rather same sized due to thinning, and this was also observed within the sample plots. Low variation in tree diameter may have caused less true competition effect within sample plots and thus bias in BAL.

Each sample plots' distance from the nearest forest edge (excluding north-facing edges) was calculated, because generally stands with increased light and temperature are more susceptible to *I. typographus* infestation (Hilszczahski et al., 2006). Fresh forest edges are especially susceptible to infestation, as *I. typographus* prefers breeding material exposed to sun, and at the same time edge trees formerly located within closed stand are not adapted to the sudden increase in solar radiation (Schroeder & Lindelöw, 2002). Sudden sun exposure may cause heat damage to the phloem, elevate transpiration rates and ultimately expose trees to drought stress, which all together weaken trees'

resistance against bark beetles (Kautz et al., 2013). This can be observed especially at the south-facing cleared edges, whereas trees on forest edges with a northern exposure are usually not stressed (Jakuš et al., 2011). Bark beetle larvae develop faster and are able to produce more generations per year on warmer, south-facing slopes that are exposed to sun (Stadelmann et al., 2013). Moreover, according to Kautz et al. (2013) higher bark temperatures increase VOC emissions form trees, attracting *I. typographus* and making it easier for them to detect susceptible host trees.

In this study, sample plots' distance from the nearest forest edge did not have an unambiguous effect on *I. typographus* infestation status. Infested trees had slightly higher median, suggesting that increase in the distance from the forest edge actually increased *I. typographus* incidence. However, scatter plot shows that infested and non-infested trees were rather evenly distributed along the different distances from the forest edge. Still, including the variable Plot into the GLMM as nested random effect improved model performance, indicating that sample plots' location had an effect on the *I. typographus* infestation incidence. However, this is probably due to the choice of sample plot location made in the field rather than the distance itself.

Among the factors that were not studied in this thesis, crown structure, especially its length and self-shading capacity, is often associated with the trees susceptibility to *I. typographus* infestation (Jakuš et al., 2011; Kautz et al., 2013; Korolyova et al., 2022). The height of the crown from top to the lowest branches determines the proportion of stem shaded by canopy. Under normal conditions a tree trunk is protected from direct solar radiation either by its own branches (individual shading) or by the canopies of nearby trees (collective shading) (Jakuš et al., 2011). When gap-inducing disturbance, such as bark beetle related mortality occurs, adjacent trees or their foliage no longer protect trees form the direct solar radiation. In dense stands with short tree crowns, a larger part of the tree trunk is now exposed to sunlight, which may eventually affect the water transpiration (Jakuš et al., 2011). Thus, the effect is very similar to a situation where trees are standing next to the edge of freshly cut down forest. As conclusion, it is not necessarily the distance from the nearest gap or forest edge itself that makes trees susceptible to *I. typographus* infestation, but rather the trees crown length and self-

shading capacity combined with the increased solar radiation within the forest edge/gap.

Indeed, the higher level of tree self-shading by canopy appears to increase trees resistance against bark beetles (Jakuš et al., 2011; Korolyova et al., 2022). Jakuš et al. (2011) concluded that trees with higher level of stem shading, i.e., longer crown length, were more likely to survive form the *I. typographus* outbreak. Similarly, Korolyova et al. (2022) demonstrated that probability of survival exhibited a consistent increase with higher levels of self-shading, reaching close to 100% for trees with complete crowns. Moreover, Baier (1996) discovered a negative correlation between the length of the crown in spruce trees and the frequency of boring attempts by *I. typographus* into the phloem. However, Sproull et al. (2015) found that trees with relatively longer crowns did not survive better, instead they were attacked more severely by bark beetles.

It is also suggested that trees with bigger crowns are more resistant to *I. typographus* attacks because of their enhanced photosynthetic capacity and higher carbon reserves (Korolyova et al., 2022). Larger crowns improve the net carbon uptake in trees, and further influence allocation of carbon within the tree (Korolyova et al., 2022). Christiansen et al. (1987) suggested that trees ability to resist bark beetle attacks is associated with the amount of carbohydrates available for immediate use in defensive responses, such as resin flow. Thus, any abiotic or biotic factor that limits the size of the tree's crown and thus its photosynthetic capacity may weaken trees' resistance against bark beetles (Christiansen et al., 1987).

Christiansen (1991) further hypothesized, that trees carbon balance may be a common denominator between all these above-mentioned factors, which are linked to increased risk of *I. typographus* infestation. As discussed in the introduction, trees defend themselves against fungal attack by forming reaction zone (Shain, 1979). Reaction zone formation requires synthesis of secondary metabolites and re-allocation of resources towards the compartmentalization of decay, and this may deplete trees carbon reserves (Christiansen et al., 1987; Oliva et al., 2010). Also, competition, drought stress, defoliation and old age, which is connected to the larger diameter of the tree, are known to reduce C availability (Jakuš et al., 2011).

# 4.3 Environmental factors and climate change

Another thing that was not considered in this study was the effect of environmental factors. Marini et al. (2017) found that higher summer temperatures, water deficit and availability of wind-felled trees increased timber loss caused by *I. typographus*. Drought has both direct adverse effects on tree growth and survival, but it also may trigger more frequent or severe outbreaks of forest insects (Jactel et al., 2012). Especially bark beetles and wood borers benefit from drought (Huberty & Denno, 2004). Warmer spring and summer temperatures accelerate bark beetle development, and the ability of *I. typographus* to modify its generation time with changes in temperature regimes, allows the species to take advantage of improved thermal conditions (Jönsson et al., 2009).

Korolyova et al. (2022) discovered that the negative effects of competition were pronounced, and the positive effects of self-shading were decreased when long-term water supply was limited. *I. typographus* infestation probability of individual trees increased steeply when mean water availability was consistently below the average conditions (Korolyova et al., 2022). Water stress causes decrease in concentrations of carbohydrates and nitrogen in the stem as discussed above (Jactel et al., 2012). Production of carbon-rich defensive compounds, such as terpenes and phenols is potentially reduced, as well as sap flow and oleoresin production and pressure (Christiansen et al., 1987; Jactel et al., 2012).

Pathogenicity may either be reduced or enhanced with increasing drought, as it is highly dependent on the pathogen species considered (Jactel et al., 2012). In general, direct effect of drought on forest pathogens are expected to be mainly negative, because fungi require high humidity conditions for spore dispersal, germination and infection (Jactel et al., 2012). However, wood moisture content is not critical for the stump infection of *Heterobasidion* sp. (Bendz-Hellgren & Stenlid, 1998). Instead, further growth of the fungus is significantly decreased with increasing stump moisture, suggesting that in contrast to Norway spruce, *Heterobasidion* sp. may not be negatively affected from the decreased water availability (Bendz-Hellgren & Stenlid, 1998). This was demonstrated as Terhonen et al. (2019) inoculated Norway spruce saplings with *H*.

*parviporum* and *H. annosum* s.s. and discovered that pathogen growth was increased under drought in saplings. Moreover, drought affected the growth of Norway spruce saplings making them more susceptible for root rot infection (Terhonen et al., 2019).

Gori et al. (2013) found that *H. parviporum* was more aggressive, caused more rapid decline, and increased drought stress in Norway spruce at lower elevations in Alps compared to higher elevations. Higher tolerance of Norway spruce to root rot in the higher elevations was suggested to be related to worse growth conditions to the fungus, e.g., lower temperature and higher water availability, rather than genetic variation in host tree tolerance (Gori et al., 2013). This indicates that as climate warms, *H. parviporum* could be more destructive at high elevation or latitude sites.

The probability of longer summer droughts and other extreme weather events are expected to increase in response to the climate change (Seidl et al., 2017). *Heterobasidion* sp. and *I. typographus* pose a serious and gradually increasing threat to the European Norway spruce forests, which are already troubled. Both *I. typographus* and *Heterobasidion* sp. are expected to benefit from increasing temperatures and drought, as discussed above. Drought may intensify water stress and damages caused by root rot, making trees even more vulnerable to subsequent bark beetle attacks. Thus, the interaction between *Heterobasidion* sp. and I. *typographus* may be highlighted in the future.

As these two disturbance agents are linked, protecting trees from root rot infection may help to protect trees from *I. typographus* infestation as well. Stump treatment is an effective way to prevent root rot infection when trees are harvested in a warm season, i.e., during the time of the sporulation of *Heterobasidion* sp. As climate warms, the time slot when temperature is below  $+5^{\circ}$ C gets narrower, and increasing amount of harvesting is done during the warm season. Therefore, stump treatment will have an increasingly significant role in the future in the control of root rot, and indirectly in the control of *I. typographus* as well.

# 4.4 Limitations of the study

In this study, there are two clear limitations that may impact the reliability of the results. First, the amount of root rot infected stumps was relatively small, and second, all the stumps could not be found after the final felling.

The unpredictability of the date of the final felling, set challenges for the field work. The final fellings were made according to the schedules of forestry companies, and on many stands, the planned harvesting date changed multiple times and was significantly delayed due to e.g., varying weather conditions and economic fluctuations. This unpredictability also affected how soon the stands could be measured after harvesting. If the time between harvesting and the second measurements was long, measuring the growth from the stumps proved challenging. To obtain more reliable results from the diameter growth, it should be measured with increment borer or at least from the fresh stump surface. Since the final fellings were not planned according to the purposes of this study, logging residues were often left on the sample plots and/or stumps were severely damaged during harvesting. To avoid unnecessary "stump loss" like this, this type of study should be conducted in close collaboration with the company implementing the fellings.

Due to a lack of time and resources, the species causing the root rot was not determined, as species identification would have required DNA sequencing. *Heterobasidion* sp. is estimated to cause approximately 80% of spruce root rot in Southern Finland (Piri et al., 2019). However, the second most common root rot causing fungi in Finnish Norway spruce stands are *Armillaria* sp., and it cannot be entirely excluded that some of the rot would have been caused by them. In addition, the formation of reaction zone was not measured. Thus, it remains unclear whether the tree has allocated resources to compartmentalization of decay or not.

#### 4.5 Suggestions for future research

The study results and limitations highlight several directions for future research. Results suggest that on a tree level, root rot is one of the factors that exposes trees to *I. typographus* infestation. However, the study does not fully capture the spatial variation of the phenomenon and the influence of tree and stand characteristics, and this needs to be further investigated. Environmental factors, especially drought, seem to favor both *Heterobasidion* sp. and *I. typographus*. Therefore, it would be useful to study how annual variations in temperature sums and precipitation affect the interaction between these two disturbance agents.

The carbon balance of the tree is believed to have an important role in the tree's defense reactions, and this could be studied in more detail in the context of root rot-bark beetle interactions. One approach could be to investigate whether decay is strictly confined to the heartwood, or if the tree has formed a reaction zone, thus allocating resources to compartmentalize the decay. This may have implications for the tree's ability to defend itself against *I. typographus* attacks. As reaction zone is characterized by increased pH, fresh stump surfaces could be sprayed with pH indicator to identify whether tree has formed a reaction zone or not, as in the study by Oliva et al. (2010).

# 5 CONCLUSIONS

This thesis investigated the direct interaction between Heterobasidion root rot and *I. typographus*, and their impacts on Norway spruce. More specifically, the aim was to examine if root rot and the stress it poses to a tree increases the risk for bark beetle attack. Trees infested with *I. typographus* were not consistently infected with root rot. However, based on the quantitative analyses, root rot infection appears to be a significant factor making trees susceptible to *I. typographus* infestation. Root rot seems to have a greater impact on the subsequent *I. typographus* infestation in the beginning of the outbreak when population density of the bark beetle is low. However, stand structure and tree characteristics also have an impact on the occurrence of *I.* 

*typographus*. Among other factors studied, larger diameter at breast height and reduction in diameter growth increased the risk of *I. typographus* infestation.

Norway spruce is one of the most economically important tree species in Europe, and it has expected to face many challenges under the climate change. The increase in temperatures and water deficit in themselves induce stress on the spruce. Moreover, both Heterobasidion root rot and the *I. typographus* benefit from increasing drought, which may potentially cause cascading disturbances on Norway spruce dominated forests. However, it is important to bear in mind that interactions between disturbance agents are not straightforward and may have damping effects in the longer time scale. Nevertheless, it is obvious that forest managers need to be prepared and adapted to the increased disturbance risks associated with Norway spruce.

Management-wise, results of this study suggest that protecting trees from root rot infection may help to protect trees from *I. typographus* infestation as well, at least when bark beetle population densities are low and stable. Mixed-species stands are usually less susceptible to large-scale bark beetle infestations, and the presence of non-host species also slows down the spread of root rot infection. Furthermore, adequate thinning could improve water availability and decrease competition among trees within the stand. On the other hand, thinning may predispose standing trees to root rot infection and if done too intensively, decrease trees self-shading capacity. That is, forest management measures often have multiple, sometimes conflicting effects on different disturbance agents. Making compromises and balancing between different risks will have an increasingly important role in future forest management.

Complex interactions and feedback dynamics will continue to govern the future disturbance dynamics in the forests. Biotic disturbance agents, in particular, may become more vulnerable to further intensification through the influence of other disturbance agents. Therefore, it is important to consider both individual disturbances and their interactive effects. This thesis provides a new perspective on the interaction between root rot and *I. typographus*. As it appears, root rot is linked to the *I. typographus* not only through wind-induced damages, but also directly by reducing tree vigor and its ability to defend itself against bark beetle attacks. However, future studies

are needed to further investigate the underlying mechanisms of this phenomenon, as well as its spatial variation.

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