Dissertationes Forestales 382

Contribution of stand, landscape and climatic attributes to *Ips typographus* damage and its spatial distribution in Finland

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Academic dissertation

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ABSTRACT

Large-scale damage caused by the European spruce bark beetle (SBB; *Ips typographus* L.) to Norway spruce (*Picea abies* (L.) H. Karst.) forests have increased in recent decades. This thesis evaluate how stand, landscape and climatic attributes contribute to SBB damage and its spatial distribution in Finland. Sub-study I analysed the differences between SBB-damaged and undamaged stands, and the contribution of landscape attributes to the formation of new SBB damage. Sub-study II examined the spatial patterns of SBB damage and the contribution of stand and landscape attributes to the formation of SBB damage hotspots. Sub-study III developed spatially explicit probability models of SBB damage, considering stand, landscape and climatic attributes. The studies covered the southern Finland (11.4 million ha with more than two million Norway spruce stands) and utilised forest-use notifications of salvage loggings during 2012–2022, and Norway spruce forest stock data (Sub-study II).

Chi-squared and Mann-Whitney U tests were used to analyse differences between SBB-damaged and undamaged stands. Generalised linear mixed effects models were used to analyse the contribution of landscape attributes to the formation of new SBB damage (Sub-study I) and SBB-damage hotspots (Sub-study II), as well as to predict the probability of stand-level SBB damage (Sub-study III). Local Moran's I was used to identify hotspots.

Mature Norway spruce stands with higher age and mean diameter, and those near recent clear-cuts, wind and SBB damage were most susceptible to SBB damage (Sub-study I) and those near recent SBB damage were most prone to form hotspots (Sub-study II). The best predictors of SBB damage were proximity to clear-cuts, mean stand diameter, distance to previous SBB damage and the number of consecutive days above 25°C (Sub-study III). Based on these findings effective proactive risk management options are needed to tackle the increasing risk of SBB damage under climate change.

Keywords: salvage logging; forest protection; quantitative and occurrence modelling; boreal forest; areal data; evidence-informed decision-making.

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Joensuu, November 27, 2025

John Alexander Pulgarín

LIST OF ORIGINAL ARTICLES

This thesis is based on data presented in the following articles, referred to by the Roman Numerals I-III:

I Pulgarín Díaz JA, Melin M, Ylioja T, Lyytikäinen-Saarenmaa P, Peltola H, Tikkanen O-P (2024) Relationship between stand and landscape attributes and *Ips typographus* salvage loggings in Finland. Silva Fennica, 58, article id 23069. https://doi.org/10.14214/sf.23069

II Pulgarín Díaz JA, Pérez-Pérez J, Melin M, Peltola H, Tikkanen O-P (2025) Assessing the impacts of forest stand structure and landscape on the formation of *Ips typographus* damage hotspots in Finland. Forestry: An International Journal of Forest Research https://doi.org/10.1093/forestry/cpaf058

III Pulgarín Díaz JA, Melin M, Mehtätalo L, Polade S, Aalto J, Peltola H, Tikkanen O-P (2025). Stand, climatic and landscape attributes contributing to the probability of *Ips typographus* damage in Finland. Manuscript under review.

The present author was the principal and corresponding author for all articles, and was responsible for the data analysis, visualisation and the original draft of articles. The other co-authors participated in model validation, visualisation, reviewing and revisions of the articles.

TABLE OF CONTENT

1 INTRODUCTION

1.1 Increasing damage by the European spruce bark beetle

Insect pests like the European spruce bark beetle (*Ips typographus* L.; SBB) – the most damaging insect pest to Norway spruce (*Picea abies* (L.) Karst.) – have been expanding their ranges due to climate change (Hlásny et al. 2021; Melin et al. 2020; Pulgarin et al. 2022). Large-scale SBB outbreaks have caused severe damage in Norway spruce forest across Europe, as environmental conditions favouring outbreaks are becoming more common (Økland et al. 2015; Tikkanen and Lehtonen 2023). Although SBB-related damage in Finland currently remains modest compared to Central Europe, an increasing number of SBB-damage-induced salvage loggings reports in Southern Finland since the 2010s signal an alarming increase in SBB risk (Figure 1 and Figure 2). This escalation in damage highlights an urgent need for improved proactive risk management strategies to increase forest resilience, which will require a better understanding of how various stand, landscape and climatic attributes contribute to the likelihood of SBB damage and its spatial distribution, complements existing knowledge from Central Europe at the northern distribution limit.

1.2 Stand, landscape and climatic attributes affecting SBB damage risk

Several climatic, stand and landscape attributes have been reported to affect the risk of SBB damage. Low temperatures have historically limited beetle development and reproduction (Annila 1969; Doležal and Sehnal 2007; Økland et al. 2015). However, under a warming climate, favourable conditions for SBB development and damage are becoming more frequent. During heat waves, oviposition and population growth reach their maximum (Grodzki et al. 2006), beetles fly further and more frequently (Funke and Petershagen 1994; Hinze and John 2019; Wermelinger and Seifert 1999) and dispersal flights synchronise. This increase in the number of simultaneous beetle attacks can overwhelm host tree defences (Wermelinger 2004). Higher thermal sums also increase the probability that two generations per year and/or sister broods occur (Jönsson et al. 2007; Marini et al. 2017). When heat weaves are combined with drought, Norway spruce defences are substantially weakened and the species' susceptibility to SBB increases, creating favourable conditions for the development of SBB epidemics (Netherer et al. 2015, 2024; Schiebe et al. 2012).

Among forest stand attributes, the diameter at breast height strongly affects SBB host selection, meaning mature Norway spruce stands (with larger diameters) are more prone to SBB damage (Wermelinger 2004). Whereas Norway spruce stands growing on soils under chronic stress tend to experience fewer SBB attacks (Netherer et al. 2019).

Different landscape attributes, such as forest diversity and proximity to recent disturbances (e.g. clear-cuts, wind damage, earlier beetle damage), also affect the spatial patterns of SBB damage (Eriksson et al. 2007; Klapwijk and Björkman 2018) and the SBB population levels (Gohli et al. 2024). Forest diversity, both in tree species composition and structural characteristics, may decrease susceptibility to SBB damage (de Groot et al. 2023; Felton et al. 2016). Previous studies have indicated that greater forest diversity improves soil moisture retention, creating greater natural enemy activity, physical barriers to beetle movement and disrupted olfactory cues (Jactel et al. 2021; Kozhoridze et al. 2024). Because

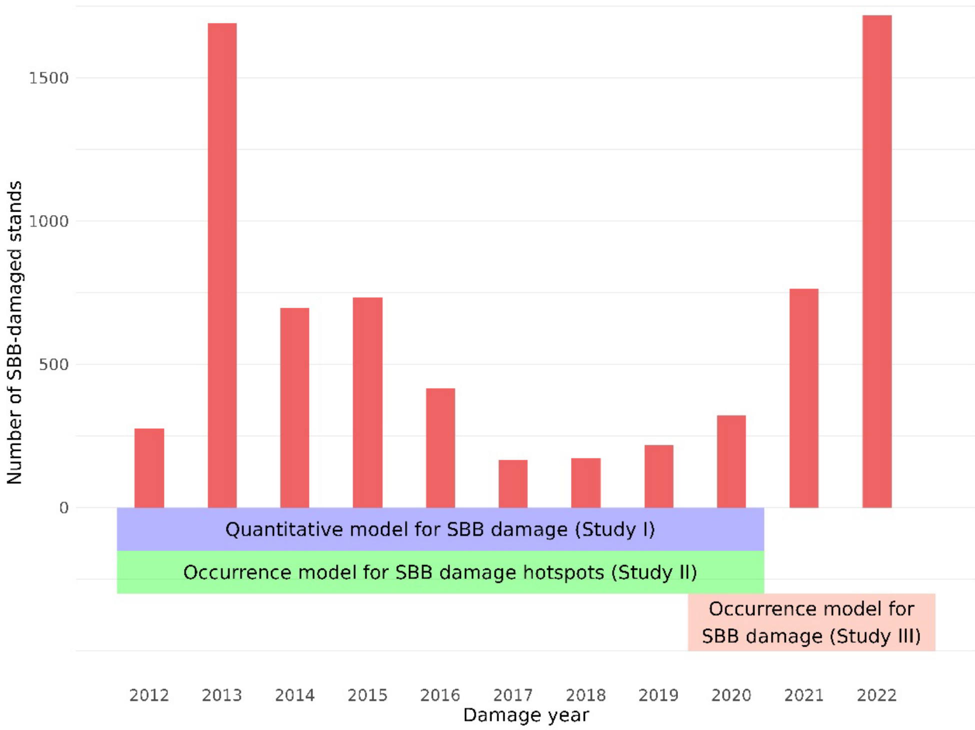

Figure 1. Salvage loggings reported in Finland due to *Ips typographus* (SBB) damage during 2012–2022. The timeline of studies in this dissertation is shown underneath. Data from forest-use notifications are freely available from the Finnish Forest Centre (see Section 2.1 for details).

mature Norway spruce stands are the most susceptible to SBB damage, a diverse forest structure where not all stands are mature disperses the risk of damage (de Groot et al. 2023; Klapwijk and Björkman 2018). In contrast, clear-cuts due to salvage logging or other forestry operations can increase the probability of SBB damage by exposing forest edges and weakening tree resistance there (de Groot and Ogris 2019; Kautz et al. 2013; Kozhoridze et al. 2024; Stříbrská et al. 2022). Trees in forest edges are exposed to new conditions, such as direct sun heat and wind force, especially those facing southward (Lindman et al. 2023), which cause stress and increase suitability to SBB attacks.

1.3 Stand, landscape and climatic attributes affecting SBB damage distribution

Proximity to wind damaged areas increases the likelihood of new SBB damage, as wind damage creates ideal beetle breeding habitats (Louis et al. 2015). Similarly, prior beetle damage increases the probability of subsequent attacks (Økland et al. 2016). Although salvage logging of wind- and SBB-damaged stands has commonly been used to prevent further SBB damage in nearby forests (Hlásny et al. 2021; Wermelinger 2004), it often triggers new SBB damage, especially if the stand is only partially salvaged.

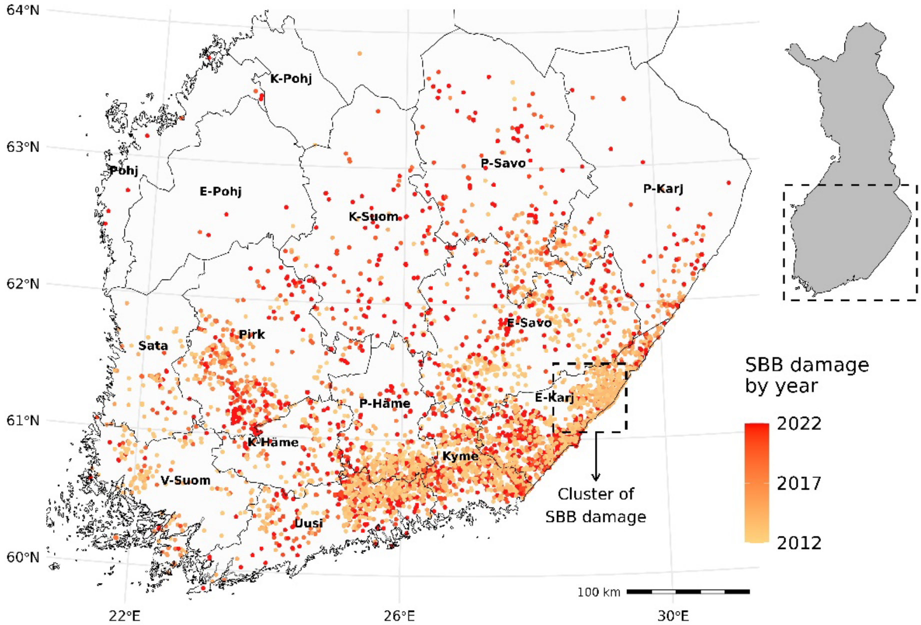

Figure 2. Spatial distribution of loggings due to *Ips typographus* (SBB) damage in the southern half of Finland during 2012–2022. Data from forest-use notifications are freely available from the Finnish Forest Centre (see Section 2.1 for details). Regions in the map include Etelä-Karjala (E-Karj), Etelä-Pohjanmaa (E-Pohj), Etelä-Savo (E-Savo), Kanta-Häme (K-Häme), Keski-Pohjanmaa (K-Pohj), Keski-Suomi (K-Suom), Kymenlaakso (Kyme), Päijät-Häme (P-Häme), Pirkanmaa (Pirk), Pohjanmaa (Pohj), Pohjois-Karjala (P-Karj), Pohjois-Savo (P-Savo), Satakunta (Sata), Uusimaa (Uusi) and Varsinais-Suomi (V-Suom).

The population dynamics of SBB include an epidemic (high density) and endemic (low density) phases. The epidemic phase occurs when favourable weather conditions, such as high temperatures, coincide with an abundance of weakened host trees. Often this happens near areas that have been previously damaged (Hlásny et al. 2021; Wermelinger 2004) and is especially intensified by drought (Müller et al. 2022). During epidemics, beetles disperse over short distances (0–500 m; Kärvemo et al. 2014; Kautz et al. 2011) and attack Norway spruce trees regardless of their size or vitality (Hlásny et al. 2021). Damage typically forms spatial clusters, as illustrated in Etelä-Karjala region in Figure 2. Aggregation of SBB damage has previously been reported (Kamińska 2022; Lausch et al. 2013; Stereńczak et al. 2019), albeit based on studies conducted at relatively small spatial scales.

The endemic phase occurs when natural enemies are abundant, breeding material is scarce, and weather conditions are unfavourable (Hlásny et al. 2021; Wermelinger 2004). In this phase, beetles mainly attack weakened trees, windthrows or old trees with low vigour, causing limited mortality (Louis et al. 2015). Because suitable hosts are less common, beetles disperse over further distances than they do during epidemics (Hlásny et al. 2021; Netherer et al. 2019).

Although our understanding of SBB damage patterns and drivers has significantly improved in recent years, the influence of different stand, landscape and climatic attributes on SBB hotspot formation and damage likelihood remains underexplored across broad regions (e.g. countrywide). Advancing this knowledge can help identify areas prone to damage (Økland et al. 2015), improve forest health monitoring and operational planning, allowing forest managers to prioritise high-risk regions for intervention (de Groot and Ogris 2019; Hlásny et al. 2021; Kuhn et al. 2022). It could also support the development of forest simulators, to assess how controlling key drivers of damage using proactive risk management strategies may affect the provision of ecosystem services such as timber yield, carbon stocks and the recreational value of forests (Potter et al. 2016; Tobin, Haynes and Carroll 2023).

The lack of this knowledge across country regions is primarily driven by methodological challenges, including limited access to fine-scale infestation data (Fernández-Carrillo et al. 2024; Nardi et al. 2023; Seidl et al. 2011). Among the relatively few available studies, de Groot and Ogris (2019) introduced an early warning system to facilitate timely risk management responses. Müller et al. (2022) analysed how environmental factors affect forest susceptibility to beetle damage. Kovárník et al. (2025) assessed the role of stand, tree, and climate attributes in Norway spruce survival under SBB attack, while Jönsson et al. (2012) focused on the likelihood of damage occurrence. Blomqvist et al. (2018) investigated the susceptibility of an urban forests to SBB in southern Finland. Modelling studies have included the phenology of SBB at the landscape level using mechanistic models (Baier et al. 2007), and the effects of climatic conditions on the host (Pirtskhalava-Karpova et al. 2024).

Examining how various attributes affect Norway spruce susceptibility to SBB at the northern distribution margin, covering countrywide study areas, offers a basis for comparison with Central Europe, where damage has intensified in recent years. Developing a national risk model for Finland would thus extend existing Central European knowledge by identifying both common and region-specific risk factors across Europe. A better understanding of the spatial and temporal drivers of SBB damage remains crucial for proactive risk management and the identification of long-term solutions when integrating risk analyses into forest simulators.

1.4 Objectives

This dissertation, consisting of three sub-studies, aimed to evaluate how various stand, landscape and climatic attributes contribute to SBB damage and its spatial distribution in Finland. Sub-study I analysed the differences between SBB-damaged and undamaged stands and the contribution of landscape attributes to the formation of new SBB damage. Sub-study II examined the spatial distribution of SBB damage and the contribution of stand and landscape attributes to the formation of SBB damage hotspots. Sub-study III developed spatially explicit probability models and maps for SBB damage, considering stand, landscape and climatic attributes.

The study area for all sub-studies consisted of the southern half of Finland (below 64°N). The studies employed forest-use notifications of salvage loggings during 2012–2022 as a proxy for wind and SBB damage and forest stock data for Norway spruce-dominated forests for timber production. This open-access forest stock data and up-to-date, spatially accurate nationwide salvage logging data offered a unique opportunity to develop a better understanding of how various stand, landscape and climatic attributes contribute to the probability of SBB damage and its spatial distribution.

2 METHODS

2.1 Study area and datasets

The study area used in this dissertation covered the southern half of Finland (Figure 2), encompassing 11.4 million ha of forestry land used for wood production, of which 78% is privately-owned (Korhonen et al. 2021).The region includes southern and middle boreal zone vegetation, with hemiboreal and boreal forests (Ahti et al. 1968). Productive forests in this area are mainly composed of *Pinus sylvestris* L., *Picea abies* (L.) H. Karst., *Betula pendula* Roth and *Betula pubescens* Ehrh. (Korhonen et al. 2021).

Data were collected from two publicly available spatial datasets covering privately-owned forests, provided by the Finnish Forest Centre (Metsäkeskus). The first includes forest-use notifications made by the forest owners, indicating harvesting operations, such as salvage loggings from wind or SBB damage (Metsäkeskus 2025). These notifications serve as a proxy for actual wind and SBB damage, identifying areas – either whole stands or partial cuts – harvested in response to these disturbances, which is the standard forestry management practice in Finland. This dataset represents the only extensive, spatially detailed record of salvage logging in Finland that specifically pinpoints areas cleared in response to SBB damage. The second dataset contains detailed forest structure information at the stand level, derived from remote sensing and field assessments (Metsäkeskus 2025). An overview of the methodological workflow for Sub-studies I–III is presented in Figure 3 (additionally, see Figure 2 in Sub-study I, Figure 2 in Sub-study II and Figure 3 in Sub-study III).

Forest-use notification data were downloaded on 18 October 2021 for Sub-studies I and II and 26 June 2023 for Sub-study III. Norway-spruce-dominated stands harvested due to wind or SBB damage were selected from this data for further analyses. The dataset indicated damage aggregated at the stand level, and the dataset did not include salvage logging volumes or counts of individual damaged trees. Sub-studies I and II used damage data from 2012 to 2020, and Sub-study III damage data from 2020 to 2022, as Sub-study III required a different methodological approach (see Section 2.3.3 for details).

The forest structure dataset used in all three sub-studies to identify Norway spruce-dominated stands susceptible to SBB damage and recent clear-cuts was initially downloaded on 18 November 2021. Susceptible stands were defined as those with a mean stand diameter at breast height greater than 15 cm and a mean age greater than 25 years in 2021, which are typical thresholds for SBB damage in Finland, based on results from Sub-study I. Recent clear-cuts were also identified as potential drivers of SBB damage, due to the resulting edge creation (Kautz et al. 2013). Stands younger than five years in a study year were identified as clear-cuts. An updated dataset was downloaded for Sub-study III on 3 January 2024.

2.2 Data analysis

2.2.1 Stand and landscape attributes contributing to SBB damage (Sub-study I)

The stand attributes used to examine the differences between Norway spruce stands with and without SBB damage included site fertility class, stand development class, soil type, mean stand diameter at breast height and mean stand age (see Table 1 in Sub-study I). The landscape attribute considered was the distance from each stand to the nearest disturbance

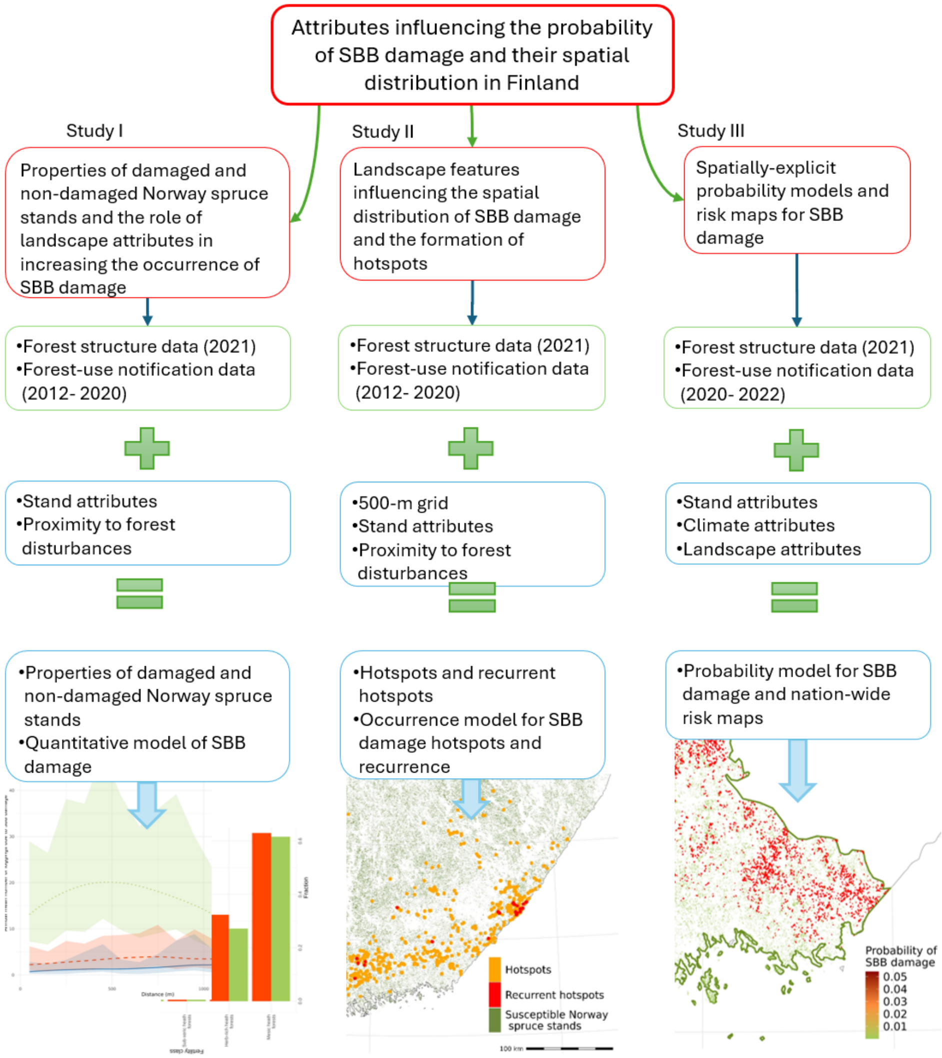

Figure 3. Workflow for identifying the stand, landscape and climatic attributes influencing the probability of *Ips typographus* (SBB) damage and its spatial distribution in Finland.

(i.e. clear-cut, previous-year wind or SBB damage). The number of SBB-damaged stands was modelled using a generalised linear mixed model (GLMM) with a negative binomial distribution, log link and year of damage (2012–2020) as random effects. Fixed effects included distance class (from 0 to 1500 m, at 100 m intervals) for each disturbance type and their interactions. Overdispersion was assessed by the dispersion statistic (Pearson X^2 divided by the residual degrees of freedom).

2.2.2 Spatial patterns of SBB damage (Sub-study II)

To analyse the spatial distribution of SBB damage in Sub-study II, two squared grids with cell sizes of 500 × 500 m and 1000 × 1000 m were laid over the study area. The 4,579 SBB damage notifications occurring during the study period (2012–2020) were then assigned to the grid cells. Global Moran's I (Moran 1950) was used to examine the spatial autocorrelation between SBB-damaged stands. Neighbourhoods were defined using two approaches. The first considered all adjacent cells, while the second used distance thresholds: cells within 1000 m formed the neighbourhood for the 500-m grid and within 2000 m for the 1000-m grid. The weights were assigned to decrease with increasing distance, reflecting the lower probability of damage farther from prior infestations (Kautz et al. 2011; Müller et al. 2022; Stereńczak et al. 2019).

Local Moran's I (Anselin 1995) was used to identify SBB damage hotspots based on the 500-m grid and the queen contiguity method, which best represents SBB dispersal (Wermelinger 2004). For this, annual damage notifications were grouped into three 3-year time windows (2012–2014, 2015–2017, 2018–2020), following earlier bark beetle studies (e.g. Potter et al., 2016). Then, each SBB-damaged stand was classified based on whether its centroid fell within a hotspot cell (see Figure 2, part 3 in Sub-study II).

To investigate the effect of stand-level and forest disturbances on hotspot formation, two binary GLMMs were used. The first model evaluated the probability of a damaged stand becoming a hotspot, while the second assessed the probability of a hotspot recurring. Stand-level predictors included mean stand diameter at breast height, age, site fertility class and development class. The Euclidean distances from each damaged stand to the nearest SBB-damaged stand from the previous two years and the nearest clear-cut, were the landscape predictors. Model fit was assessed using the dispersion statistic, the sample variogram to test the spatial autocorrelation of the residuals and the Durbin–Watson test to assess the temporal autocorrelation over simulated residuals.

2.2.3 Modelling the probability of SBB damage (Sub-study III)

Sub-study III developed probability models for SBB damage by employing two binary GLMMs. The dataset used in Sub-study III integrated newly observed SBB damage from 2020–2022 that was not previously analysed in Sub-studies I and II. It offers extensive spatial coverage of both infestation and non-infestation records with accurate stand-level geolocation and incorporates a set of predictors not considered in the earlier sub-studies.

Fourteen independent predictors were used: one stand attribute, seven landscape attributes and six climatic attributes (Table 1 in sub-Study III). The stand attribute was mean stand diameter at breast height. The landscape attributes included the Euclidean distance from target stands (i.e. SBB-damaged or susceptible Norway spruce) to the nearest forest disturbance (i.e. clear-cut, wind and SBB damage from the previous two years), as well as the volume of Norway spruce within a 500-m buffer around each target stand and the volume of other tree species within the same buffer. The climatic attributes, measured from May to August, were extracted from climatic rasters produced by the Finnish Meteorological Institute (Aalto et al. 2016). They included the maximum number of consecutive hot days (>25°C), total precipitation and cumulative thermal sum above 5°C. To address overdispersion in a countrywide model, the study area was split into southern and northern sub-areas for modelling purposes. The southern sub-area included the regions with the highest number of SBB damage and hotspots between 2012 and 2020, according to Sub-study II. The model fit was assessed as in Sub-study II. All data processing was done in RStudio v.2023.12.0+369 (RStudio Team 2023), with the specific packages used described in each Sub-study.

3 RESULTS

3.1 Stand and landscape attributes contributing to SBB-damage

Between 2012 and 2022, a total of 22,897 salvage logging operations due to SBB damage were recorded in Finland (Figure 1 and Figure 2). Annual SBB damage events first peaked in 2013 and declined before peaking again in 2021 (Figure 4 in Sub-study I). Most SBB damage occurred in southeastern Finland between 60° and 62°N (Figure 2). SBB damage was not randomly distributed among Norway spruce-dominated stands, as the characteristics of damaged stands (i.e. mean stand diameter, mean stand age, fertility class, stand development class and soil type) differed from undamaged Norway spruce stands (Figure 4; Table 2 in Sub-study I). Most SBB damage occurred in Norway spruce stands on mesic heath or herb-rich heath forests (Figure 4) and in stands located on semi-coarse or coarse and fine-grained heath forest soils. SBB damage generally occurred also in mature, older stands, with a mean stand diameter of 20–35 cm, peaking at 27.5 cm (Figure 7 in Sub-study I).

Proximity to clear-cuts clearly increased the number of new SBB-damaged stands, but previous-year wind and SBB damage had a weaker effect (Figure 5; Table 3 in Sub-study I). Damage peaked at 450–600 m from the clear-cuts, while the effects of previous-year wind and SBB damage were stronger at greater distances.

3.2 Spatial patterns of SBB damage

The results of Sub-study II exposed low-to-moderate statistically significant spatial autocorrelation in the distribution of SBB-damaged stands (Table 1 in Sub-study II), confirming a robust spatial signal. SBB damage formed statistically significant hotspots, concentrated in the southeast of Finland (Figure 6), present throughout the study period but less common during the 2018–2020 period. The proximity to SBB-damaged stands in the previous two years affected both the formation of hotspots and their recurrence (Tables 3–4 in Sub-study II). From them, distance to previous-year SBB damage was the most influential attribute, with probabilities dropping sharply beyond 500 m. The probability of hotspot formation also increased with stand age. When assessing the overall effect of site fertility class and stand development class, only the effect of the latter was statistically significant and only in the recurrent hotspots model.

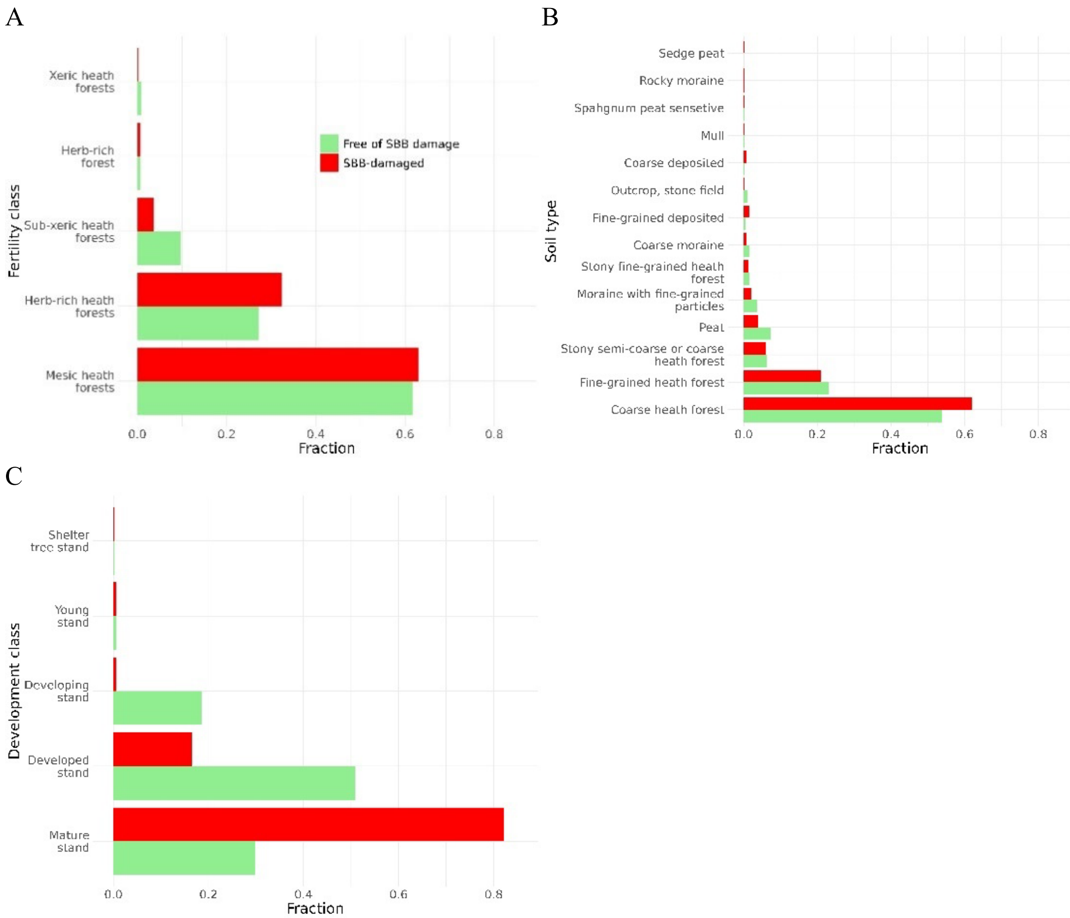

Figure 4. Fraction of *Ips typographus* (SBB)-damaged and non-damaged Norway spruce stands in Finland between 2012 and 2020, categorised by (A) site fertility class, (B) stand development class and (C) soil type. Adapted from Sub-study I, Pulgarín et al., (2024), figure licence CC BY SA.

3.3 Probability of SBB damage

In Sub-study III, the probability of a Norway spruce stand becoming SBB-damaged was low, ranging from 0 to 0.125 (mean = 0.00034; Figure 7). The most influential attributes on the probability of SBB damage in both sub-areas were distance to clear-cuts and the mean stand diameter at breast height. Also, the maximum number of consecutive hot days in the current year greatly affected the probability of SBB damage in the northern sub-area (Table 2 in Sub-study III). In the southern sub-area, the volume of Norway spruce slightly increased the probability of SBB damage. Meanwhile, in the northern sub-area, the probability of SBB damage increased with both a greater number of consecutive hot days during the study year and shorter distance to wind damage from two years before. In the southern sub-area, the distance to earlier wind- and SBB-damaged areas, volume of other tree species, precipitation in the previous year, precipitation in the current year and the number of consecutive hot days

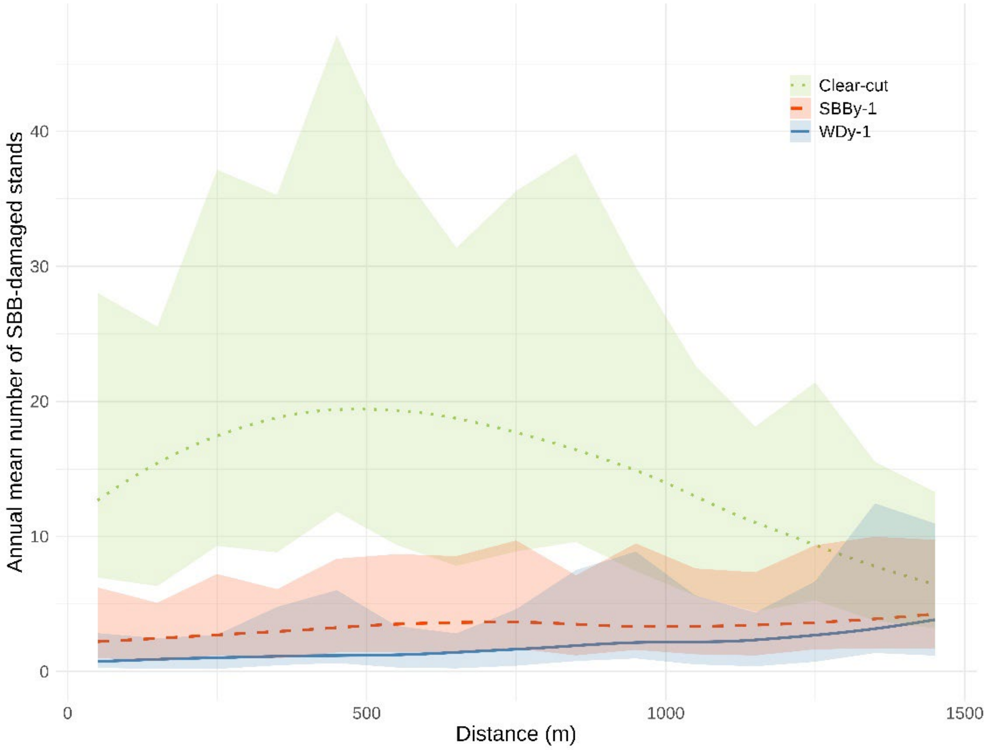

Figure 5. Mean number of *Ips typographus* (SBB)-damaged stands based on the distance from clear-cuts, previous year SBB damage (SBB_{y-1}) and previous year wind damage (WD_{y-1}), according to the generalised linear mixed model developed in Sub-study I. Shaded areas indicate the 95% Wald-type confidence intervals for the predicted mean count. Adapted from Sub-study I, Pulgarín et al., (2024), figure licence CC BY SA.

in the previous year had reduced the probability of SBB damage. In the northern sub-area, distance to earlier SBB-damage and clear-cuts, the volume of other tree species and precipitation in the current year had similar negative effects on the probability of SBB damage.

The probability of SBB damage declined sharply as the distance from clear-cuts increased, with the highest probabilities occurring within 0.5 km (Figure 4 and Figure 5 in Sub-study III). The small area depicted in Figure 8 illustrates the spatial distribution of forest disturbances (i.e. wind damage, beetle damage, other clear-cuts) and highlights the complex spatial patterns of SBB damage. It shows how highly susceptible Norway spruce stands are often located close to clear-cuts.

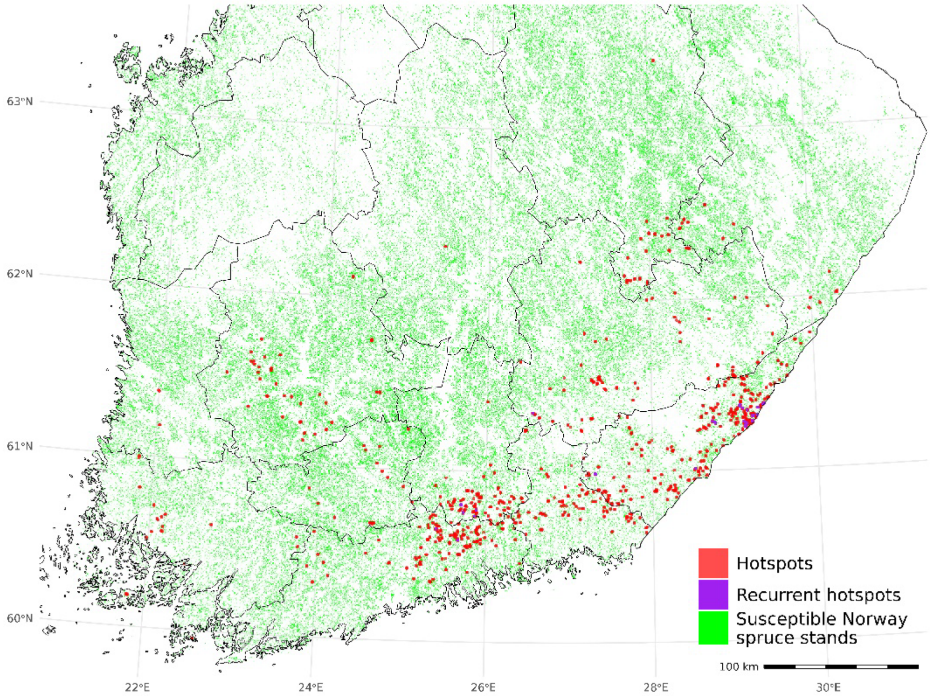

Figure 6. Norway spruce stands (green), hotspots (red) and recurrent hotspots (purple) of *Ips typographs* (SBB) damage in Finland. Adapted from Sub-study II, Pulgarín et al. (2025), figure licence CC BY.

4 DISCUSSION

4.1 Effects of stand attributes on SBB damage

In Sub-study I, SBB-damaged stands were concentrated in mature, older stands with a larger mean stand diameter at breast height. This is likely because trees with thicker bark and more phloem offer better conditions for larval development than younger or slower-growing trees (Kärvemo et al. 2014; Wermelinger 2004). However, small stands with low mean diameters were also affected, which may indicate epidemic population levels, where even smaller-diameter trees succumb (Hlásny et al. 2021)

The formation of hotspots in Sub-study II was similarly found to be affected by the stand age. After SBB damage, susceptible mature Norway spruce stands form subsequent hotspots. A similar pattern has been observed for *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae; Nelson and Boots, 2008). In Sub-study III, mean stand diameter was the second most important predictor of SBB damage, and its importance has been emphasised in earlier studies (Göthlin et al. 2000; Wermelinger 2004). Tree size and age are closely correlated, which may partially explain the concentration of SBB damage and their hotspots in mature stands. Also, diameter is closely related with height, though these two relationships can be influenced by factors such as site quality and stand density. Similar to tree diameter, greater tree height increases the likelihood of SBB attack (Müller et al. 2022). Nevertheless,

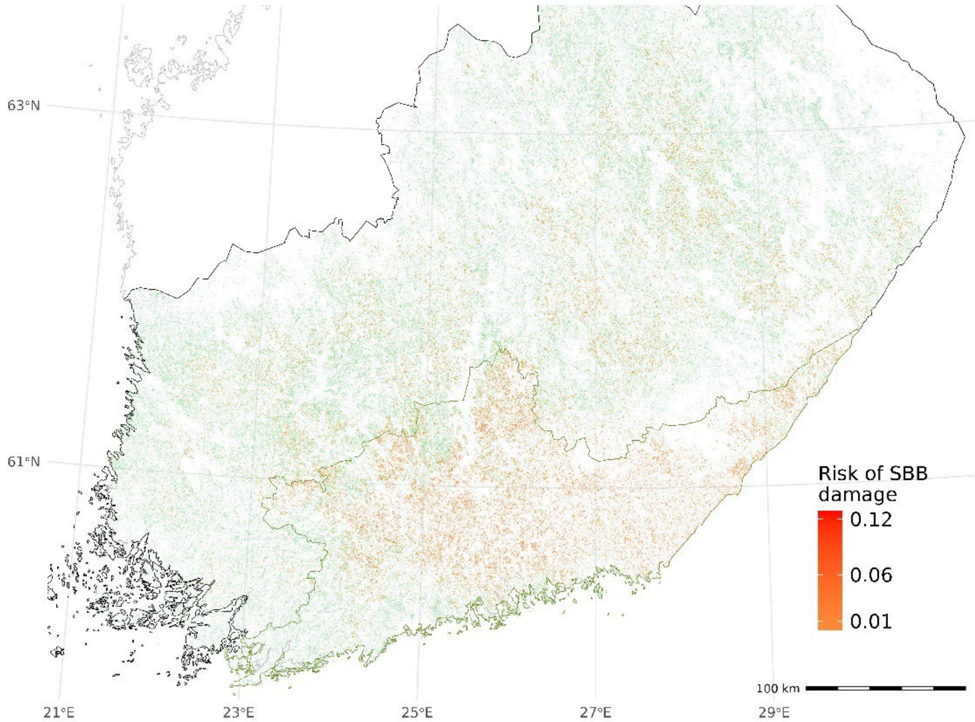

Figure 7. Predicted probability of *Ips typographus* (SBB) damage in Norway spruce stands in southern and northern sub-areas. The probability is indicated by colour intensity, with most stands showing low values (green). Adapted from Sub-study III (manuscript under review).

during epidemic population levels even younger, smaller trees may also be attacked (Hlásny et al. 2021).

In Sub-study I, SBB-damaged stands tended to occur on the most prevalent site fertility types (i.e. mesic heat and herb-rich forest), but were comparatively rare on dry, nutrient-poor sites. Observed SBB damage has similarly been lower in soils with limited water retention (Netherer et al. 2019). Especially when linked to soil wetness, as low wetness predispose the Norway spruce to SBB attack (Müller et al. 2022).

4.2 Effects of landscape attributes on SBB damage

Sub-studies II and III evaluated the probability of hotspot formation and SBB damage, respectively, across the entire beetle-affected area of Finland, what includes its northernmost distribution limit of the species (Romashkin et al. 2020). The studied landscape attributes, namely proximity to forest disturbances, were important in explaining SBB damage. Proximity to clear-cuts was the strongest driver in Sub-studies I and III. Contrary to expectations, however, clear-cuts were not associated with hotspot formation or recurrence (Sub-study II). The effect of clear-cuts on SBB damage exceeded the combined effect of earlier wind and SBB damage, or other attributes considered in Sub-studies I and III.

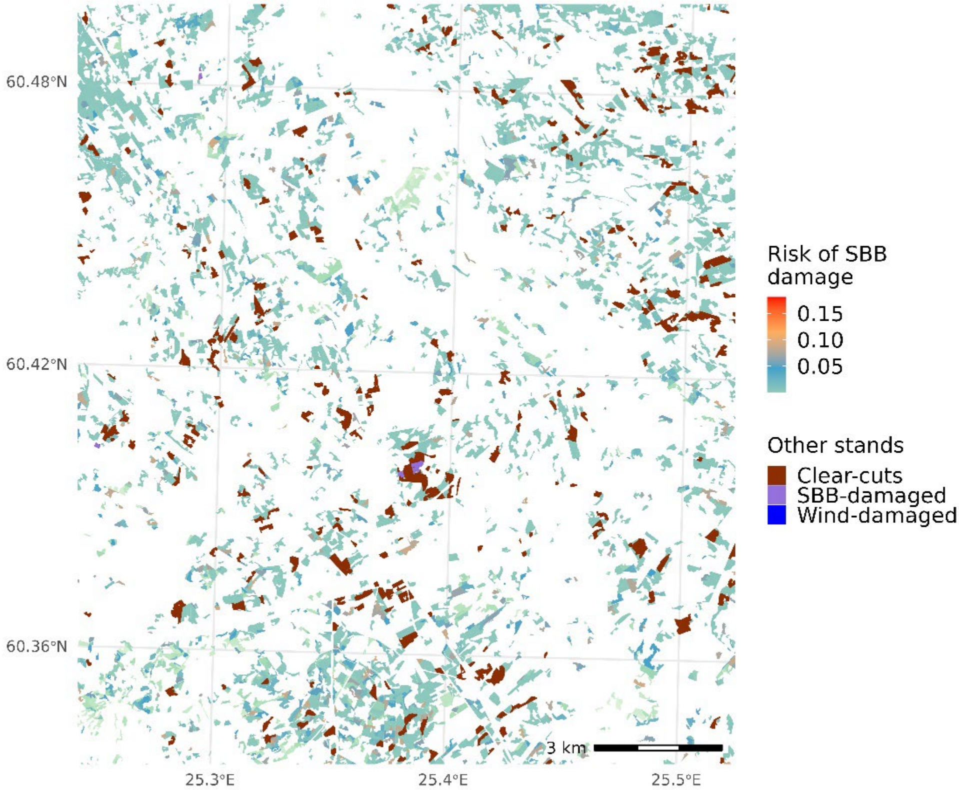

Figure 8. Detailed area of Uusimaa region showing the predicted probability of *Ips typographus* (SBB) damage in Norway spruce stands. The data for clear-cuts stands are from 2017–2022, while data from wind- and SBB-damaged stands are from 2021 and 2020. Adapted from Sub-study III (manuscript under review).

In Sub-studies I and III, clear-cut influence peaked around 500 m. This aligns with previous studies where new SBB damage appeared within 200–500 m of clear-cuts (Kärvemo et al. 2014; Müller et al. 2022). The likely reason behind this effect is that the new edges created by clear-cuts provide favourable conditions for beetle reproduction, facilitating new attacks (Stříbrská et al. 2022). Higher edge temperatures accelerate beetle development, increase flight activity and dispersal and enhance the synchrony and intensity of mass attacks (Funke and Petershagen 1994; Hinze and John 2019; Wermelinger and Seifert 1999). In addition, trees on new edges are commonly weaken and wind-damaged (Louis et al. 2015). Together, these conditions improve the beetles' ability to attack and overcome host defences.

The proximity to earlier SBB damage also influenced the occurrence of new SBB damage in Sub-study III and was the main driver of hotspot formation and recurrence in Sub-study II. This reflects the typical spread of SBB damage during epidemic conditions, where beetles attack new hosts close to previously infested trees (Hlásny et al. 2021; Netherer et al. 2019). This pattern has also been observed in *D. ponderosae* (Nelson and Boots 2008). The spatial extent of the effects of previous SBB damage varied among sub-studies. In Sub-study I, previous SBB damage increased the amount of new damage up to 1500 m, with a modest effect. In Sub-study II, however, earlier SBB damage had a strong effect on hotspot formation and recurrence within 500 m. This finding was consistent with Sub-study III, which also showed an elevated probability of SBB damage within 500 m. Earlier research has reported distances ranging from 213 m (Stereńczak et al. 2019) to 750 m (Müller et al. 2022). These is consistent with the epidemic phase of population dynamics (Hlásny et al. 2021; Wermelinger 2004).

In Sub-studies I and III, the effect of previous wind damage and SBB damage on new infestations was weaker than the influence of clear-cuts. These disturbances are closely linked: salvage of wind- or SBB-damaged stands often results in new clear-cuts, which in turn promote further SBB damage. This feedback loop, found in Sub-studies I and III, and illustrated in Figure 9, highlights the interconnected role of these disturbances in sustaining outbreaks.

Sub-study III showed that the volume of growing stock (i.e. Norway spruce vs. other tree species) had a relatively small effect on SBB probability compared with other stand and landscape attributes. However, the probability of SBB damage decreased as the volume of other tree species increased. Other studies have similarly observed that greater Norway spruce volume increases damage probability, while the presence of other species reduces it (de Groot et al. 2023; de Groot and Ogris 2019; Felton et al. 2016). In an equivalent way, Norway spruce volume is positively related to higher SBB population (Gohli et al. 2024), Mixed-species stands may reduce susceptibility to SBB damage through several mechanisms, including enhanced natural enemy activity, diverse fungal associates, physical barriers to beetle movement and disrupted olfactory cues (Felton et al. 2016; Klapwijk et al. 2016; Kozhoridze et al. 2024; Zhang and Schlyter 2004).

In Sub-study II, proximity to previous SBB damage was the most important attribute related to hotspot formation. Similar formation of SBB hotspots has been reported (Kamińska 2022; Stereńczak et al. 2020). Hotspots and recurrent hotspots were particularly common in southeast Finland, with additional dispersed hotspots elsewhere. The peak hotspot period (i.e. 2012–2014) may be explained by previous severe windstorms in southeast Finland and a warm summer with above-average temperatures (Tikkanen and Lehtonen 2023; Viiri et al. 2019), which triggered extensive SBB damage. Conversely, the low recurrence of hotspots suggests that the conditions required for persistent clusters were rarely met in Finland during the study period. These results indicate that while spatial clustering occurs, it is generally transient or dynamic rather than stable over time.

4.3 Effects of climatic attributes on SBB damage

Sub-study III revealed that climatic attributes played only a minor role in predicting the probability of SBB damage. The effects of temperature conditions on SBB damage (Annila 1969; Økland et al. 2015) and the combined effect of temperature and drought on beetle attacks (Funke and Petershagen 1994; Hinze and John 2019; Wermelinger and Seifert 1999) have also been well-documented in previous studies. The weak or non-existent influence of climatic attributes in Sub-study III may reflect non-linear effects, masking by random variables or interactions not captured in the models. Additionally, their reduced significance could result from the inclusion of other variables. Even though, climatic conditions, specifically low thermal conditions, have historically limited SBB development in our study area (Annila 1969; Tikkanen and Lehtonen 2023), also in locations where temperatures are higher than in our study area (Kovárník et al. 2025; Wermelinger 2004).

Interactions between climatic attributes, such as periods of high temperature combined with low precipitation, play a particularly important role in influencing SBB damage (Netherer et al. 2015; Potterf et al. 2025). The mechanism behind the effect of hot droughts is driven by the positive effect of high temperatures on the beetle population and the negative effect of droughts on the Norway spruce defence system (Netherer et al. 2015). Offering support for the effect of hot droughts, the number of consecutive hot days was the most influential climatic attribute in Sub-study III, what is explained by the increasing attack success that higher temperatures have (Funke and Petershagen 1994; Hinze and John 2019; Wermelinger and Seifert 1999). However, the conflicting north–south influence that number of consecutive hot days have on the probability of SBB damage suggests complex thermal responses, warranting further study. Precipitation had little effect on SBB probability in Sub-study III, although low precipitation has previously been linked to beetle damage (Grodzki et al. 2006; Kozhoridze et al. 2024). However, it is possible that drought-induced weakening of Norway spruce has a lag of up to three years (Netherer et al. 2015; Økland et al. 2015).

4.4 Forest risk management implications

Diversified forest structure (i.e. tree species composition and age) may reduce SBB damage risk at the forest landscape level. The findings of all three sub-studies suggest that reducing the proportion of mature Norway spruce stands and increasing both species and age diversity can reduce forest vulnerability to SBB damage. This is especially relevant in southern Finland, where mature Norway spruce is widespread and SBB hotspots are concentrated (Korhonen et al. 2021).

In the coming years, climate warming is expected to increase the susceptibility to both wind and SBB damage (Venäläinen et al. 2022). Wind and SBB damage can initiate new SBB outbreaks, fostering hotspot formation and recurrence. In Finland, the usual response to wind and SBB damage is salvage logging, which creates new clear-cuts. Although clear-cuts can limit beetle spread in some situations (Wermelinger 2004; Hlásny et al. 2021), Sub-studies I and III showed that they are also drivers of new SBB damage (Figure 9). Infested trees should instead be managed in ways that reduce outbreak likelihood. One alternative is *timely selective removal* – removing infected trees on time, before completing the development of the new beetle generation. This may help to reduce vulnerable forest edges and lower infestation probability (Komonen et al., 2020). However, selective removal can also increase harvesting damage (Hantula et al. 2025; Nevalainen 2017) and reduce the long-term wood supply, which can have a negative impact on financial revenues (Brunner et al. 2025).

Considering the forest areas vulnerable to SBB attacks, annually updated risk maps, similar to the ones produced in Sub-study III, can help identify areas requiring monitoring or intervention (Figure 7 and Figure 8). Risk maps can support operational forest management planning by helping identify and prioritise cuttings of the stands most vulnerable to SBB outbreaks. This can significantly increase the effectiveness of detection efforts, whether conducted manually (Kautz et al. 2023), with scent detection dogs (Vošvrdová et al. 2023) or with large-scale aerial remote sensing technologies (Turkulainen et al. 2025). The identified hotspots highlight areas where SBB activity tends to cluster, enabling forest managers to prioritize surveillance and reduce the need for blanket monitoring across large regions. This approach also supports more efficient allocation of limited resources, such as personnel, machinery, and funds, to the areas of greatest concern.

4.5 Advantages, limitations and future research

The data and methodology used in Sub-studies I-III were selected to progressively build a comprehensive understanding of the studied phenomena. The datasets used in all sub-studies generated robust findings, including damage risk maps, given the huge amount of national stand-level data they provided (11.4 million ha with more than two million Norway spruce stands). Such data is not commonly available for forest health studies countrywide (Fernández-Carrillo et al. 2024; Nardi et al. 2023; Seidl et al. 2011). Other key advantages of the spatial datasets used are that they signal the agent causing the damage and are publicly available (Metsäkeskus 2025). This is in contrast to aerial imagery data, where it can be difficult to identify the agent causing the damage (Junttila et al. 2024).

However, the forest-use notifications dataset based on salvage logging may contain time gaps. Because records precede logging, some operations may not have been executed, some damage may have gone unreported and older damage may have been misclassified. A major shortcoming of this dataset is the absence of damage intensity data (e.g. timber volume or affected area), which could improve the inference of SBB damage levels (Hlásny et al. 2021; Kautz et al. 2011). Damage intensity can be derived from remotely sensed data, but such data are costly and not always readily accessible for analysis. Future efforts integrating remote sensing with ground-based observations may help fill gaps in damage intensity information and improve overall assessment accuracy. It should also be noted that the soil-type data used in this study were not based on thorough field inventories, which is a limitation for assessing the role of soil type in the damage events.

Future studies on hotspot formation may include attributes based on climate, soil and beetle population levels to better explain hotspot formation and recurrence. Similarly, future modelling endeavours may include data on combined heat and drought effects and beetle population levels, which may result in better-fitting models at the national level.

The developed models explained a substantial portion of the variation in SBB damage probability, but system complexity, multiple drivers and the large study area left some variation unexplained. Possible additional explanations include unconsidered local factors such as microclimate, beetle populations, soil conditions, prior tree health and unreported disturbances. For example, root rot (*Heterobasidion* spp.) also predisposes trees to SBB attacks (Wahlman et al. 2025) but sufficient data on root rot occurrence is unavailable. Full-area probability models may become feasible with longer time series, additional predictors for local conditions and higher spatial resolution of SBB damage. More advanced approaches– such as geographically weighted regression, Bayesian spatial models, or other modelling techniques – could also be valuable for developing a comprehensive, full-area model (Seidl et al. 2011).

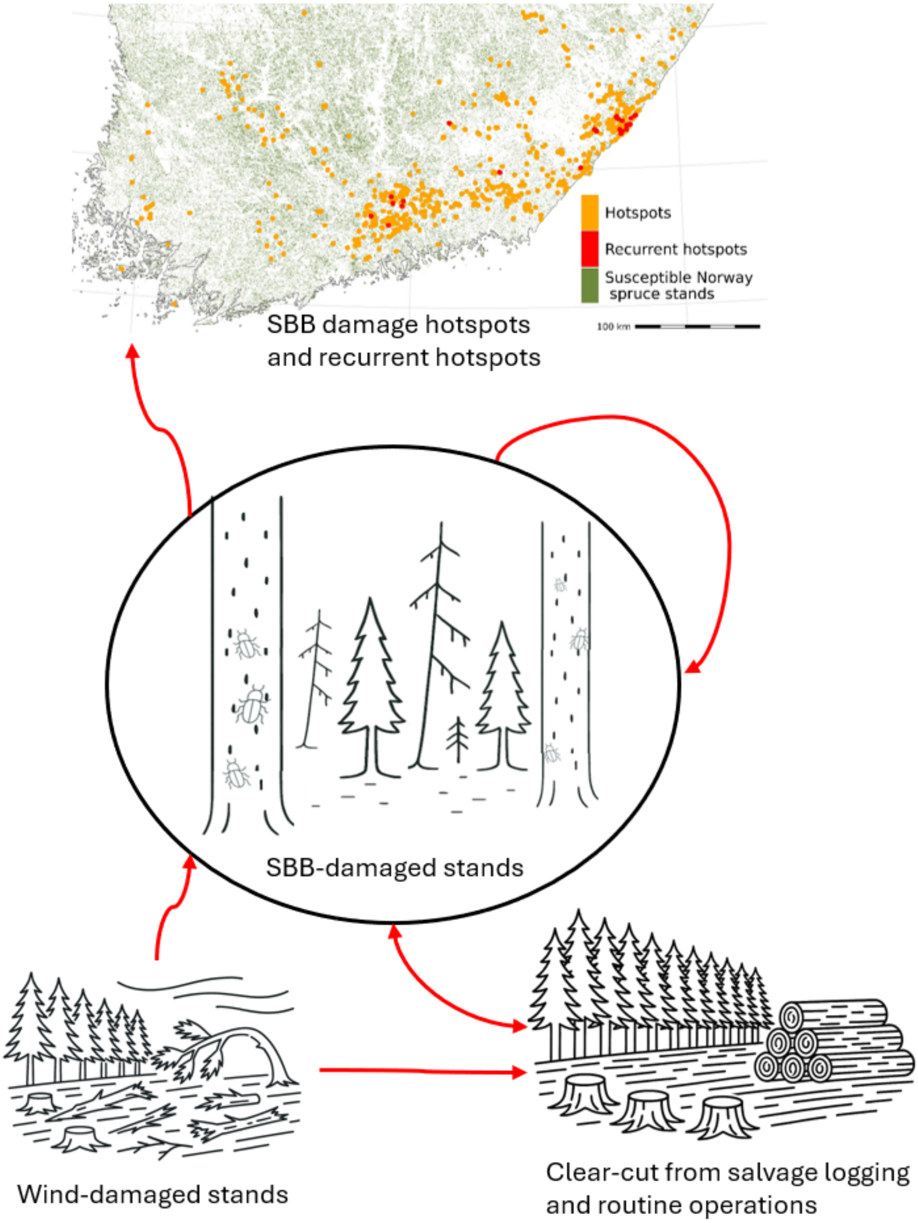

Figure 9. Self-reinforcing sequence of *Ips typographus* (SBB) damage. Wind or SBB damage leads to the removal of affected trees. This is typically carried out through salvage logging, which may involve clearing entire stands or portions of them. However, such interventions can inadvertently promote further bark beetle outbreaks and contribute to the development of damage hotspots.

5 CONCLUSIONS

This comprehensive dissertation showed how forest stand, landscape and climatic attributes strongly influence SBB damage and its spatial distribution in Finland. Sub-study I showed that SBB damage was concentrated in mature, older stands with greater mean stand diameter at breast height and that nearby disturbances (i.e. wind and SBB damage) also increased the number of SBB-damaged stands. Sub-study II showed that hotspots were more frequently formed in southeastern Finland and were linked to stand age and proximity to recent SBB damage. Recurrent hotspots correlated with stand development class and proximity to older damage. Sub-study III showed that the probability of SBB damage was primarily driven by proximity to clear-cuts, mean stand diameter at breast height and consecutive hot days above 25°C, with higher probabilities in the southern study sub-area. The findings show that as Norway spruce stands mature and get older, they become more vulnerable to beetle attacks, which is further exacerbated by hot days. Mature stands not only attract infestations but also foster the formation of damage hotspots and their recurrence, especially when located near areas previously affected by SBB.

The typical response to SBB damage is salvage logging the affected stand, either fully or partially, creating clear-cuts. However, this may trigger new outbreaks, as proximity to clear-cuts contributes to SBB damage. In the short term, risk maps can guide forest managers to harvest high-risk stands and enable targeted monitoring and timely, cost-effective intervention. In the long term, SBB risk will depend on the structural and compositional diversity of forests. Further research is needed to identify which kind of proactive management options are most effective under future climatic conditions. To tackle the increasing risk of SBB outbreaks and damage under climate change, it is crucial to improve forest health monitoring and management to reduce the likelihood of future large-scale SBB outbreaks.

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