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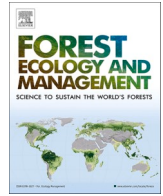
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Root rot increases the vulnerability of Norway spruce trees to *Ips typographus* infestation

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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 the European spruce bark beetle (*Ips typographus*) are major disturbance agents of Norway spruce and are expected to increasingly affect spruce-dominated forests as the climate warms. This study investigated the direct interaction between root rot and *I. typographus*, with the aim of examining whether root rot and the stress it causes to a tree increases the risk of subsequent bark beetle attack.

In total, 442 Norway spruce trees from nine different mature, even-aged forest stands were studied. First, symptoms caused by *I. typographus* were evaluated before final felling from each tree based on visual assessments of crown and stem conditions. After the felling, the sample plots were relocated from the clearcut areas, and the stumps of sampled trees were reassessed for root rot. Exploratory analysis and binomial Generalized Linear Mixed Model (GLMM) were used to analyze relationships between explanatory variables and their effect to *I. typographus* infestation.

The best predictors for *I. typographus* infestation at individual tree level were presence of root rot and to a lesser extent, tree diameter at breast height. Seventy-five percent of root rot-infected trees were also infested with *I. typographus*, and most of those trees were either dead or severely infested. Results suggest that root rot weakens trees, making them more vulnerable to subsequent *I. typographus* infestation, especially early in outbreaks when bark beetle population densities are low.

1. Introduction

Norway spruce (*Picea abies* (L.) H. Karst.) is one of the most common and economically significant conifer tree species in Northern and Central Europe (Jansson et al., 2013). It 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). However, climate change poses significant challenges to Norway spruce, including increased susceptibility to drought stress due to its shallow root system (Lévesque et al., 2013), and vulnerability to biotic disturbances such as pests and pathogens (Jactel et al., 2012). European spruce bark beetle (*Ips typographus* (L.), Coleoptera: Curculionidae) and root rot caused by *Heterobasidion* spp. are the most severe biotic disturbance agents on Norway spruce, causing great

economic losses (Asiegbu et al., 2005; Hlásny et al., 2019). Both of these agents are likely to have greater impact on spruce-dominated forests as the climate warms (Müller et al., 2014; Seidl et al., 2016). Therefore, understanding potential interactions between *I. typographus* and *Heterobasidion* spp. is crucial for managing the health and sustainability of Norway spruce-dominated forests.

Heterobasidion annosum sensu lato is a species complex comprising of five species, three of which are native to Europe: *H. abietinum* Niemelä and Korhonen, *H. annosum* s.s. (Fr.) Bref. and *H. parviporum* Niemelä and Korhonen (1978). These species have different and partly overlapping host preferences, however, the main host species are firs (*Abies* sp., *H. abietinum*), pines (*Pinus* sp., *H. annosum* s.s.) and spruces (*Picea* sp., *H. parviporum*) (Korhonen, 1978). *Heterobasidion* spp. are common in intensively managed forests, especially if logging activities are

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conducted during the growing season. Primary infection by *Heterobasidion* spp. occur, when basidiospores disperse in the air and land on freshly exposed wood substrate such as freshly cut stumps or wounds in stem or roots (Redfern and Stenlid, 1998). After primary infection, fungus spreads to the next tree generation or neighboring uninjured trees through vegetative growth of the mycelium and root contacts (Garbelotto and Gonthier, 2013). This is the main pathway for infections to spread within the stand, and makes silvicultural control of the disease difficult (Garbelotto and Gonthier, 2013; Nevalainen and Piri, 2020). Pathogen may remain viable and infective in the stumps for decades and serve as inoculum source for the following tree generations (Piri et al., 2021).

Armillaria spp. are the second most significant fungi causing root rot in Norway spruce, after *Heterobasidion* spp. (Kedves et al., 2021; Vainio et al., 2022). Like *Heterobasidion* spp., *Armillaria* basidiospores infect tree stumps and wounded roots, but the primary dispersal method is through root-like rhizomorphs, which allow the fungus to spread efficiently through the soil and colonize new trees (Heinzelmann et al., 2019; Kedves et al., 2021). As highly diverse group, *Armillaria* spp.'s pathogenicity varies greatly and they are often found in trees already weakened by drought or *Heterobasidion* root rot (Kedves et al., 2021; Vainio et al., 2022).

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 and Hammerbacher, 2022). *Ips 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 breeding material for *I. typographus* (Komonen et al., 2011).

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). Primary disturbance may drive a direct 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 types is often termed as a "linked disturbance" and the latter one a "compound disturbance" (Paine et al., 1998; Simard et al., 2011). Interaction between different disturbance agents may lead to cascading effects, when primary disturbance increases the severity of the following disturbances caused by another agent (Buma, 2015). 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). 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).

Bark beetles are typically associated with trees of low vigor and root pathogens are known to be important agents in making trees more susceptible to infestations by certain bark beetle species (Cobb, 1989; Goheen and Hansen, 1993; Hlásny et al., 2019). It is frequently suggested that root rot reduces trees' resistance against bark beetles by disrupting the water uptake, which increases moisture stress and reduces resin exudation pressure and thus the trees' ability to pitch out beetles (Alexander et al., 1980; Tkacz and Schmiz, 1985; Goheen and Hansen, 1993). Additionally, the formation of reaction zones to restrict advancing decay demands significant carbohydrate resources,

potentially compromising the trees' ability to defend against beetles (Shain, 1979; Christiansen et al., 1987). Some studies also suggest that chemicals released by diseased trees might attract certain beetle species, although evidence for this is varied (Moeck et al., 1981; Gara et al., 1984; Goheen et al., 1985; Tkacz and Schmiz, 1985; Jirošová et al., 2022).

Interactions between root pathogens and bark beetles has been studied especially in North America and with primary focus on the genus *Dendroctonus* and pine trees. For example, *Armillaria* species have been found to increase the incidence of mountain pine beetles (*D. ponderosae*) on ponderosa pine and lodgepole pine, as demonstrated by Lessard (1985) and Tkacz and Schmiz (1985). Similarly, Hadfield et al. (1986) reported that *Heterobasidion annosum* infections led to increased attacks by mountain pine beetles and western pine beetles (*D. brevicornis*), while (Alexander et al., 1980) found that the same pathogen increased the susceptibility of trees to southern pine beetle (*D. frontalis*) attacks in thinned stands located at high risk *Heterobasidion* root rot sites. In contrast, less research has been done on spruce trees and their related pathogens and insect pests. However, Lewis and Lindgren (2002) explored the relationship between the root disease fungus *Inonotus tomentosus* and the spruce beetle (*D. rufipennis*). Their findings suggest that while *I. tomentosus*-infected trees are not necessarily more attractive to spruce beetles as such, they have the potential to support greater beetle populations at low densities compared to healthy trees.

Disturbances caused by root rot and bark beetles have also indirect interaction through wind damages (Giordano et al., 2012; Honkaniemi et al., 2017). *Heterobasidion* root rot predisposes Norway spruce to uprooting and windthrow by weakening their root system and stem base, which reduces trees' ability to anchor to the ground and increases the risk of stem breakage (Giordano et al., 2012). *Ips typographus* then colonizes and breeds on weakened wind-fallen trees (Komonen et al., 2011). Even though this indirect interaction between *Heterobasidion* root rot and *I. typographus* through wind disturbances is well-known and described, direct interaction between *Heterobasidion* spp. and *I. typographus* has not been studied in the field.

This study aimed to investigate the potential direct interaction between *Heterobasidion* root rot and *I. typographus* and their impacts on Norway spruce. Specifically, the aim was to analyze if decay in stem base and the stress it poses to a tree increases the risk for bark beetle attack. Our research objective was to measure and quantify the impacts of bark beetles in Norway spruce stands in Southern Finland, and 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. We hypothesized that (1) trees infested with bark beetles are consistently also infected with root rot; (2) advanced decay of root rot weakens the tree resistance and make it easier for bark beetles to colonize and kill the tree; (3) when bark beetle population density is low, a higher proportion of trees infested with bark beetles are also infected with root rot.

2. Materials and methods

2.1. Study area

Our study was done in the southern Finland in Pirkanmaa, Uusimaa, and Kanta-Häme regions (Fig. 1). Managed forests in the study area are being increasingly characterized by Norway spruce dominated stands, as planting share of Norway spruce has been more than 70 % in these three regions during the years 2016–2020 (Ruotsalainen et al., 2022). All of the stands were private-owned Norway spruce-dominated stands located at mineral soil. Stand area varied between 1.1 and 10.8 ha, with an average of 3.3 ha.

2.2. Data collection

Nine mature, even-aged Norway spruce dominated stands were measured during the year 2023: first before their final felling to screen

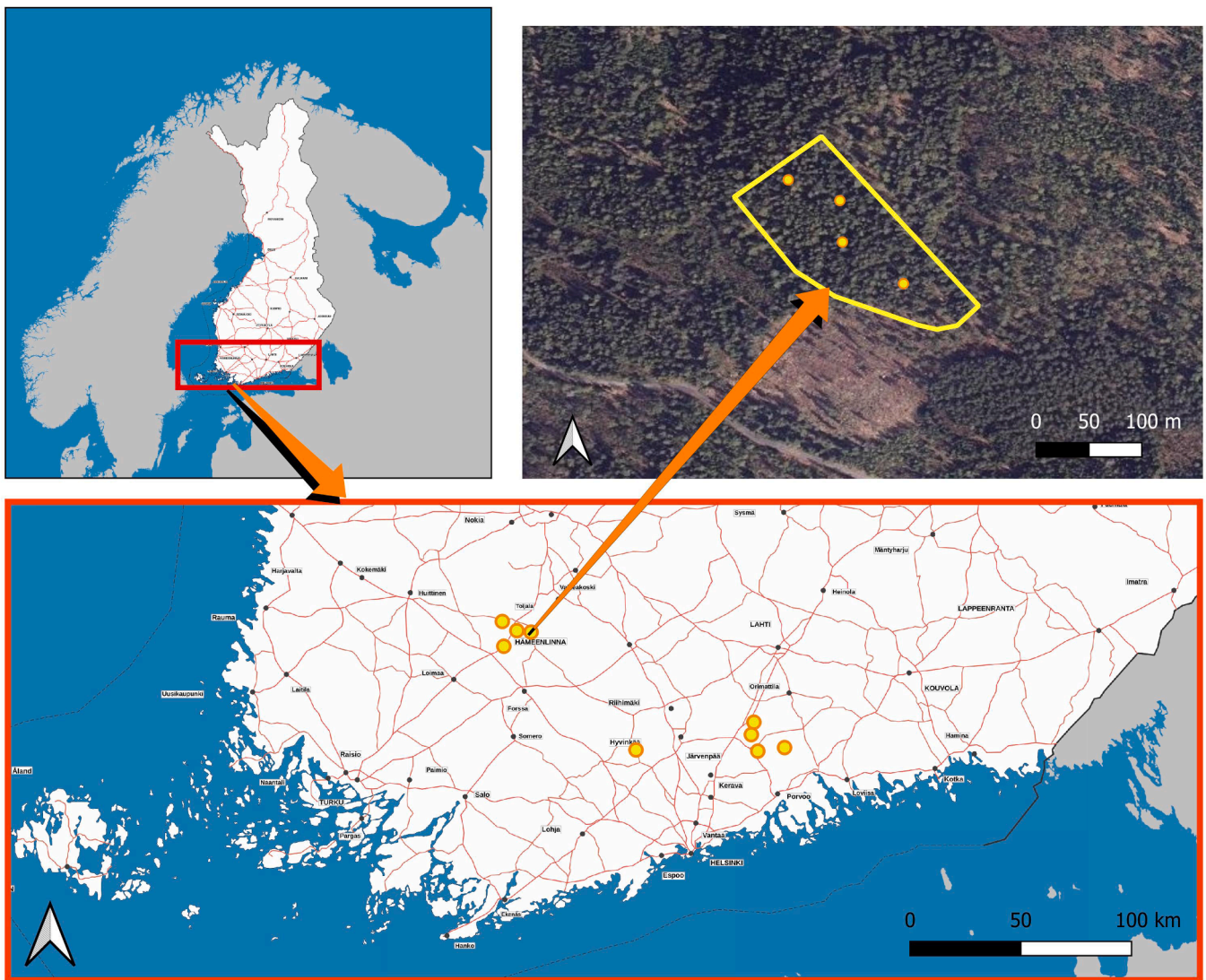


Fig. 1. The locations of the nine Norway spruce stands included in the study. Aerial map of one of the studied Norway spruce stands, and the locations of sample plots within that stand.

bark beetle damages and afterwards to observe root rot on the stump surfaces. Four circular sample plots with a radius of 8.92 m were measured from each stand. Thus, in total 36 sample plots with varying bark beetle infestation levels were measured. The locations of the sample plots were chosen in situ to comprehensively represent different degrees of bark beetle damages present within the stand.

Before the final felling, symptoms caused by *I. typographus* were assessed from each tree following the classification method described by Blomqvist et al. (2018) (Table 1). 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).

Ips typographus can be reliably recognized based on entrance holes, galleries, brown frass and debarking (Blomqvist et al., 2018; Kautz et al.,

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

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 %

2023). When bark is still attached to trees, making a distinction from other bark beetle species is more difficult. However, other possible species, such as *Ips duplicatus*, *Ips amitinus* and *Pityogenes calographus*

typically colonize upper thin-barked parts of smaller spruce trees, whereas *I. typographus* prefers lower, thick-barked sections (Jeger et al., 2017; Kavčič et al., 2023; Schebeck et al., 2023). Here, we assessed only the lowest two meter of the tree trunk, which makes it more likely that the species in question was *I. typographus*. To conclude, all the trees were assessed collectively, considering the typical biology and symptoms associated with various bark beetle species. This approach led to a reliable conclusion that the observed symptoms were caused by *I. typographus* rather than another bark beetle species.

Tree diameter at breast height (DBH), tree species, and distance of tree 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. General information on the plots including DBH range, average DBH and basal area can be found in appendixes (Table A1). 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 on stand located in Mäntsälä. The rest of the pre harvest measurement were done in a two-week 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 reassessed for root rot. Species causing the decay was identified based on visual assessments of the rot patterns on the stump surface. *Heterobasidion* infection first appears as a violet ring-shaped discoloration at the boundary between the heartwood and sapwood (Piri et al., 2019). Over time, this discoloration expands into a complete circle and gradually transforms into a hard, light brown rot that later softens as the decay process progresses (Piri et al., 2019). *Armillaria* spp. causes a dark brown rot with a dark, sharply defined boundary from healthy wood (Vainio, 2023). Decay caused by *Armillaria* spp. often leads to hollowing at the tree base and typically rhizomorphs can be observed on the stump (Vainio, 2023).

All stumps were photographed with a scale and the diameter of rot was measured in situ, from two directions (see appendixes, Fig. A1). 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 (Fig. A1).

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 after 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 (See Fig. A1). 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 from the stump impossible. In addition, in some cases trees with smaller diameter were left standing.

2.3. Statistical analysis

In addition to the variables measured directly in the field, we derived two other variables afterwards with potential significance. First, basal area of larger trees (BAL) was calculated for each Norway spruce 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 (Burkhardt and Tomé, 2012). We hypothesized that dominant trees would have better vigor and thus be less impacted by bark beetle attacks. Formula for calculating BAL is:

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

Where BA_j is the basal area (m^2) of trees which are larger than the subject tree per ha in the plot.

Secondly, 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 assuming that warm forest edges may be more favorable for bark beetle infestations (Schroeder and Lindelöw, 2002; Jakuš et al., 2011).

Point-biserial correlation analysis was conducted to examine the relationship between *I. typographus* infestation and four key variables: DBH, BAL, distance from the forest edge and 5-year growth. To examine the association between root rot and *I. typographus* infestation, a Pearson's chi-squared test with Yates' continuity correction was conducted.

Binomial Generalized Linear Mixed Model (GLMM) was used to predict trees' *I. typographus* infestation status based on the fixed predictors (DBH, Rot, BAL, Growth), while 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.

Explanatory variables with significant effects on tree infestation status were selected using the backward stepwise method, starting with variables DBH, Rot, BAL and Growth. 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 metric, the Area Under the Curve (AUC), were used to evaluate model performance. The ROC curve graphically represents a model's ability to distinguish between "Infestation" and "No infestation" by plotting the True Positive Rate (Sensitivity) against the False Positive Rate (1 - Specificity). AUC, ranging from 0 to 1, summarizes the ROC curve, with higher values indicating better performance (Fawcett, 2006). Finally, Q-Q plots and Residual vs. Fitted plots, were used to evaluate the goodness of fit of the final model.

The final model included only DBH and Rot as fixed predictors and Stand and Plot as nested random effects:

$$\begin{aligned} P(\text{Infestation} = 1) &= \text{logit}^{-1}(\beta_0 + \beta_1 \times \text{DBH} + \beta_2 \\ &\times \text{Rot} + \upsilon_{\text{Stand/Plot}}), \end{aligned} \quad (2)$$

Where:

- $P(\text{Infestation}=1)$ is the probability of infestation being 1.
- logit^{-1} is the logistic function that transforms the linear combination of predictors to the probability scale.
- β_0 is the intercept.
- β_1 is the vector of coefficients for variable DBH.
- β_2 is the vector of coefficients for variable Rot.
- $\upsilon_{\text{Stand/Plot}}$ represents the vector of random effects for the grouping structure Stand/Plot.

All analyses were performed using R Statistical Software (R Core Team, 2023) Data visualization and exploration was conducted using the *ggplot2* R package (Wickham, 2016), which facilitated the creation of boxplots, bar plots, scatter plots, and grid layouts of multiple plots. The *gridExtra* R package (Auguie, 2017) was used to arrange multiple plots

into a single layout for comparative visualization, complemented by the *cowplot* R package (Wilke, 2023) for extracting and arranging legends and multiple plots. Cross-tabulation tables to summarize relationships between categorical variables were generated using the *sjPlot* R package (Lüdtke, 2023). Data manipulation and transformation were carried out with the *dplyr* R package (Wickham et al., 2023) enabling efficient grouping, summarization, mutation, and filtering of data.

Generalized linear mixed models (GLMMs) were fitted using the *lme4* R package (Bates et al., 2015), allowing for the inclusion of random effects in the models. ROC curves and the Area Under the Curve (AUC) were calculated using the *pROC* R package (Robin et al., 2011) to evaluate the performance of binary classifiers. Model diagnostic checks, including residual analysis and visualization, were conducted using the *DHARMA* R package (Hartig, 2022) to ensure the validity of the model assumptions. *DHARMA* simulates residuals based on the fitted model and compares them to the observed residuals, emphasizing the distribution and patterns of residuals rather than assuming normality (Hartig, 2022).

3. Results

In total, 442 Norway spruce trees from 9 different stands were measured in this study. 47 % of Norway spruce trees were infested with *I. typographus*, while 53 % had no signs of infestation. After the final felling, 87 % (N=384) of the stumps were found, identified and assessed for root rot. Root rot was recorded 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 58 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 % and 37 %, with a median value of 11 %. Fig. 2a-b shows the distribution of *I. typographus* and root rot infested trees by stand.

A Pearson's chi-squared test with Yates' continuity correction was performed to assess the relationship between the root rot and *I. typographus* incidence. The analysis revealed a statistically significant association between the variables (X-squared = 8.7358, df = 1, p-value = 0.003), indicating that the presence of root rot is associated with *I. typographus* infestation. The p-value of 0.003 suggests that the association is unlikely to have occurred by chance.

Of *I. typographus* infested trees 51 % of the trees were in class "Moderate infestation" while 49 % were 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". 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 infested trees was two-fold among the dead trees compared to living trees (Fig. 3). 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.

Ips typographus incidence did not increase or decrease together with the root rot incidence (Table 2). Results indicate that the relationship between *I. typographus* and root rot is not linear. 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 the stand located in Purola, which had both high *I. typographus* and high root rot incidence.

There was a weak but statistically significant positive correlation between *I. typographus* infestation and diameter at breast height (DBH), $r = 0.17$, $p = 0.0003$ (Fig. 4a). This implies that trees with *I. typographus* infestation tend to have slightly larger diameters at breast height compared to those without infestation, although the relationship is not particularly strong. The correlation coefficient (r) between *I. typographus* infestation and BAL (Basal Area of Larger trees) was found to be -0.099 , with a p-value of 0.037 (Fig. 4b). This suggests that there is a weak negative correlation between infestation presence and tree dominance within the forest stand, as measured by BAL. Specifically, as the infestation level increases, there is a slight increase in the competitive position or dominance of the affected trees within the forest stand.

There was also a weak but statistically significant positive

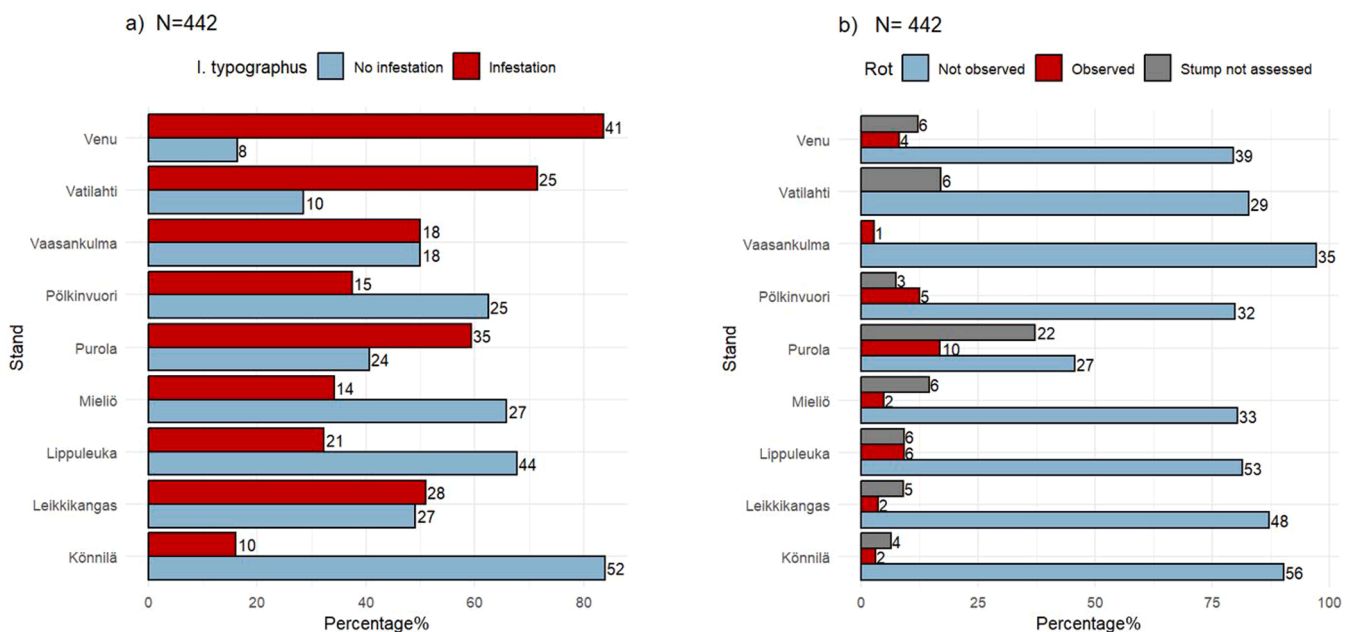


Fig. 2. *Ips typographus* infestation and root rot observations across different stands. 2a) represents the count and percentage of observations for *I. typographus* infestation status, and 2b) provides a similar breakdown for root rot observations, including the stumps that could not be assessed in the field.

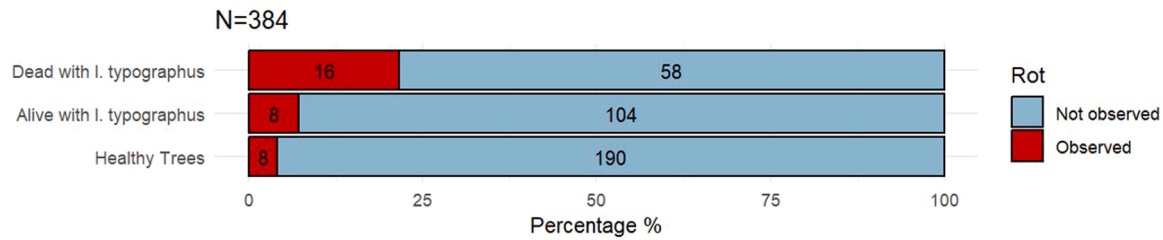


Fig. 3. The distribution of root rot observations in three categories: Healthy trees, Alive trees with *I. typographus* infestation, and Dead trees with *I. typographus* infestation. The bars represent the percentage of trees in each group, with numbers showing the count of trees. The proportion of NAs in the three categories were as follows: 12 % in Dead with *I. typographus*, 9 % in Alive with *I. typographus* and 16 % in Healthy trees.

Table 2

The proportion of *I. typographus* infested trees, and proportion of rot in trees infested with *I. typographus* in each stand.

Stand	Proportion of <i>I. typographus</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 %

correlation between *I. typographus* infestation and sample plots' distance from the forest edge, $r = 0.135$, $p = 0.0046$ (Fig. 4c). This indicates that trees with *I. typographus* infestation are slightly more likely to be located further from the forest edge compared to non-infested trees. Furthermore, the correlation coefficient (r) between *I. typographus* infestation and 5-year growth was -0.169 , with a p -value of 0.015 (Fig. 4d). This negative correlation suggests that the presence of *I. typographus*

infestation may be associated with a slight decrease in tree growth over a 5-year period, although the correlation is relatively weak and the number of observations low.

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 to 34 cm 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. 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 and 29 cm, but otherwise stumps with root rot were evenly distributed among the DBH classes. 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 30–34 cm.

The selection of explanatory variables for GLMM with significant effect on tree infestation status was made with the backward stepwise method, and the final model included DBH and Rot as fixed predictors and Stand and Plot as nested random effects. Also, growth was included into the GLMM at first, as it showed significant effect ($P = 0.03$), but as the amount of growth observations was small ($N=207$), it had to be

I. typographus No infestation Infestation

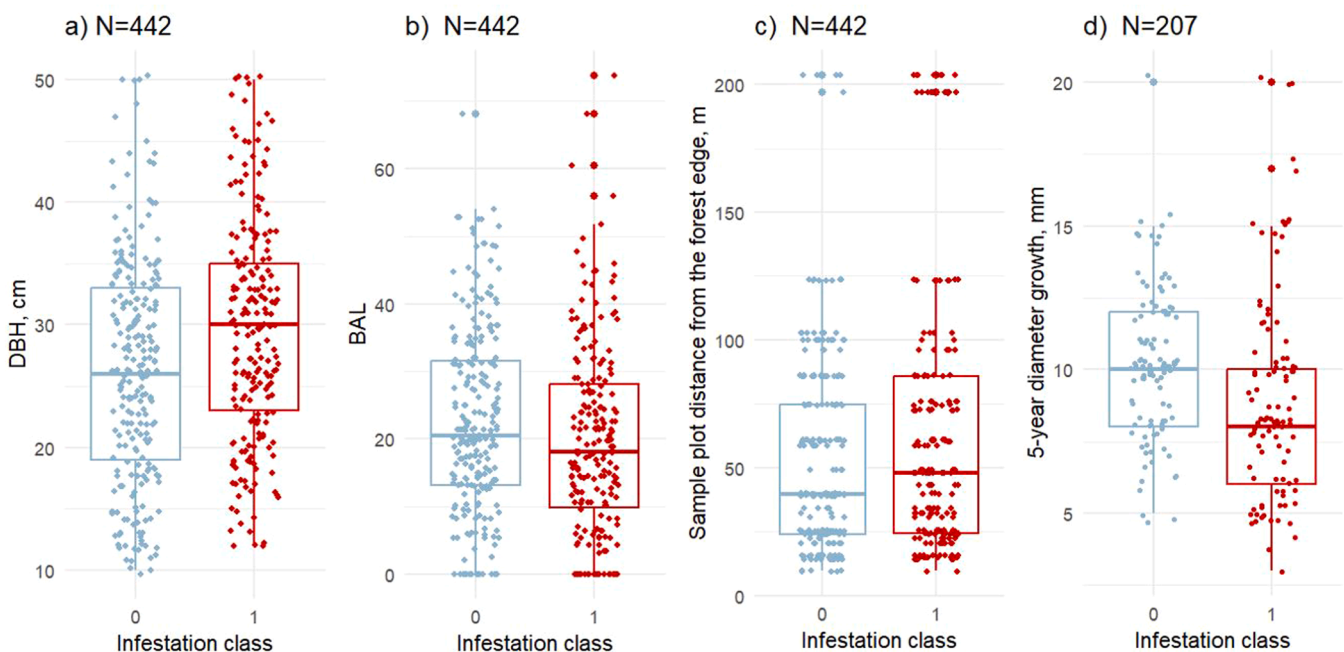


Fig. 4. Relationship between different explanatory variables and the *I. typographus* infestation status on a tree-level.

excluded from the final model. The best predictor of infestation was presence of root rot ($P < 0.01$), while DBH was not statistically significant ($P = 0.055$) (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. Positive coefficient for DBH suggests that an increase in DBH increases the probability of *I. typographus* infestation.

The ROC curve of the final model hugs the upper left corner of the plot, indicating it has a relatively high true positive rate and a low false positive rate (Fig. 5). The AUC value is 0.8249, suggesting that the model has a high probability of ranking a randomly chosen positive instance higher than a randomly chosen negative instance approximately 82 % of the time. This implies that the model performs well at differentiating the cases into classes “Infestation” and “No Infestation.” Moreover, in the Q-Q plot, points closely follow the diagonal line (Fig. A2). There are no departures from linearity that would indicate model misspecification or outliers. Also, residuals are rather evenly distributed suggesting that on average the model’s predictions are unbiased (Fig. A3). 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.

4. Discussion

Disturbance interactions have potential to either cascade or dampen the impacts on forests. Here, we studied the potential direct interactions between two of the most important biotic disturbance agents in European coniferous forests, *I. typographus* and Heterobasidion root rot. Our study results indicate that the best predictors for *I. typographus* infestation on a single-tree level are presence of root rot and to a lesser extent, larger diameter at breast height. Unlike hypothesized, trees infested with *I. typographus* were not consistently infected with root rot, as only 12 % 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 them more vulnerable 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).

Results of this study support the third hypothesis and previous interaction studies, 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 and Hansen, 1993; Lewis and Lindgren, 2002). In this study, root rot incidence was highest among the trees that were in the infestation class “Severe infestation”. Trees within this class were either dead or severely damaged by bark beetle, i.e., 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

Table 3

Coefficient table for the final model. n=384.

The final model: Infestation ~ DBH + Rot + (1 Stand/Plot)				
Fixed effects	Coefficient	Standard Error	Z-Value	P
(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	< 0.01

Bold values are significant at $P < 0.01$.

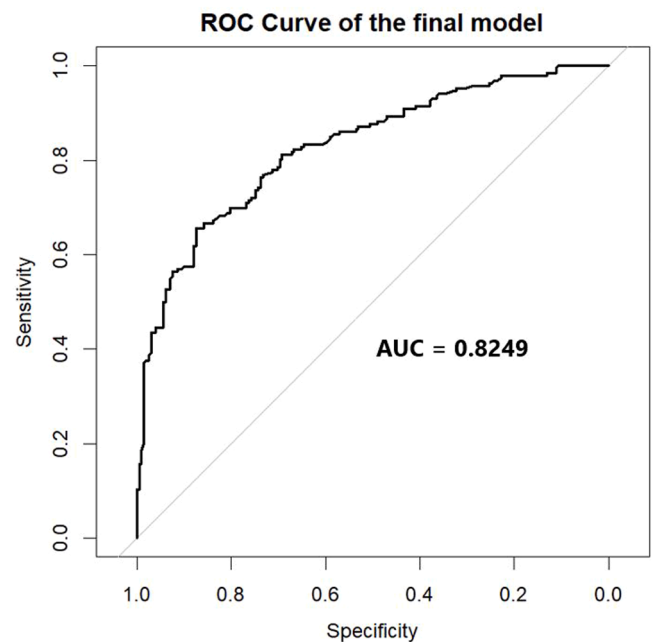


Fig. 5. ROC curve and AUC of the final model. Rot and DBH as explanatory variables. N=384.

beetle is relatively low. When the outbreak progresses, impact of root rot 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 Puroola, where both the proportion of *I. typographus* infested trees within the stand and proportion of stumps with root rot and bark beetle infestation was among the three highest in this study.

Heterobasidion root rot spreads within the stands to adjacent trees via root contacts, and propagation of decay from roots further to the stem base of the tree may take several years (Stenlid and 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. Thus, root infection may at least partly explain *I. typographus* infestation of trees that are adjacent to the trees with identified root rot on the stump surface. On the other hand, even though *I. typographus* has a dispersal range of 500 m 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). Therefore, root rot weakened trees may attract *I. typographus* and once these trees have been colonized, beetles move to the adjacent healthy trees. In this sense, trees with root rot may even serve as focal point for a new bark beetle infestation.

Even though root rot had statistically significant effect on the occurrence of *I. typographus* infestation, it was only observed from 12 % of the *I. typographus* infested trees. Moreover, trees with root rot but without *I. typographus* infestation were found from three stands, where both proportional and absolute root rot incidence was highest, suggesting that root rot alone is not the only factor contributing to bark beetle incidence. Sproull et al. (2015) concluded that stand structure characteristics, especially tree diameter, is a key predictor of *I. typographus* attack. Similarly, Zolubas et al. (2009) noted 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. Also, there was weak but statistically significant positive correlation between DBH and *I. typographus* infestation in point-biserial correlation test. The reason 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. When comparing the dataset containing all the DBH observations to the dataset included in the final model, *I. typographus* infested trees' slight trend towards larger diameter narrows. This may explain why DBH is not statistically significant predictor in the final model. 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*.

Ips 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. Hilszczański 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 the present study, growth was on average slower among infested trees compared to non-infested trees, and negative correlation between growth and *I. typographus* suggests that the presence of *I. typographus* infestation may be associated with a slight decrease in tree growth over a 5-year period. However, there was also lot of variation between individual trees and the sample size was relatively small. 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.

The growth of an individual tree is largely influenced by its vigor, and tree's vigor 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 died on or survived from the *I. typographus* attack. Superior trees were mostly alive, while majority of the dominant trees were found dead. Korolyova et al. (2022) used stand density as a simple proxy for competition and found that variation in stand density was the key factor affecting the *I. typographus* infestation. BAL was included in this study as a measure of tree competition and relative dominance, since competition-induced stress in subordinate trees may predispose them to *I. typographus* attacks. However, BAL did not have an effect on the probability for *I. typographus* infestation in present study. Contrary to expectations, BAL value had a weak negative correlation with *I. typographus* infestation, suggesting that trees in a better competitive position were more frequently infested compared to subordinate trees. Since larger trees have lower BAL values, this may reflect a preference of *I. typographus* for larger-diameter trees. Another factor to consider is BAL-resolution which reflects size variation of trees within plots. The plot size determines a specific BAL-resolution, defined as the variations in BAL among adjacent trees in the DBH distribution (Ledermann and Eckmüllner, 2004). Smaller DBH differences increase BAL-resolution, introducing potential bias when plots have few, similarly-sized trees (Ledermann and Eckmüllner, 2004). In this study, tree counts per plot

ranged from 8 to 29. While small diameter variation was observed in some, but not all, plots due to thinning practices in Finnish commercial forests, this uniformity may have reduced true competition effects and potentially biased BAL measurements.

Each sample plots' distance from the nearest forest edge (excluding north-facing edges) was calculated, as increased light and temperature at forest edges make stands more susceptible to *I. typographus* infestation (Hilszczański et al., 2006). Fresh forest edges are particularly vulnerable, as *I. typographus* prefers breeding material exposed to sun, and trees unaccustomed to sudden increase in solar radiation may suffer from heat damages to phloem, increased transpiration and drought stress, reducing their resistance against bark beetles (Schroeder and Lindelöw, 2002; 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). Moreover, according to Kautz et al. (2013) higher bark temperatures increase VOC emissions from trees, attracting *I. typographus* and making it easier for them to detect susceptible host trees.

In the present study, distance from the nearest forest edge did not show clear effect on *I. typographus* infestation status, though infested trees had a slightly higher median distance from the edge, suggesting a minor trend towards beetles preferring trees further from edges. However, given that the correlation is weak and scatter plot showing similar distribution of infested and non-infested trees across different distances, distance from the edge alone may not be a major factor. Additionally, all trees over 150 m from the edge were in the same stand, potentially biasing results. Including "Plot" as a nested random effect in the GLMM improved model performance, but likely due to sample plot location choices rather than distance itself. Also, as the crown length and self-shading capacity are often associated with the trees susceptibility to *I. typographus* infestation (Jakuš et al., 2011), it may be these crown characteristics, rather than distance from the forest edge alone, that make trees vulnerable to bark beetle attacks when exposed to increased solar radiation at the forest edge.

The unexplained variability in stands with high levels of *I. typographus* damages could be attributed to the lack of data on prior bark beetle infestations or disturbances occurring outside the stand. In this study, we focused on within-stand variability, specifically examining the relationship between root rot and bark beetle damages at the individual tree level. Although we accounted for the presence of clear-cut edges as a proxy for major past disturbances, this variable did not yield significant effects. Incorporating a detailed analysis of past disturbance events or nearby bark beetle attacks at the landscape-level might have provided additional insights, but it was beyond the scope of this study. We recognize that these factors could be critical for understanding the spatio-temporal dynamics of bark beetle activity, and we recommend further research to explore these potential influences.

Furthermore, the present study faced a few key limitations: a small number of root rot-infected stumps and the inability to re-measure all the stumps after the final felling. Unpredictable felling schedules by forestry companies, influenced by weather and economic factors, complicated fieldwork and affected the timing of measurements. Measuring stump growth was challenging when the time between harvesting and measurements was long, and logging residues or stump damage further complicated data collection. Additionally, species causing root rot in the stumps were not identified in the laboratory and the causal agents were here identified only visually based on the decay shape and degree at stump surface. However, in practice there are two alternatives that cause spruce root rot in Finland: *Heterobasidion* spp. and *Armillaria* spp. (Piri et al., 2019). Of these two, *Heterobasidion* spp. is estimated to cause approximately 80–90 % of spruce root rot within our sampling areas in Southern Finland (Piri, 2002), while *Armillaria* spp. is the second most common root rot fungus in Finnish Norway spruce stands (Vainio et al., 2022). *Heterobasidion* spp. causes hard, light brown rot that later softens as the decay process progresses, while *Armillaria* spp. causes a darker brown rot with a dark, sharply defined boundary

from healthy wood (Piri et al., 2019; Vainio, 2023). *Armillaria* spp. is also very easy to recognize based on rhizomorphs (Vainio, 2023), which were not observed in any of the assessed stumps. While we remain confident that the decay we observed on the stump surfaces was caused by *Heterobasidion* spp., we acknowledge that other root rot agents, such as *Armillaria* spp., may also have been present but undetected. However, the specific root rot agent causing the decay may be irrelevant in terms of the phenomenon, since *I. typographus* as an opportunistic bark beetle species is likely to attack trees weakened by decay, whether caused by *Heterobasidion* spp. or *Armillaria* spp.

As climate change progresses, the probability of longer summer droughts and other extreme weather events is expected to increase, posing a growing threat to European Norway spruce forests (Seidl et al., 2017). Drought not only directly affects tree growth and survival but also increases the frequency and severity of bark beetle outbreaks (Jactel et al., 2012; Korolyova et al., 2022). Warmer conditions accelerate bark beetle development, and the ability of *I. typographus* to modify its generation time with changes in temperature regimes, allows the species to exploit improved thermal conditions (Jönsson et al., 2009). While drought generally hampers the growth of many forest pathogens that rely on high humidity (Jactel et al., 2012), *Heterobasidion* species appear less affected by water deficits (Bendz-Hellgren and Stenlid, 1998). Their growth may even increase under drought conditions, as demonstrated by Terhonen et al. (2019), who found increased pathogen growth under drought in saplings inoculated with *H. parviporum* and *H. annosum* s.s. Thus, the interaction between *Heterobasidion* spp. and *I. typographus* may be highlighted in the future, though these interactions are complex and may have damping effects in the longer time scale.

To mitigate these risks, results of this study suggest that protecting trees from root rot infection may help indirectly to protect trees from *I. typographus* infestation as well, at least when bark beetle population densities are low. Stump treatment with chemical or biological control agent is an effective way to prevent primary *Heterobasidion* root rot infection (Thor and Stenlid, 2005; Garbelotto and Gonthier, 2013). Additionally, effective long-term strategies include silvicultural management to reduce forests' susceptibility to *I. typographus*, such as increasing landscape heterogeneity with mixed-species stands and creating buffer zones with non-host trees between high-risk areas characterized by mature Norway spruce forests (Fettig and Hilszczański, 2015; Seidl et al., 2016; Honkaniemi et al., 2020). 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 (Felton et al., 2016). Reducing stressors such as competition and drought through careful thinning may also help, although thinning may predispose standing trees to root rot infection and if done too

intensively, decrease trees' self-shading capacity. Balancing these multiple risks will be crucial for the future management of Norway spruce-dominated forests.

5. Conclusions

Heterobasidion root rot appears to be one of the significant factors making Norway spruce trees more vulnerable to *I. typographus* infestation. Results suggest that root rot has 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 a significant role in the occurrence of *I. typographus*, as trees infested with *I. typographus* were not consistently infected with root rot. Among other factors studied, larger diameter at breast height seems to be connected to increased risk of *I. typographus* infestation. Future studies are needed to further investigate the underlying mechanisms of interaction between *Heterobasidion* root rot and *I. typographus*, as well as spatio-temporal variation of this phenomenon.

CRediT authorship contribution statement

Werna Wahlman: Writing – original draft (lead), Investigation (lead), Formal analysis (lead), Writing – review & editing. **Risto Kasanen:** Conceptualization, Writing – review & editing. **Lauri Lappalainen:** Conceptualization, Writing – review & editing, Funding acquisition. **Juha Honkaniemi:** Conceptualization (lead), Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Co-author Lauri Lappalainen is affiliated with Lallemand Finland Oy, which financially supported the thesis work for Werna Wahlman. However, there is no direct financial benefit or conflict of interest from the study results for Lallemand Finland Oy.

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Appendix A

Table A1
General information of the sampling plots.

Stand	Plot	Distance from the edge, m	No. of trees	No. of Spruce trees	DBH range (spruce), cm	Average DBH (spruce), cm	DBH range (all trees), cm	Average DBH (all trees), cm	Basal area (all trees), m ² /plot	Basal area (all trees), m ² /ha
Könnilä	1	39,1	14	14	13–50	29	-	-	1,08	43,2
	2	15,5	17	17	18–47	31	-	-	1,37	54,8
	3	23,9	17	17	20–42	29	-	-	1,18	47,2
	4	25,2	14	14	23–50	34	-	-	1,35	54,0
Leikki-kangas	1	22,5	14	14	22–50	40	-	-	1,88	75,2
	2	15,6	13	13	27–38	34	-	-	1,18	47,2
	3	58,6	12	12	16–50	36	-	-	1,32	52,8
Lippuleuka	4	14	17	16	18–45	31	18–45	31	1,37	54,8
	1	39,9	29	25	10–21	15	10–25	16	0,58	23,2
	2	74,6	18	17	12–28	19	12–28	19	0,55	22,0

(continued on next page)

Table A1 (continued)

Stand	Plot	Distance from the edge, m	No. of trees	No. of Spruce trees	DBH range (spruce), cm	Average DBH (spruce), cm	DBH range (all trees), cm	Average DBH (all trees), cm	Basal area (all trees), m ² /plot	Basal area (all trees), m ² /ha
Mieliö	3	49,3	14	12	15–27	21	14–31	21	0,5	20,0
	4	34,1	16	11	12–24	18	12–33	20	0,55	22,0
	1	123,1	11	10	12–33	23	12–33	23	0,49	19,6
	2	102,8	16	13	14–32	21	14–39	23	0,73	29,2
Purola	3	25	9	6	19–29	24	19–35	26	0,51	20,4
	4	85,7	13	12	25–36	31	25–44	32	1,06	42,4
	1	60,8	24	23	12–41	21	12–41	21	0,96	38,4
	2	32,4	11	11	13–43	34	-	-	1,03	41,1
Pölkinvuori	3	72,6	14	9	12–45	31	12–45	29	1,09	43,7
	4	86	19	16	12–36	24	12–36	24	0,78	31,2
	1	123,5	10	8	20–32	26	20–45	28	0,67	26,7
	2	60,3	11	8	10–44	28	10–44	26	0,66	26,4
Vaasan-kulma	3	24,3	12	11	10–37	28	10–37	28	0,81	32,4
	4	100	14	13	27–43	31	15–43	30	1,04	41,8
	1	14,8	9	9	25–37	29	-	-	0,62	24,8
	2	20,3	10	10	25–42	31	-	-	0,79	31,6
Vatilahti	3	9,6	8	8	24–41	31	-	-	0,63	25,2
	4	20,5	9	9	21–43	32	-	-	0,76	30,4
	1	76,1	8	8	30–47	39	-	-	0,99	39,6
	2	25,6	14	11	12–37	27	12–37	26	0,80	31,8
Venu	3	43,3	6	6	31–42	36	-	-	0,62	24,7
	4	96	10	10	26–44	36	-	-	1,05	42,1
	1	47,9	14	14	16–42	31	-	-	1,12	44,9
	2	203,5	14	14	20–37	27	-	-	0,81	32,2
	3	196,7	15	14	14–35	24	14–37	24	0,73	29,4
	4	30,8	9	7	18–34	26	18–34	26	0,50	19,9



Figure A1. Top left-side picture: stump with root rot. Top right-side picture: the condition of the stumps varied a lot between and within the sample plots, sometimes making it difficult to calculate annual rings. Bottom left-side picture: a stump that has been run over with a forest machine. Bottom right-side picture: a pile of logging residues on the sample plot.

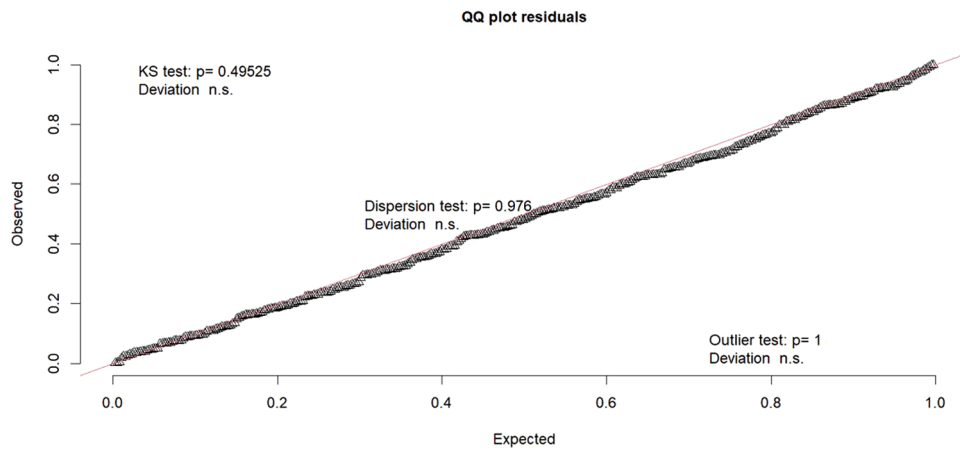


Figure A2. Q-Q plot of the final model.

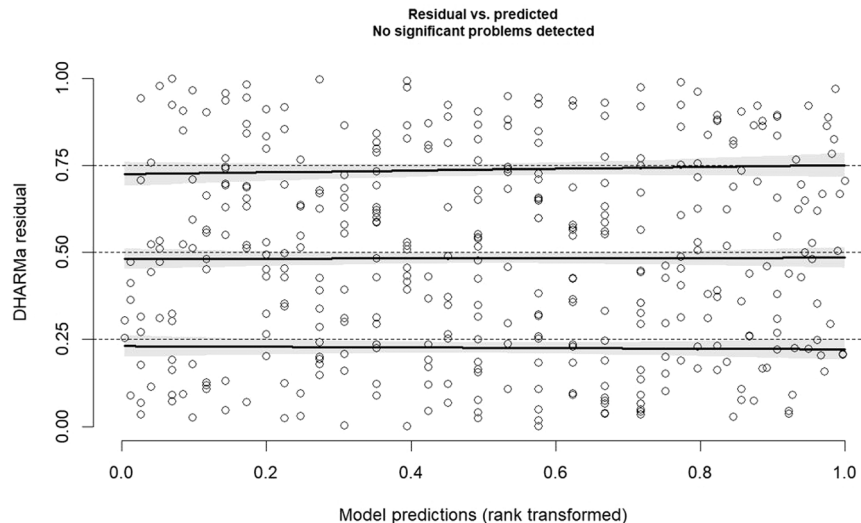


Figure A3. Residual plot of the final model.

Data availability

To preserve private forest owner information and the state of their forest property, detailed coordinates of the forest stands in the study remain confidential. Otherwise, the measured data collected for this publication is published openly in Zenodo <https://doi.org/10.5281/zenodo.13841857>.

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