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# Weak performance of the Eurasian spruce bark beetle in the non-native lodgepole pine

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**ABSTRACT**
The North American lodgepole pine is the most used non-native tree species in Sweden. The performance of the Eurasian spruce bark beetle (*Ips typogaphus*) and the occurrence of other insects were recorded from bark samples from 19 *I. typographus*-killed lodgepole pines in central Sweden. The occurrence of blue-stain fungi and the mean radial increment were recorded from cut stem sections from 10 trees. Mean colonization density (± SE) per $m^2$ bark was 331 ± 38 for males (based on entrance holes) and 329 ± 39 for females (maternal galleries) at 2.5 m height. The mean production of new generation *I. typographus* adults per $m^2$ bark was 8.6 ± 2.6 and mean reproductive success (daughters per mother) was 0.01 ± 0.003. The mean density per $m^2$ bark of the bark beetle enemies *Thanasimus* sp. (Coleoptera) was 2.2 ± 2.2, *Medetera* spp. (Diptera) 41.8 ± 10.3 and parasitoids 30.8 ± 10.1. Blue-stain covered most of the surfaces of the cut stems and the annual ring widths decreased steadily during the last 20 years. The study demonstrates that *I. typographus* can colonize weakened lodgepole pines, but the reproductive success is very low. *Ips typographus* does not escape its enemies in the non-native host.

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Colonization density; *Ips typographus*; natural enemies; non-native tree species; *Pinus contorta*; reproductive success

## Introduction

In recent decades, global forestry has seen the widespread planting of non-native tree species to boost the production of timber, pulp, and fuelwood, as well as to mitigate erosion (Richardson and Rejmánek 2011; Brundu and Richardson 2016). On a global scale, 44% of plantation forests are now dominated by non-native tree species (Food and Agriculture Organization of the United Nations 2010). Diversifying forest production with the use of non-native tree species has also increased in Scandinavia, first to increase forest production, and in more recent years to help maintain sustainable forestry under climate change (Felton et al. 2013; Kjær et al. 2014; Mårald et al. 2024). The most used non-native tree species in Sweden is lodgepole pine (*Pinus contorta* Douglas var. *latifolia*). The species is native to the northwestern USA and western Canada and has been used at a large scale in Swedish forestry since mid-1970s to overcome a predicted future timber shortage (Elfving et al. 2001; Mårald et al. 2024). The introduction of lodgepole pine into Sweden is one of the largest introductions of non-native tree species in Europe, covering about 6000 square kilometers or about 5% of production forest land in northern Sweden (Mårald et al. 2024). Thus, it is important to evaluate to what extent native pests may be a threat to these lodgepole pine stands.

Tree-killing bark beetles are one of the most important disturbance factors in conifer forests (Raffa et al. 2008). In Europe, the Eurasian spruce bark beetle *Ips typographus* (L.) (Coleoptera, Curculionidae) is the most important species, causing the mortality of millions of $m^3$ of Norway spruce [*Picea abies* (L.) Karst] during outbreaks (Schelhaas et al. 2003; Seidl et al. 2011; Marini et al. 2017). Damages have also increased in recent decades (Hlásny et al. 2021). Outbreaks are triggered by large-scale storm fellings and warm and dry summers (Schroeder and Lindelöw 2002; Kärvemo et al. 2014; Hlásny et al. 2021; Rousi et al. 2023). After the exceptionally warm and dry summer of 2018, Sweden experienced the largest outbreak ever recorded with an estimated 31 million $m^3$ of mature spruce forest killed during the years 2018–2023 (Schroeder and Kärvemo 2022; Wulff and Roberge 2023).

In Europe, Norway spruce is the main host tree of *I. typographus*. The males initiate tree colonization by tunneling into the bark and releasing aggregation pheromones that strongly attract females and males. The females establish maternal galleries under the bark in which they lay their eggs and the hatched larvae feed on the phloem. Tree-killing bark beetles, including their associated microorganisms, attempting to colonize living trees encounter both constitutive and induced tree defences (Franceschi et al. 2005; Raffa 2014; Krokene 2015; Whitehill et al. 2023). These defences may be overcome by bark beetle mass attacks, coordinated by aggregation pheromones that rapidly attract high numbers of beetles, and by the beetles vectoring blue-stain fungi that

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are considered to contribute to the breakdown of tree defences. For successful colonization, the density of attacking beetles must exceed a critical threshold (Raffa and Berryman 1983; Mulock and Christiansen 1986; Christiansen et al. 1987; Pineau et al. 2017). If the attack density is below the critical threshold, reproduction will be strongly reduced or fail.

There are only a few earlier studies about the ability of *I. typographus* to colonize and successfully reproduce in non-native tree species. Most of these have compared the performance of *I. typographus* in Norway spruce (its historical host) with the performance in congeneric North American spruce species (Økland et al. 2011; Flø et al. 2018; Isitt et al. 2023a) while only one has considered a non-native pine species, lodgepole pine (Schroeder and Cocoş 2018). The studies on spruce suggest that *I. typographus* can colonize and reproduce in the North American spruce species but that the reproductive success is somewhat lower or similar compared with Norway spruce. The comparison of *I. typographus* performance in lodgepole pine and Norway spruce showed a much lower reproductive success in lodgepole pine (Schroeder and Cocoş 2018). Only two of the earlier studies of *I. typographus* performance on non-native tree species were conducted on living trees which means that the beetles encounter tree defences (Økland et al. 2011; Schroeder and Cocoş 2018). In both these studies, the trees were baited with *I. typographus* pheromones to induce attacks which may have influenced colonization densities and helped the beetles to overcome the tree defences. Thus, there is a need to study bark beetle performance on non-native tree species under more natural conditions, i.e. when the beetles themselves select trees to attack. This means that colonization density will depend on the beetles' ability to produce pheromones in the non-native tree species which influences the probability of overcoming tree defenses of living trees and thus also the reproductive success.

The performance of *I. typographus*, and other native bark- and woodboring beetles, in lodgepole pine is of interest for not only European forestry but also forestry in western North America where lodgepole pine is one of the most common tree species. This is because *I. typographus* is one of the most commonly intercepted non-native *Ips* species (Turner et al. 2021). Up until 2008, *I. typographus* was intercepted 465 times at North American ports (Liebhold et al. 2017). This means that there is a considerable risk that the species at some point may establish there.

In 2023, two lodgepole pine stands have been attacked by *I. typographus* in Sweden. No Norway spruce trees in the stands could have induced the attacks on the lodgepole pines. Thus, the stands provided an opportunity to study the performance of *I. typographus* in naturally attacked lodgepole pines. The specific questions addressed in the study were (1) What were the colonization density and reproductive success of *I. typographus*? (2) Which other bark- and woodboring species colonized the trees? (3) Which bark beetle enemies were present and at what densities? (4) How much of the wood surface was covered by blue-stain fungi? (5) What was the yearly increment growth in the last twenty years? In addition, we checked for signs of bark beetle attacks on nearby living lodgepole pines and Norway spruces.

## Materials and methods

### Study sites

The study was conducted in two small stands (0.8 and 0.6 ha), age 35 years and approximately 90% dominated by lodgepole pine, and attacked by *I. typographus*. The stands are located close to the Baltic Sea in the county of Upland in central Sweden (Figure 1). Norway spruce and Scots pine (*Pinus sylvestris,* L) are the dominant tree species in this region, with some deciduous trees, consisting mostly of birch [*Betula pendula* (Roth.) and *B. verrucosa* (Ehrh.)], and aspen [*Populus tremula* (L.)]. Only a few lodgepole pine stands have been established in this region. The mean diameter at breast height (DBH hereafter; ± SE) for the unattacked lodgepole pines in the two stands was 15.4 ± 0.4 cm ($N = 50$, stand 1) and 14.6 ± 0.4 cm ($N = 50$, stand 2), respectively. The mean DBH for spruce trees found within the two stands was 15.6 ± 0.8 cm ($N = 22$, stand 1) and 15.1 ± 0.7 cm ($N = 32$, stand 2), respectively. The mean diameter of a pure Norway spruce stand bordering stand 1 was 16.3 ± 0.6 cm ($N = 50$). The lodgepole pine stands were thinned about three years before the study was conducted. Both stands were situated on small hills with rocky outcrops. Based on five soil profiles per stand, the organic soil layer was situated directly on the bedrock with mean depths of 12.6 ± 0.6 cm (stand 1) and 9.2 ± 0.5 cm (stand 2). For the spruce stand bordering stand 1, the organic soil layer was 22.1 ± 0.2 cm, and situated on a coarse layer of the soil.

Research questions (1) – (3) were answered by analyzing bark samples, and questions (4) and (5) by inspecting surfaces of cut stem sections from killed lodgepole pines in stand 1. In stand 2, the killed lodgepole pines had been cut in winter 2023/2024, thus sampling was not possible there. In stand 1, 25 lodgepole pines were killed and in stand 2 about 11 lodgepole pines. The cut trees from stand 2 were stored nearby and these trees were also colonized by *I. typographus*. No Norway spruces were killed in the two lodgepole pine stands, or in adjacent spruce stands, and thus no comparison of *I. typographus* performance in the native host tree species and lodgepole pine in the same locality was possible.

### Bark samples

The bark sampling was done between the 6th of February and the 8th of March in 2024 before insect emergence. Nineteen of the 25 killed lodgepole pines in stand 1 were sampled: ten by felling the trees and cutting 50 cm long stem sections at five different heights and nine by taking one bark sample at 2.5 m height without felling the trees. The mean DBH for the 19 sampled trees was 16.3 ± 0.7 cm and the mean thickness of the bark samples was 3.3 ± 0.2 mm. For the felled trees, stem sections were cut at (1) the base, (2) 2.5 m, (3) 5 m, (4) 8 m and (5) the top of the tree. In addition, one branch was collected at 2–3 m height. The 2.5 m height was chosen to be able to compare the results with a previous study in which healthy lodgepole pines and Norway spruces were baited with *I. typographus* pheromone dispensers (to induce attacks) and subsequently checked for bark beetle performance in bark

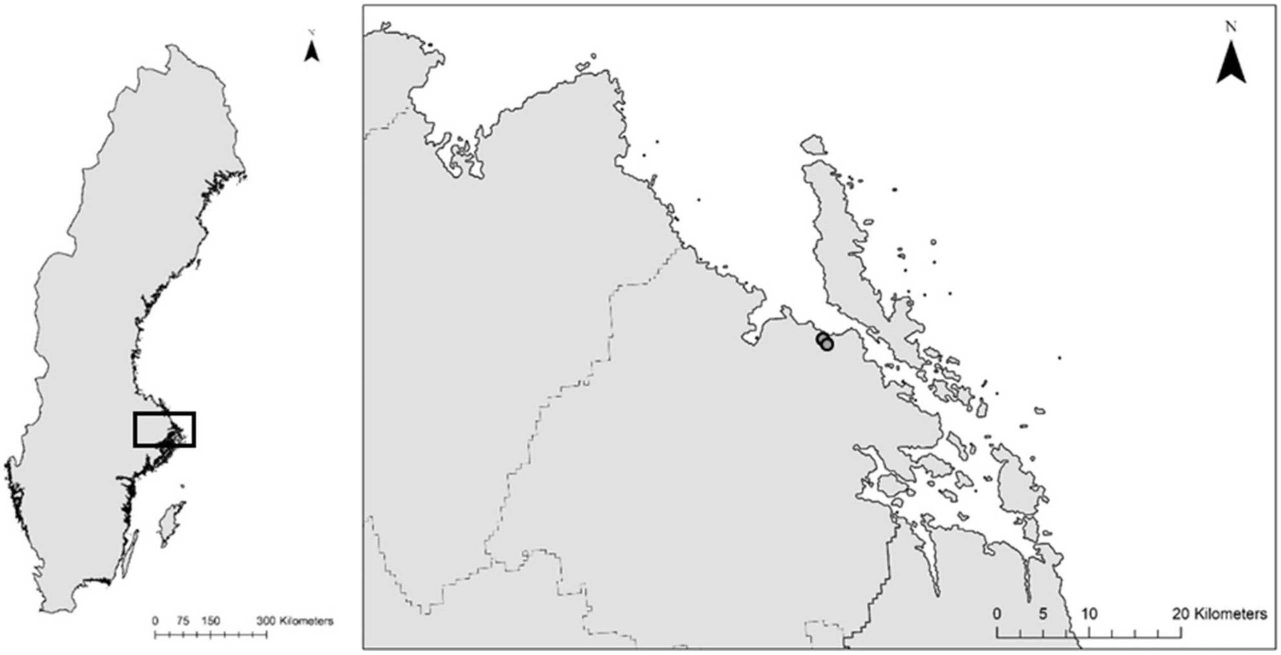

**Figure 1.** Map showing the locations of the two stands (red circles) in which lodgepole pines were killed by *Ips typographus* in 2023. The distance between the two attacked stands was 650 m. Central coordinates (WGS84) for Stand 1: 60°19′54.7"N 18°23′18.2"E and Stand 2: 60°19′39.2"N 18°23′46.0" E.

samples from 2.5 m height (Schroeder and Cocoş 2018). The other heights, and branches from the felled trees, were included to check how large parts of the trees were colonized by *I. typographus* and which other insect taxa occurred in the trees.

All stem sections, branches and bark samples were brought to the laboratory where they were stored at +5°C until analyzed. One bark sample was taken from each stem section in the laboratory (except the top section). The bark sample size was $15 \times 45$ cm and the bark thickness of each sample was recorded. Tops and branches were analyzed by removing the bark on the whole length (mean $54 \pm 3$ cm and $55 \pm 5$ cm, respectively). For the ten cut trees, the diameter of each stem section was measured.

For each bark sample, the following *I. typographus* variables were recorded: number of male entrance holes and maternal galleries (representing male and female colonizations), number of mating chambers, number of maternal galleries per mating chamber, maternal gallery length and number of live individuals of different developmental stages in the samples (i.e. larvae, pupae, adults) and emergence holes from the new-generation adults. All variables were recalculated to densities because the bark sample differed somewhat in size (mean size $0.07 \pm 0.001$ m$^2$). Reproductive success was calculated as the number of daughters per mother beetle (defined as the number of beetles produced x 0.5)/(number of maternal galleries) (Hedgren and Schroeder 2004).

For other bark beetle species, we recorded gallery system coverage and development stage in the bark samples. In addition, densities of live individuals and cocoons of bark beetle enemies were recorded as well. The enemies were not identified at the species level, but grouped into parasitoids (larvae or cocoons), predatory flies of the genus *Medetera* (larvae), and predatory beetles of the genus *Thanasimus* (larvae). These three groups include the most common insect enemies of *I. typographus* under bark (Weslien 1992; Hedgren and Schroeder 2004; Kenis et al. 2004). *Thanasimus* larvae may be either *T. formicarius* or *T. femoralis*. Both parasitoids and *Medetera* include several species. As the sampling was done in the early spring after the year of attack, most *Thanasimus* larvae should have already left the stems of the trees, whereas some parasitoids and most *Medetera* hibernate in the bark colonized by *I. typographus* (Weslien 1992; Schroeder 1999; Hedgren and Schroeder 2004). Thus, our results will underestimate *Thanasimus*, and somewhat underestimate parasitoids, but be accurate for *Medetera* regarding the densities produced in the trees.

### Failed bark beetle attacks on living trees

In both lodgepole pines stands and the adjacent Norway spruce stand, all diameter-measured living trees, including the few existing Norway spruces and Scots pines within the lodgepole pine stands, were visually inspected for failed bark beetle attacks from the base up to 3 m height. If holes or resin exudations were present, a knife was used to debark the area around the attack and the fate of the attack was recorded.

### Blue-stain fungi and tree growth

The percentage of the cut surface of each stem section and branch stained by blue-stain fungi was recorded. To quantify the yearly growth for the ten cut trees, the lower cut surface of the stem sections cut at 2.5 m was polished. The widths of the last 20 annual rings were measured with a digital caliper and calculated as the mean of two sets of measurements taken at 90 degrees from each other starting from the pith.

Tree age was determined by counting the annual rings on the basal stem section.

### Temperature and precipitation

Daily maximum and minimum temperatures, and precipitation, for the period March 1st–July 31st 2023 were derived from the nearest Swedish Meteorological and Hydrological Institute (SMHI) weather stations. Precipitation: Söderby-Karlsäng, distance 5.5 km (coastal, no temperature readings); Temperature: Film, distance 30 km (inland), Örskär, distance 21 km (coastal) and Gävle, distance 75 km (coastal) (Figure S1).

### Statistical analyses

All statistical analyses were performed in R studio, version 2023.09.1 (R Core Team 2023). Separate analyses were conducted for bark samples from 2.5 m (first dataset, 19 trees) and bark samples from the cut trees (second dataset, 10 trees). For the first dataset, we used linear models (LM) to analyze the relationship between the *I. typographus* male and female colonization densities (response variables) and the two explanatory variables tree diameter at 2.5 m and bark thickness. For the second dataset, linear mixed-effect models were used to analyze the relationship between the male and female colonization densities (response variables) and bark thickness (explanatory variable). The tree was included as a random factor (to account for differences between the sampled trees). Linear models (LM) were used to analyze the relationship between the above-mentioned response variables and the bark sample height (i.e. base, 2.5, 5 and 8 m) as a predictor. Tops and branches were excluded from these analyses due to very low colonization of *I. typographus*. No models were run on the *I. typographus* reproductive success and number of offspring produced per m$^2$ bark area, due to too many zeroes. Levene's test was used to check for homogeneity of variance in the residuals (Levene Test; car-package, Fox and Weisberg 2019). The package multcomp (Hothorn et al. 2008) was used for Tukey's pairwise comparisons.

## Results

No live *I. typographus* larvae, pupae or adults were found in any of the bark samples. However, emergence holes demonstrated that a few new-generation adults had been produced. *Ips typographus* larval galleries developed from all maternal galleries. However, the pupal stage was only reached in 68% (based on the presence of pupal chambers), and new generation adults in only 42% of the bark samples (the presence of emergence holes).

### Performance of **I. typographus** in bark samples at 2.5 m (first dataset)

*Ips typographus* colonization occurred in 18 out of the 19 samples, and the mean colonization density per m$^2$ bark (including all 19 samples) was 331 ± 38 for males (entrance holes) and 329 ± 39 for females (maternal galleries). Only 51% of the entrance holes resulted in a mating chamber with maternal galleries. No significant relationship was found between the male ($F_{1,17} = 0.08$, $p = 0.79$) or the female ($F_{1,17} = 0.51$, $p = 0.49$) colonization density and the tree diameter at 2.5 m. The mean number of maternal galleries per mating chamber was 1.82 ± 0.14 and the mean maternal gallery length was 7.1 ± 0.6 cm. There was a positive and significant relationship between *I. typographus* male attack density and the density of maternal galleries ($r = 0.64$, $n = 19$, $p = 0.003$) (Figure 2A).

The mean production of new-generation adults per m$^2$ bark was 8.6 ± 2.6 ($N = 19$, based on emergence holes). *Ips typographus* mean reproductive success (daughters per mother) was 0.01 ± 0.003. New-generation adults were only produced when the density of entrance holes exceeded 200 per m$^2$ bark (Figure 2B).

### Performance of **I. typographus** in bark samples at different heights (second dataset)

Male and female *I. typographus* colonizations occurred from the base up to the 8 m section but not in the tops (except for one, with both male entrance holes and maternal galleries present), or branches (Figure 3A and B). Male and female colonization densities were significantly lower in the 8 m sections than in the lower sections (male: $F_{3,36} = 2.96$, $p = 0.04$; female: $F_{3,36} = 2.72$, $p = 0.05$). There was a significant negative relationship between bark thickness and both male ($p = 0.05$) and female ($p = 0.03$) colonization densities. The decrease in bark thickness with height above ground for the ten killed trees that were cut is shown in Figure S2. No new generation adults of *I. typographus* were produced at heights above 5 m (Figure 3C and D).

### Presence of other species

Nine taxa of bark and wood-boring beetles were recorded from the killed lodgepole pines (Table 1). The most common species (based on a number of colonized trees) in the samples taken at 2.5 m height were *I. typographus*, *Acanthocinus griseus* (Fabricius) and *Pityogenes chalcographus* (L). For the 10 cut trees, including all six heights and branches, the most common species were *I. typographus, A. griseus, P. chalcographus* and *Polygraphus poligraphus* (L). Most bark and wood-boring species occurred in the base (seven species), followed by the 5 m sample (six species) and the 2.5 m sample (five species).

In addition, several bark beetle enemies and other species associated with bark beetle-killed trees, representing four different insect orders, were present in the bark samples (Table 2). The densities per m$^2$ bark in the 2.5 m samples of three of the most common enemy groups were *Thanasimus* spp. (Coleoptera) 2.2 ± 2.2, *Medetera* spp. (Diptera) 41.8 ± 10.3 and parasitoids (Hymenoptera) 30.8 ± 10.1.

### Failed bark beetle attacks on living trees

A few entrance holes and mating chambers filled with resin (i.e. failed bark beetle attacks) were observed on four

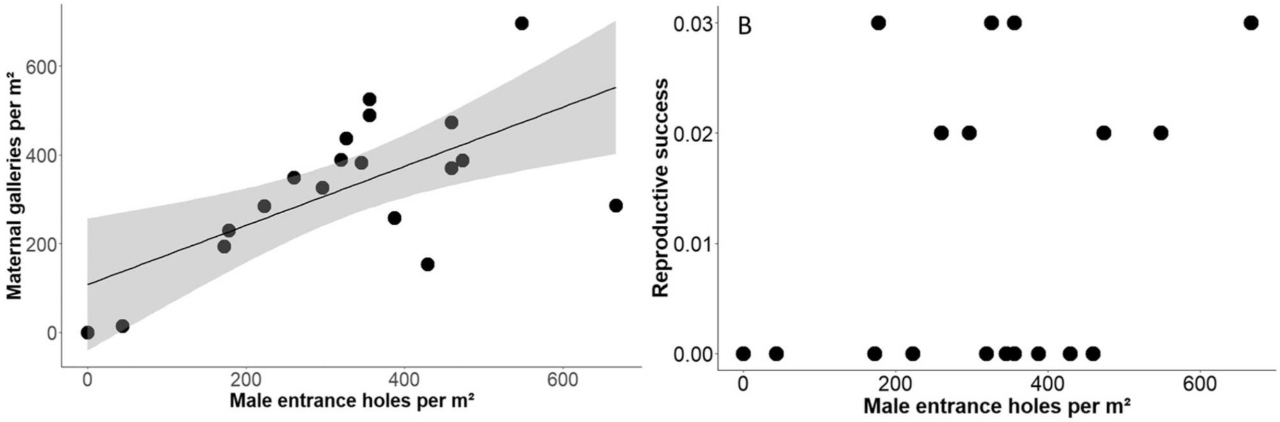

**Figure 2.** Relationship between densities of (A) *Ips typographus* male entrance holes and maternal galleries and (B) *Ips typographus* male entrance holes and female reproductive success in naturally colonized lodgepole pine. Each symbol represents one sampled tree at 2.5 m height.

lodgepole pines in stand 1, and none in stand 2. No failed attacks were recorded on Norway spruces or Scots pines within stands 1 and 2 or in the adjacent spruce stand. Very few, and very short pitch tubes were observed on both successfully and failed attacked lodgepole pines. No *I. typographus* attacks occurred on spruce trees growing within 100 m of the lodgepole stands in 2023. Bark beetle-killed spruces were recorded at a distance of 450 m from stand 1 (four trees), and 600 m from stand 2 (six trees).

## Blue-stain fungi and tree growth

Almost all cut stem sections and branches (except one base, one top and one branch) were affected by blue-stain fungi. The mean coverage for the blue-stain (Figure 4) was high to the top of the trees, with no significant difference between the different heights ($F_{5,54} = 1.54$, $p = 0.19$).

The analysis of tree ring widths for the last twenty years showed a steady decrease over time with an especially strong dip in 2017 and in the exceptionally dry and warm

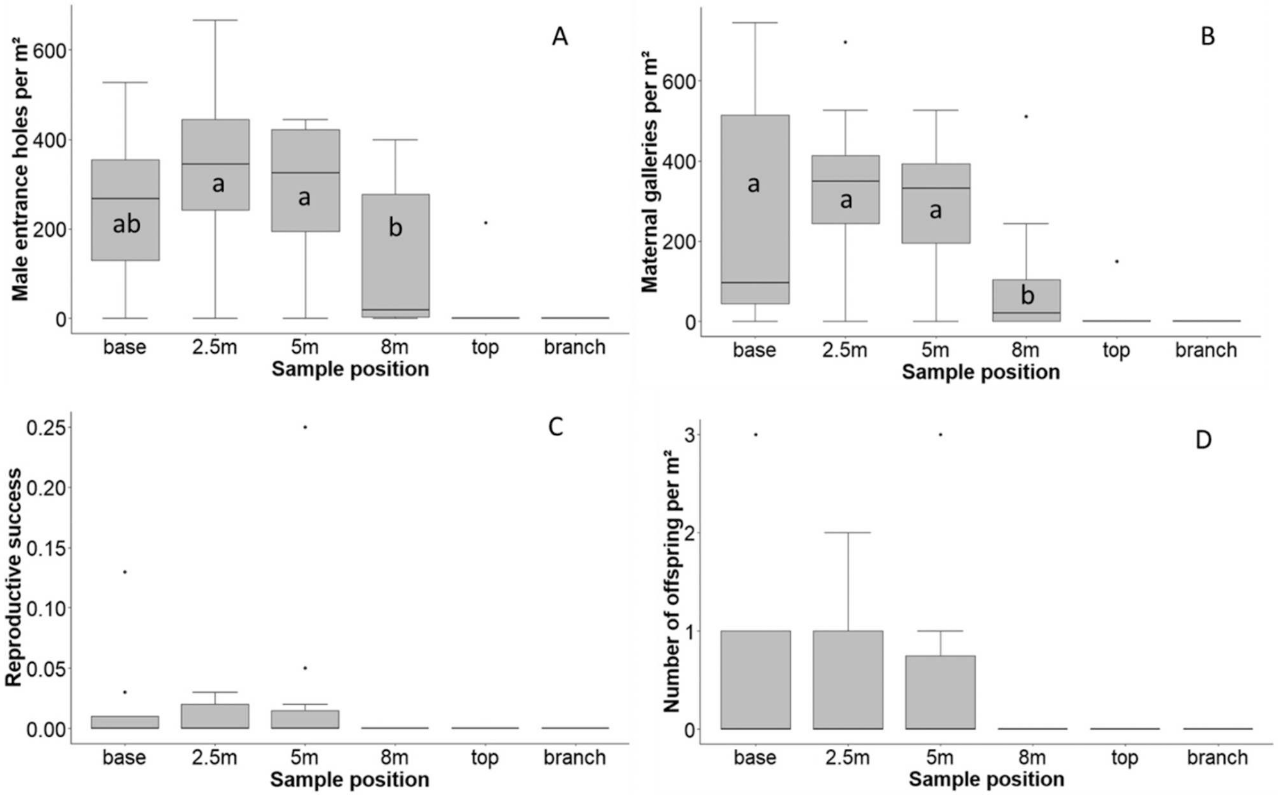

**Figure 3.** *Ips typographus* male (A) and female (B) colonization densities, reproductive success (C), and offspring production (D) in bark samples from different heights of the stems of ten killed lodgepole pines and in branches. The central lines of the box plot represent the median, the box indicates lower and upper quartiles and the whiskers represent the largest and smallest observations that fall within 1.5 times the box size from the nearest quartile. Only samples from the base, 2.5, 5 and 8 m are included in the analyses. Black dots represent outliers. Means with different lowercase letters are significantly different at $p < 0.05$.

**Table 1.** Number of killed lodgepole pines colonized at different heights by different species/taxa of bark- and wood-boring beetles based on analysis of bark samples.

| Species | Number of colonized trees and percentage of sample area covered by galleries | | | | | | | Total | Present as | Native host |
|---|---|---|---|---|---|---|---|---|---|---|
| | Base | 2.5 m | | 5 m | 8 m | Top | Branch | | | |
| Replicates | 10 | 10 | 19 | 10 | 10 | 10 | 10 | | | |
| Curculionidae | | | | | | | | | | |
| Scolytinae | | | | | | | | | | |
| Pityogenes chalcographus | 2 (18) | 4 (40) | 9 (30) | 8 (41) | 10 (54) | 10 (73) | 9 (59) | 15 | GS, AD | S,(P) |
| Ips typographus* | 9 | 9 | 18 | 9 | 7 | 1 | | 19 | GS | S |
| Polygraphus poligraphus | | 1 (50) | 6 (24) | 3 (4) | 3 (37) | 4 (22) | 5 (38) | 12 | GS, LA | S |
| Crypturgus sp. | 1 (1) | 2 (60) | 4 (50) | 3 (21) | | | | 5 | GS, AD | S,P |
| Tomicus piniperda | | | | 1 (1) | | | | 1 | AD | P |
| Curculioninae | | | | | | | | | | |
| Pissodes sp. | 3(33) | | | | | | | 3 | GS, AD | S,P |
| Cerambycidae | | | | | | | | | | |
| Acanthocinus griseus | 6(21) | 9 (24) | 17 (22) | 10 (20) | 8 (15) | 10 (12) | 9 (8) | 18 | GS, AD | S,P |
| Rhagium inquisitor | 5(28) | | | | | | | 5 | GS, AD | S,P |
| Asemum/Arhopalus | 1 (2) | | | | | | | 1 | GS | S,P |

In parenthesis percentage of the bark sample covered by galleries of the species. At 2.5 m height, nine additional trees to the 10 cut trees were sampled. Native host trees of the species: S, Norway spruce; P, Scots pine. Colonization recorded from the presence of AD, adults; GS, gallery systems; LA, larvae. Empty cells represent zero counts.

*For *Ips typographus* no data were collected on the percentage of bark samples covered by galleries.

summer of 2018 (Figure 5). In 2019, there was an increase and thereafter the decrease continued.

### *Temperature and precipitation*

The spring and summer of 2023 were dry with little precipitation until the beginning of July and with temperatures often exceeding 20°C (Figure S1).

## Discussion

This is the first documented natural attack of *I. typographus* on standing lodgepole pines in Sweden. This is even though this non-native tree species have been used for a considerable time in Sweden and are established on about 6000 square kilometers (Mårald et al. 2024). In some cases, attacks by *I. typographus* on the native non-host Scots pine have been induced by switching of attack from adjacent ongoing attacks on Norway spruces (Komonen et al. 2011) due to pheromones produced by *I. typographus* in the attacked spruces in combination with host volatiles released from the bark beetle entrance holes. This was not the case in our study because there were no *I. typographus*-killed spruces within the lodgepole pine stands or in nearby spruce stands. Attacks by *I. typographus* on storm-felled lodgepole pines, in the absence of nearby attacked Norway spruces, have been recorded but in much lower incidence than for storm-felled Norway spruces (Schroeder and Cocoş 2018). Thus, lodgepole pine is generally not conceived as a potential host by *I. typographus*.

The attacks by *I. typograhus* were most probably the major factor contributing to the killing of the lodgepole pines. First, it was the only bark beetle species recorded in all 19 inspected trees and generally also present at relatively high attack densities over large parts of the stems. Second, the killed trees were heavily infested by blue-stain fungi that are known to be vectored by *I. typographus* and that can kill Norway spruces when inoculated (Christiansen and Solheim 1990; Krokene and Solheim 1998). Third, the two other bark beetle species found (i.e. *P. chalcographus* and *P. poligraphus*) may sometimes kill Norway spruces but are considered to be more secondary than *I. typographus* and

**Table 2.** Densities of bark beetle natural enemies and other taxa present in the bark samples from killed lodgepole pines.

| Species | Densities (± SE) per m$^2$ bark | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Base | 2.5 m | | 5 m | 8 m | top | branch | |
| Replicates | 11 | 10 | 19 | 10 | 10 | 10 | 10 | Stage |
| Coleoptera | | | | | | | | |
| Thanasimus | 0 | 0 | 2.2 (± 2.2) | 1.5 (± 1.5) | 0 | 1.7 (± 1.7) | 0 | L |
| Plegaderus | 0 | 0 | 0 | 0 | 1.5 (± 1.5) | 0 | 0 | L |
| Corticeus | 2.7 (± 2.7) | 1.4 (± 1.4) | 6 (± 3.9) | 1.5 (± 1.5) | 4.5 (± 3.2) | 15.1 (± 6.4) | 17.2 (± 10.3) | A |
| Staphylinidae | 20.5 (± 10.4) | 7.3 (± 3.3) | 3.8 (± 1.9) | 1.5 (± 1.5) | 5.7 (± 3.1) | 10.1 (± 7.3) | 5.1 (± 3.5) | L, A |
| Rhizophagus | 0 | 0 | 0.6 (± 0.6) | 0 | 0 | 0 | 0 | L |
| Diptera | | | | | | | | |
| Medetera | 32.5 (± 11.6) | 44 (± 11.3) | 41.8 (± 10.4) | 80.6 (± 34.2) | 47.5 (± 14.9) | 113.2 (± 22.2) | 33.2 (± 10.3) | L |
| Lonchaea | 169 (± 85.1) | 5.7 (± 5.7) | 44.2 (± 30.5) | 22.9 (± 10.8) | 78.5 (± 41.8) | 61.4 (± 24.7) | 22.2 (± 8.1) | L, A |
| Stratiomyidae | 60 (± 31.7) | 11.8 (± 6.9) | 7 (± 3.8) | 1.4 (± 1.4) | 1.5 (± 1.5) | 0 | 0 | L |
| Cecidomyiidae | 0 | 142.2 (± 132.4) | 85.4 (± 69.6) | 19.2 (± 8.5) | 12.1 (± 3.8) | 21.8 (± 7.8) | 61.3 (± 30.2) | L |
| Sciaridae | 20.2 (± 20.2) | 0 | 0 | 4.3 (± 3.1) | 34.4 (± 22.9) | 26.7 (± 26.7) | 2.5 (± 2.5) | L |
| Hymenoptera | | | | | | | | |
| Parasitoids | 11.4 (± 8.1) | 30.1 (± 13.5) | 30.8 (± 10.1) | 38.2 (± 13.9) | 11.1 (± 5.9) | 17.2 (± 11.2) | 0 | L, C |
| Heteroptera | 1.3 (± 1.3) | 1.5 (± 1.5) | 3 (± 2.3) | 2.9 (± 1.9) | 3.0 (± 2.0) | 1.2 (± 1.2) | 0 | A |

A, adult; L, larvae; C, cocoon.

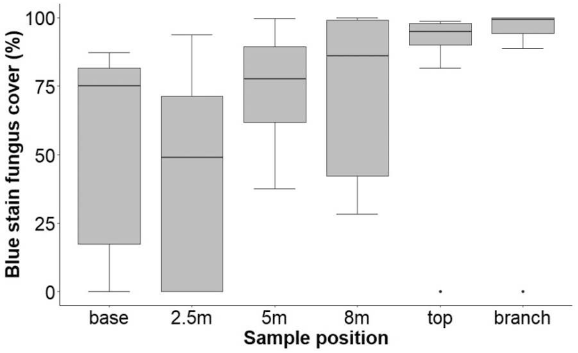

**Figure 4.** Percentage of blue stain fungus covering the lower end of each stem section and branch.

also have flight periods that peak later in the season than *I. typographus* (Schroeder 2013; Viklund 2024). None of the other recorded bark- and wood-boring species is known to be able to kill trees.

The most probable explanation for the *I. typographus* attacks, and successful killings, of the lodgepole pines is that the trees were severely weakened and thus had low defenses against bark beetle attacks. The analysis of annual ring widths demonstrated a steadily declining growth over the past 20 years with a strong negative effect of the exceptionally warm and dry summer of 2018. In addition, the early summer of 2023 (the year of tree-killing) was exceptionally warm and dry and thus may have been the triggering factor for the attacks. This in combination with the poor ground conditions may have predisposed the lodgepole pines to the bark beetle attacks. In addition, lodgepole pines are known to have more shallow root systems, especially on rocky outcrops (Lotan and Critchfield 1990). Generally, pines defend themselves against bark beetle attacks with a copious resin flow that prevents beetle establishment (Kane and Kolb 2010; Boone et al. 2011; Zhao and Erbilgin 2019). The fact that there were few signs of resin flow or pitch tubes on the killed trees also indicates low tree defenses. The Norway spruces (and Scots pines) within the lodgepole pine stands coped better in these conditions because they showed no signs of bark beetle attacks.

The mean *I. typographus* female colonization density of 329 maternal galleries per m$^2$ bark in the killed lodgepole pines is only somewhat lower than the mean density of 509 maternal galleries per m$^2$ bark recorded on killed Norway spruces during five outbreaks in Sweden (Kärvemo and Schroeder 2010; Komonen et al. 2011). *Ips typographus* is only weakly attracted to host tree volatiles alone (Lindelöw et al. 1992; Schroeder 2003; Lehmanski et al. 2023). Thus, the fact that the colonization density was comparable to that in killed Norway spruces is a strong indication that *I. typographus* males can produce their aggregation pheromones also in lodgepole pine. The two main components of the pheromone are 2-methyl-3-buten-2-ol and cis-verbenol (Schlyter et al. 1987). 2-Methyl-3-buten-2-ol is produced de novo (i.e. no specific precursor required), whereas cis-verbenol is produced from the precursor (-)-α-pinene (Lanne et al. 1989; Lindström et al. 1989). This precursor is present in lodgepole pine but accounts for only 5% on average of total monoterpene content (Pureswaran et al. 2004), which is a much lower proportion than in Norway spruce (Schiebe et al. 2012). It has previously been shown that *I. typographus* produce similar amounts of its aggregation pheromone (2-methyl-3-buten-2-ol and cis-verbenol) in stem sections of the North American spruce species *P. sitchensis* and *P. glauca x lutzii* as in its historical host Norway spruce (Flø et al. 2018).

The reproductive success of *I. typographus* in the killed lodgepole pines was very low. New generation adults were only produced in 42% of the sampled attacked trees and the mean reproductive success was only 0.01 daughters per mother (maximum offspring production of 30 adults per m$^2$ bark). In killed Norway spruces, average reproductive success is often about 200 times higher with about two daughters per mother (Kärvemo and Schroeder 2010; Komonen et al. 2011). In a previous experiment in which healthy Norway

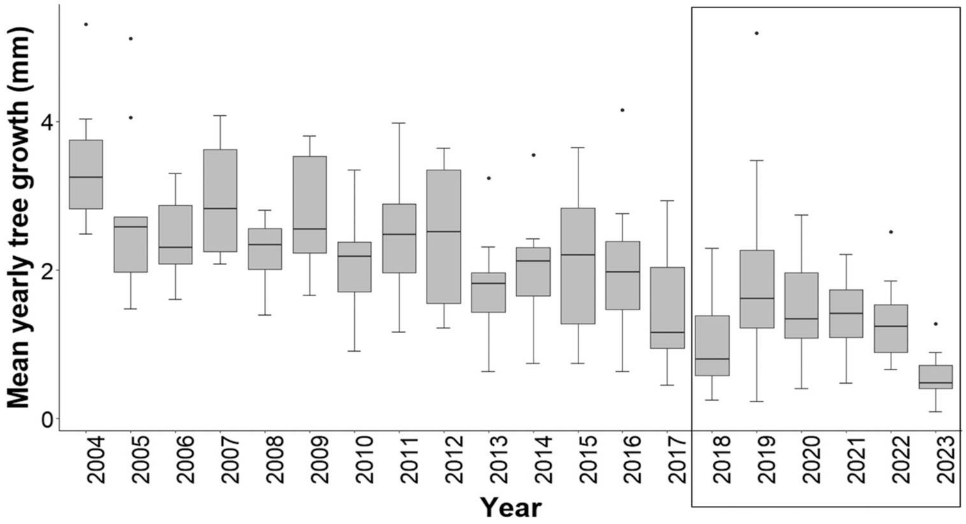

**Figure 5.** Mean annual increment for the last twenty years including the year of *Ips typographus* colonization (2023) for ten killed lodgepole pines. The black box represents the growth years from the very dry summer of 2018.

spruces and lodgepole pines were baited with *I. typographus* pheromone dispensers, the reproductive success was much higher in spruce than in lodgepole pine: 1.43 and 0.08 daughters per mother, respectively (Schroeder and Cocoş 2018). The low reproduction in the present study was not caused by the failure of larvae to establish, as larval galleries were present from all maternal galleries. Although the pupal stage was present in some of the bark samples, only a few larvae reached it. In an earlier study conducted on *I. typographus*-killed Norway spruces average maternal gallery length was 6.0 cm (range 5.3–6.9 cm) but at a somewhat higher colonization density (mean 460 per $m^2$ bark) (Hedgren and Schroeder 2004) which is comparable to a mean length of 7.1 cm on lodgepole pine in the present study. Thus, shorter maternal galleries (and room for fewer eggs) is neither an explanation for the low reproductive success. Also, the number of maternal galleries per mating chamber was similar in the two studies: 1.6 in Norway spruce and 1.8 in lodgepole pine. The females were as prone to enter a mating chamber created in the non-native lodgepole pine as in the traditional host Norway spruce. The thinner phloem thickness of lodgepole pine compared to Norway spruce (Schroeder and Cocoş 2018), and differences in chemistry and nutritional quality compared with the traditional host, in combination with the negative effect of enemies (see below) are probable explanations for the low reproduction. A somewhat lower reproduction of *I. typographus* in non-native species of spruce compared to the native Norway spruce has previously been demonstrated (Økland et al. 2011; Flø et al. 2018; Isitt et al. 2023a) but the differences were much smaller than those in the present study. This may be explained by a larger difference in chemistry and physical attributes between lodgepole pine and Norway spruce than between different species of spruce.

In a field experiment, Christiansen and Solheim (1990) observed no blue-stain fungi growth in any of the *Ophiostoma polonicum* Siem-inoculated lodgepole pines while all inoculated Norway spruces were heavily stained and the trees died. In contrast, all *I. typograp*hus-killed lodgepole pines in our study were stained by blue-stain fungi. However, we do not know which of the blue-stain fungi species were present in our study. In addition, the trees in our study were more stressed than the trees in the earlier study. Blue-stain fungi are often associated with *I. typographus* and cause tree death after bark beetle attacks (Christiansen and Solheim 1990; Krokene and Solheim 1998; Lieutier et al. 2009; Zhao et al. 2019).

Larvae from the most important groups of bark beetle enemies were present in the *I. typographus*-attacked lodgepole pines. A similar bark beetle enemy community was also found in attacked lodgepole pines baited with *I. typographus* pheromones (Schroeder and Cocoş 2018). A comparison between the enemy community in the present study and earlier studies on *I. typographus*-killed Norway spruces showed similar enemy complexes (Hedgren and Schroeder 2004; Weslien et al. 2024). Thus, natural enemies can track their prey species also in the non-native lodgepole pine. This might be the result of many enemy species being generalist predators, responding to pheromones from several bark beetle species inhabiting different tree species (Kenis et al. 2004; Isitt et al. 2023b).

The cerambycid beetle, *Acanthocinus griseus*, (Fabricius), was the second most common species when it comes to the number of colonized trees and the most common when looking at the number of samples (including all heights). *Acanthocinus griseus* utilizes both Norway spruces and Scots pines attacked by bark beetles (Martikainen 2002; Foit 2010) and is attracted to bark beetle pheromones (Cocoş et al. 2017). It is also included in the Swedish red list as Near Threatened (Swedish Species Information Centre 2020).

To conclude, our study shows that *I. typographus* can colonize and kill non-native lodgepole pine. However, this seems to be a rare phenomenon because this is the first report of *I. typographus* killing lodgepole pines despite being a common tree species in parts of Sweden. One important factor for the attacks may be that the stands were growing on unfavourable sites and were stressed by drought. The reproductive success was extremely low which is in accordance with an earlier study with baited trees. Thus, if lodgepole pines are killed by *I. typographus* the trees will act as a sink for the bark beetle population. Despite being a novel host tree, the bark beetles did not escape their enemy complex. Several bark- and wood-boring beetle species and bark-beetle-associated taxa were present in the killed trees.

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## References

Boone CK, Aukema BH, Bohlmann J, Carroll AL, Raffa KF. 2011. Efficacy of tree defense physiology varies with bark beetle population density: a basis for positive feedback in eruptive species. Can J For Res. 41:1174–1188. doi:10.1139/x11-041.

Brundu G, Richardson DM. 2016. Planted forests and invasive alien trees in Europe: a code for managing existing and future plantings to mitigate the risk of negative impacts from invasions. NeoBiota. 30:5–47. doi:10.3897/neobiota.30.7015.

Christiansen E, Solheim H. 1990. The bark beetle-associated blue-stain fungus *Ophiostoma polonicum* can kill various spruces and Douglas fir. Eur J For Pathol. 20:436–446. doi:10.1111/j.1439-0329.1990.tb01159.x.

Christiansen E, Waring RH, Berryman A. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. For Ecol Manage. 22:89–106. doi:10.1016/0378-1127(87)90098-3.

Cocoş D, Etxebeste I, Schroeder M. 2017. An efficient detection method for the red-listed beetle *Acanthocinus griseus* based on attractant-baited traps. Insect Conserv Diversity. 10:294–301. doi:10.1111/icad.12224.

Elfving B, Ericsson T, Rosvall O. 2001. The introduction of lodgepole pine for wood production in Sweden – a review. For Ecol Manage. 141:15–29. doi:10.1016/S0378-1127(00)00485-0.

[FAO] Food and Agriculture Organization of the United Nations. 2010. Global forest resources assessment 2010: main report. Rome: FAO.

Felton A, Boberg J, Björkman C, Widenfalk O. 2013. Identifying and managing the ecological risks of using introduced tree species in Sweden's production forestry. For Ecol Manage. 307:165–177. doi:10.1016/j.foreco.2013.06.059.

Flø D, Norli HR, Økland B, Krokene P. 2018. Successful reproduction and pheromone production by the spruce bark beetle in evolutionary naïve spruce hosts with familiar terpenoid defences. Agric For Entomol. 20:476–486. doi:10.1111/afe.12280.

Foit J. 2010. Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. Agric For Entomol. 12:133–141. doi:10.1111/j.1461-9563.2009.00461.x.

Fox J, Weisberg S. 2019. An R companion to applied regression. 3rd ed. Thousand Oaks (CA): Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Franceschi VR, Krokene P, Christiansen E, Krekling T. 2005. Anatomical and chemical defences of conifer bark against bark beetles and other pests. New Phytol. 167:353–376. doi:10.1111/j.1469-8137.2005.01436.x.

Hedgren PO, Schroeder LM. 2004. Reproductive success of the spruce bark beetle *Ips typographus* (L.) and occurrence of associated species: a comparison between standing beetle-killed trees and cut trees. For Ecol Manage. 203:241–250. doi:10.1016/j.foreco.2004.07.055.

Hlásny T, Zimová S, Merganičová K, Štěpánek P, Modlinger R, Turčáni M. 2021. Devastating outbreak of bark beetles in the Czech Republic: drivers, impacts, and management implications. For Ecol Manage. 490:119075. doi:10.1016/j.foreco.2021.119075.

Hothorn T, Bretz F, Westfall P. 2008. Simultaneous inference in general parametric models. Biom J. 50(3):346–363. doi:10.1002/bimj.200810425.

Isitt R, Økland B, Krokene P, Sweeney J, Heard S, Pureswaran DS. 2023a. Successful colonization of novel spruce hosts by European and North American spruce bark beetles can favour trans-Atlantic range expansion. Forestry. 96:631–638. doi:10.1093/forestry/cpad015.

Isitt R, Økland B, Krokene P, Sweeney J, Heard S, Pureswaran DS. 2023b. Using semiochemicals to predict biotic resistance and facilitation of introduced species. Biol Invasions. 25:441–454. doi:10.1007/s10530-022-02925-0.

Kane JM, Kolb TE. 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. Oecologia. 164:601–609. doi:10.1007/s00442-010-1683-4.

Kärvemo S, Rogell B, Schroeder M. 2014. Dynamics of spruce bark beetle infestation spots: importance of local population size and landscape characteristics after a storm disturbance. For Ecol Manage. 334:232–240. doi:10.1016/j.foreco.2014.09.011.

Kärvemo S, Schroeder LM. 2010. A comparison of outbreak dynamics of the spruce bark beetle in Sweden and the mountain pine beetle in Canada (Curculionidae: Scolytinae). Entomologisk tidsskrift. 131:215–242.

Kenis M, Wermelinger B, Grégoire J-C. 2004. Research on parasitoids and predators of scolytidae – a review. In: F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire, H. Evans, editors. Bark and wood boring insects in living trees in Europe, a synthesis. (UK): Dordrecht: Kluwer Academic Publishers; p. 237–290.

Kjær ED, Lobo A, Myking T. 2014. The role of exotic tree species in Nordic forestry. Scand J For Res. 29:323–332. doi:10.1080/02827581.2014.926098.

Komonen A, Schroeder LM, Weslien J. 2011. *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. J Appl Entomol. 135:132–141. doi:10.1111/j.1439-0418.2010.01520.x.

Krokene P. 2015. Conifer defence and resistance to bark beetles. In: Vega FE, Hofstetter RW, editors. Bark beetles – biology and ecology of native and invasive species. USA: Academic Press; p. 177–207.

Krokene P, Solheim H. 1998. Pathogenicity of four blue-stain fungi associated with aggressive and nonaggressive bark beetles. Phytopathology. 88(1):39–44. doi:10.1094/PHYTO.1998.88.1.39.

Lanne BS, Ivarsson P, Johnson P, Bergström G, Wassgren AB. 1989. Biosynthesis of 2-methyl-3-buten-2-ol, a pheromone component of *Ips typographus* (Coleoptera: Scolytidae). Insect Biochem. 19:163–167. doi:10.1016/0020-1790(89)90087-5.

Lehmanski LMA, Kandasamy D, Andersson MN, Netherer S, Alves EG, Huang J, Hartmann H. 2023. Addressing a century-old hypothesis – do pioneer beetles of *Ips typographus* use volatile cues to find suitable host trees? New Phytol. 238:1762–1770. doi:10.1111/nph.18865.

Liebhold AM, Brockerhoff EG, Kimberley M. 2017. Depletion of heterogeneous source species pools predicts future invasion rates. J Appl Ecol. 54:1968–1977. doi:10.1111/1365-2664.12895.

Lieutier F, Yart A, Salle A. 2009. Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. Ann For Sci. 66:801. doi:10.1051/forest/2009066.

Lindelöw Å, Risberg B, Sjödin K. 1992. Attraction during flight of scolytids and other bark- and wood-dwelling beetles to volatiles from fresh and stored spruce wood. Can J For Res. 22:224–228. doi:10.1139/x92-029.

Lindström M, Norin T, Birgersson G, Schlyter F. 1989. Variation of enantiomeric composition of α-pinene in Norway spruce, *Picea abies*, and its influence on production of verbenol isomers by *Ips typographus* in the field. J Chem Ecol. 15:541–548. doi:10.1007/BF01014699.

Lotan JE, Critchfield WB. 1990. *Pinus contorta* Dougl. ex Loud. In: Burns RM, Honkala BH, technical coordinators. Silvics of North America. Vol. 1. Washington (DC): USDA Agriculture Handbook 654; p. 302–315.

Mårald E, Jönsson J, Kardell Ö, Sjögren J, Tunlind A. 2024. An exotic tree in a foreign country: a cultural biography of the Lodgepole Pine in Sweden. Environ Hist. 30:483–506. doi:10.3197/096734023X16869924234822.

Marini L, Økland B, Jönsson AM, Bentz B, Carroll A, Forster B, Grégoire JC, Hurling R, Nageleisen LM, Netherer S, et al. 2017. Climate drivers of bark beetle outbreak dynamics in Norway spruce forests. Ecography. 40:1426–1435. doi:10.1111/ecog.02769.

Martikainen P. 2002. Ecology and conservation status of *Acanthocinus griseus* (Fabricius, 1792) (Coleoptera: Cerambycidae) in Finland. Entomol Fenn. 13:41–50.

Mulock P, Christiansen E. 1986. The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. For Ecol Manage. 14:125–132. doi:10.1016/0378-1127(86)90097-6.

Økland B, Erbilgin N, Skarpaas O, Christiansen E, Långström B. 2011. Inter-species interactions and ecosystem effects of non-indigenous invasive and native tree-killing bark beetles. Biol Invasions. 13:1151–1164. doi:10.1007/s10530-011-9957-2.

Pineau X, Bourguignon M, Jactel H, Lieutier F, Sallé A. 2017. Pyrrhic victory for bark beetles: successful standing tree colonization triggers strong intraspecific competition for offspring of *Ips sexdentatus*. For Ecol Manage. 399:188–196. doi:10.1016/j.foreco.2017.05.044.

Pureswaran DS, Gries R, Borden JH. 2004. Quantitative variation in monoterpenes in four species of conifers. Biochem Syst Ecol. 32:1109–1136. doi:10.1016/j.bse.2004.04.006.

Raffa KF. 2014. Terpenes tell different tales at different scales: glimpses into the chemical ecology of conifer – bark beetle – microbial interactions. J Chem Ecol. 40:1–20. doi:10.1007/s10886-013-0368-y.

Raffa KF, Aukema BH, Bentz BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience. 58:501–517. doi:10.1641/B580607.

Raffa KF, Berryman AA. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol Monogr. 53:27–49. doi:10.2307/1942586.

R Core Team. 2023. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. https://www.r-project.org/

Richardson DM, Rejmánek M. 2011. Trees and shrubs as invasive alien species - a global review. Divers Distrib. 17:788–809. doi:10.1111/j.1472-4642.2011.00782.x.

Rousi E, Fink AH, Andersen LS, Becker FN, Beobide-Arsuaga G, Breil M, Cozzi G, Heinke J, Jach L, Niermann D, et al. 2023. The extremely hot and dry 2018 summer in central and Northern Europe from a multi-faceted weather and climate perspective. Nat Hazards Earth Syst Sci. 23:1699–1718. doi:10.5194/nhess-23-1699-2023.

Schelhaas MJ, Nabuurs GJ, Schuck A. 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biol. 9:1620–1633. doi:10.1046/j.1365-2486.2003.00684.x.

Schiebe C, Hammerbacher A, Birgersson G, Witzell J, Brodelius PE, Gershenzon J, Hansson BS, Krokene P, Schlyter F, et al. 2012. Inducibility of chemical defenses in Norway spruce bark is correlated with unsuccessful mass attacks by the spruce bark beetle. Oecologia. 170:183–198. doi:10.1007/s00442-012-2298-8.

Schlyter F, Birgersson G, Byers JA, Löfqvist J, Bergström G. 1987. Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. J Chem Ecol. 13:701–716. doi:10.1007/BF01020153.

Schroeder LM. 1999. Prolonged development time of the bark beetle predator *Thanasimus formicarius* (Col.: Cleridae) in relation to its prey species *Tomicus piniperda* (L.) and *Ips typographus* (L.) (Col.: Scolytidae). Agric For Entomol. 1:127–135. doi:10.1046/j.1461-9563.1999.00018.x.

Schroeder LM. 2003. Differences in responses to α-pinene and ethanol, and flight periods between the bark beetle predators *Thanasimus femoralis* and *T. formicarius* (Col.: Cleridae). For Ecol Manage. 177:301–311. doi:10.1016/S0378-1127(02)00441-3.

Schroeder LM. 2013. Monitoring of *Ips typographus* and *Pityogenes chalcographus*: influence of trapping site and surrounding landscape on catches. Agric For Entomol. 15:113–119. doi:10.1111/afe.12002.

Schroeder M, Cocoş D. 2018. Performance of the tree-killing bark beetles *Ips typographus* and *Pityogenes chalcographus* in non-indigenous lodgepole pine and their historical host Norway spruce. Agric For Entomol. 20:347–357. doi:10.1111/afe.12267.

Schroeder M, Kärvemo S. 2022. Rekordstort utbrott av granbarkborre – orsaker och vad man kan göra. Kungl. Skogs- och Lantbruksakademiens TIDSKRIFT. 7:16–19.

Schroeder M, Lindelöw Å. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. Agric For Entomol. 4:47–56. doi:10.1046/j.1461-9563.2002.00122.x.

Seidl R, Schelhaas MJ, Lexer MJ. 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biol. 17:2842–2852. doi:10.1111/j.1365-2486.2011.02452.x.

Swedish Species Information Centre. 2020. Rödlistade arter i Sverige 2020. Uppsala: ArtDatabanken SLU.

Turner RM, Brockerhoff EG, Bertelsmeier C, Blake RE, Caton B, James A, MacLeod A, Nahrung HF, Pawson SM, Plank MJ, et al. 2021. Worldwide border interceptions provide a window into human-mediated global insect movement. Ecol Appl. 31(7):1–18. doi:10.1002/eap.2412.

Viklund L. 2024. Aggregation pheromones in the four-eyed bark beetles *Polygraphus poligraphus, Polygraphus punctifrons, Polygraphus subopacus* and *Polygraphus proximus* [Doctoral thesis 408]. Mid Sweden University, ISBN: 978-91-89786-68-4.

Weslien J. 1992. The arthropod complex associated with *Ips typographus* (L.) (Coleoptera, Scolytidae): species composition, phenology, and impact on bark beetle productivity. Entomol Fenni. 3:205–213. doi:10.33338/ef.83730.

Weslien J, Öhrn P, Rosenberg O, Schroeder M. 2024. Effects of sanitation logging in winter on the Eurasian spruce bark beetle and predatory long-legged flies. For Ecol Manage. 554:121665. doi:10.1016/j.foreco.2023.121665.

Whitehill JGA, Bohlmann J, Krokene P. 2023. Forest insect – plant interactions. In: Allison JD, Paine TD, Slippers B, Wingfield MJ, editors. Forest entomology and pathology, volume 1: entomology. Cham: Springer; p. 169–204. doi:10.1007/978-3-031-11553-0.

Wulff S, Roberge C. 2023. Inventering av barkborreangrepp i Götaland och Svealand 2023. Umeå: Institutionen för skoglig resurshushållning, SLU, Arbetsrapport 2023-12-08.

Zhao S, Erbilgin N. 2019. Larger resin ducts are linked to the survival of lodgepole pine trees during mountain pine beetle outbreak. Front Plant Sci. 10:1459. doi:10.3389/fpls.2019.01459.

Zhao T, Kandasamy D, Krokene P, Chen JY, Gershenzon J, Hammerbacher A. 2019. Fungal associates of the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer phenolics and influence bark beetle tunneling behavior. Fungal Ecol. 38:71–79. doi:10.1016/j.funeco.2018.06.003.