Norwegian University
of Life Sciences

Master's Thesis 2024 45 ECTS
Faculty of Environmental Sciences and Natural Resource Management

Effects of competition and predation on reproductive success of the European spruce bark beetle *Ips typographus* in unmanaged vs. managed forests

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Preface

This thesis marks the end of my MSc in Natural resource management at the Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU).

I would like to thank my main supervisor, Paal Krokene, for providing guidance and thorough and constructive feedback, and for generously sharing his inspirational knowledge of *Ips typographus*. I would also like to express my sincere gratitude to my co-supervisor Milda Norkute for all her work on setting up the study that made this thesis possible, and for all the valuable help and feedback throughout the process. I am further grateful to my other co-supervisor Tone Birkemoe for providing feedback and optimism surrounding the project.

I would also like to thank Jozef Vakula for providing insight into the world of insect gallery determination, Sindre Ligaard for identifying the beetles to species, Tone Granerud for guidance in the lab, and my father for assisting with the illustrations. I also want to extend my gratitude to UNIFOR (UMBs research fund) for the financial support of the fieldwork, and to the EcoForest team for sharing data and insight into the project.

Lastly, a big thank you to my friends and classmates, for making these last two years at NMBU a joy. A special thank you to my friend Pauline for being the best study partner I could have asked for throughout this thesis. I also want to express my gratitude to my family, for their unwavering support and faith in me.

Vera Lena Fiske

Ås, May 14 2024

Abstract

The European spruce bark beetle *Ips typographus* is a severe pest in mature spruce forests, with the potential to cause widespread tree mortality. Managed forests are suggested to be particularly susceptible to *I. typographus* infestations compared to more diverse, unmanaged forests, partly because they are thought to support less natural enemies and competitors of the beetle. This study explores whether forest management practices that enhance forest diversity and populations of natural enemies and interspecific competitors can suppress *I. typographus* reproductive success and thus mitigate outbreak risks. Experimental pheromone-baited logs were placed in near-natural and previously clear-cut forest stands across 10 paired sites in SE-Norway. Analysis of bark occupation by interspecific competitors and *I. typographus* reproductive success was conducted on the bark, and data on *I. typographus* predatory beetle assemblages was collected via window traps. Results revealed a tendency for higher reproductive success of *I. typographus* in managed forests. Occurrence of predatory beetles and interspecific competitors was similar between management types and did not affect *I. typographus* reproductive success. Intraspecific competition, estimated by attack density, tended to be higher in unmanaged forests and had a significant negative effect on *I. typographus* reproductive success. Results indicate that forest management that promotes forest diversity does not increase predatory beetle or interspecific competitor populations and thus might not mitigate bark beetle outbreak risks. Instead, it appears that decreased reproductive success of *I. typographus* in unmanaged forests can be explained by increased intraspecific competition for resources, underscoring intraspecific competition as one of the main drivers of *I. typographus* population dynamics.

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1. Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) are a subfamily of weevils that predominantly breed in dead trees and tree parts (Hlásny et al., 2019). Most of the roughly 6,000 bark beetle species in the world are harmless and even beneficial, as they contribute to nutrient cycling and serve as food for other animals (Hlásny et al., 2021). However, a few species are considered problematic because they are occasionally capable of mass-attacking healthy conifer trees, leading to extensive outbreaks that can cause widespread tree mortality. These outbreaks can have major consequences for forestry and wood production, negatively impact ecosystem services like carbon storage, and create social issues and political conflicts (Morris et al., 2018; Raffa et al., 2008). There has been an alarming increase in bark beetle outbreaks in recent years; in Europe's conifer forests, damage due to bark beetle outbreaks has increased by about 700% over the last four decades (Hlásny et al., 2021). About half of this increase is attributed to the strong influence of human land use practices on forest composition and structure (Seidl et al., 2011).

The European spruce bark beetle (*Ips typographus*) is the most important outbreak species attacking spruce in Europe and is a severe pest in mature spruce forests (Weslien & Schroeder, 1999). Most of the time, *I. typographus* is limited to reproducing in dying and stressed trees (Økland et al., 2022). However, when populations of the beetle reach higher densities, mostly following abiotic disturbance events like drought periods or large windfalls, they can overwhelm tree defenses through mass-attacks, potentially resulting in major *I. typographus* outbreaks (Krokene, 2015). In Norway, *I. typographus* is the only bark beetle that can kill healthy spruce trees on a large scale. For instance, during an outbreak of *I. typographus* in SE-Norway in the 1970s, spruce with a value of 2,3 billion NOK was lost (2016 lumber prices) (Økland et al., 2022).

Because *I. typographus* can have such a large impact on spruce-dominated forests, proper management is essential. There are, however, several knowledge gaps regarding the dynamics of bark beetle outbreaks and proper management responses (Hlásny et al., 2019; Raffa et al., 2008). Today, the most common management strategies center on risk reduction or combatting ongoing outbreaks (Hlásny et al., 2021). A weakness of current management strategies is that they largely rely on *ad hoc* decisions with limited scientific backing, without properly considering preventative measures to control bark beetle outbreaks. Preventive measures mainly focus on ecological aspects, such as altering forest conditions to prevent bark beetle population build-up and reduce outbreak probability (Hlásny et al., 2019).

Conditions in unmanaged and managed forests often differ considerably, both in heterogeneity (Martikainen et al., 1999) and forest dynamics (Kuuluvainen, 2009), as well as in community composition and species interactions (Jacobsen et al., 2020; Paillet et al., 2010). It has been suggested that intensively managed forests with only one age class and one dominating tree species, may have increased risk of bark beetle outbreaks compared to more diverse near-natural unmanaged forests (Hlásny et al., 2019). This is supported by the "insurance hypothesis", which states that biodiversity enhances ecosystem functioning by increasing the ecosystem's ability to withstand and recover from disturbances such as bark beetle outbreaks, and has been used to argue for forest management fostering more diversity (Hlásny et al., 2019; Yachi & Loreau, 1999). One of the reasons diverse forests are thought to be less susceptible to outbreaks is that they could support larger populations of natural enemies and competitors of bark beetles (Hlásny et al., 2019; Martikainen et al., 1999). Thus, *I. typographu*s outbreak risks in managed forests could be reduced through preventative measures that enhance forest diversity, partly because greater richness and abundance of natural enemies and interspecific competitors may increase *I. typographus* mortality (Johansson et al., 2007; Martikainen et al., 1999).

Natural enemies of bark beetles include both predators and parasites in Coleoptera, Diptera, Hymenoptera, and other orders, which are often encountered in large numbers in infested trees (Kenis et al., 2004; Wegensteiner et al., 2015). The impact of natural enemies on *I. typographus* populations varies between studies. Field experiments where natural enemies are excluded with cages have found a range of 24-87% fewer emerged beetles from exposed logs compared to caged logs (Weslien & Schroeder, 2023), indicating that enemies can greatly reduce reproductive output of *I. typographus*. On the other hand, Marini et al. (2013) found no effect of the generalist predator *Thanasimus formicarius* on *I. typographus* population dynamics during their 16-year study period. Empirical results on whether natural enemies of *I. typographus* truly are more diverse in unmanaged forests are also divided. While Weslien and Schroeder (1999) found two to three times higher trap catches of some *I. typographus* predators in unmanaged stands versus managed stands, several studies have also found higher densities of predators outside than inside unmanaged forests (Feicht, 2006; Schlyter & Lundgren, 1993), and some have found no difference between management types (Hilszczański et al., 2007; Schroeder, 2007). In summary, although several studies show that natural enemies can strongly reduce bark beetle reproductive output (Wermelinger, 2002; Weslien & Schroeder, 1999), the importance of natural enemies on *I. typographus* population dynamics, and whether natural enemies truly are more diverse in unmanaged forests, remains uncertain (Wegensteiner et al., 2015).

Since dead and weakened host trees are a limited resource, interspecific competition between *I. typographus* and other saproxylic organisms can be quite severe (Byers, 1989; Byers, 1993). Other bark beetle species and larvae of longhorn beetles (Colepotera: Cerambycidae) are considered particularly important competitors of *I. typographus*, as they often overlap in space and time (Allison et al., 2001). Larvae of Cerambycidae also feed upon dying and stressed trees, and can have both competitive and predatory effects on bark beetles (Ray et al., 2019). For instance, studies show that *I. typographus* offspring production can be reduced by 78% due to competition with cerambycids (Weslien & Schroeder, 1999) and that predation by cerambycids can cause high mortality in bark beetle larvae (Allison et al., 2001). Other bark beetles can also have negative effects on *I. typographus*; Byers (1993) discovered that *I. typographus* avoided areas colonized by *Pityogenes chalcographus,* and Schlyter and Anderbrant (1993) found a negative effect on offspring production and body mass in interactions between *I. typographus* and *Ips duplicatus*. As for predators of *I. typographus*, there are mixed results on how the abundance of interspecific competitors varies with forest management. Although several studies have found other saproxylic beetles to be more abundant in unmanaged forests (Jacobsen et al., 2020; Martikainen et al., 1999; Stenbacka et al., 2010), some have also found no difference between management types (Karpiński et al., 2021; Similä et al., 2003). Thus, saproxylic beetles can have strong negative effects on *I. typographus* reproductive success, but findings on whether they are more abundant in unmanaged forests are mixed (Stenbacka et al., 2010; Økland et al., 1996).

Fungi can also compete with bark beetles for substrate (Juutilainen et al., 2014). The most well-known relationship between bark beetles and fungi is when fungal symbionts assist the beetles in exhausting tree defenses (Biedermann et al., 2019). However, some fungal species limit beetle development, both by competing for food and by competing with fungi that are beneficial to the beetles (Cardoza et al., 2006; Raffa et al., 2015). There are few studies on the effects of antagonistic fungi on *I. typographus*, but gallery invasion by opportunistic fungi has been found to reduce survival and reproduction for other bark beetle species (Cardoza et al., 2006; Fox et al., 1992). Although the effect of forest management on antagonistic fungi of *I. typographus* has been little studied, saproxylic fungi generally tend to be more diverse in unmanaged forests (Tomao et al., 2020). Thus, fungi might have an increased interspecific competitor effect on bark beetles in unmanaged forests.

Intraspecific competition is thought to be a main driver of *I. typographus* population dynamics (Biedermann et al., 2019). Escape from intraspecific competition is a well-documented cause of rapid population growth after large disturbance events that drastically increases the availability of suitable host trees with low defense levels (Lindgren & Raffa, 2013). Studies have found that the number of emerged offspring per mother, along with offspring body size and fat content, is negatively correlated with attack density (Anderbrant et al., 1985; Botterweg, 1983). Although intraspecific competition has a strong effect on *I. typographus,* whether this effect varies between forest management types is little studied. Theoretically, less interspecific competition and predation in managed forests could lead to increased *I. typographus* attack density.

In general, the importance of natural enemies and interspecific competitors in *I. typographus* population dynamics has been questioned. *I. typographus* populations at the non-outbreak level are influenced by several factors, such as host tree availability, weather, inter- and intraspecific competition, and natural enemies (Lindgren & Raffa, 2013; Raffa et al., 2008). Out of these factors, host tree availability and intraspecific competition are considered primary regulators of *I. typographus*, while natural enemies and interspecific competitors are thought to play a minor role (Raffa et al., 2015; Reeve, 1997). Thus, natural enemies and interspecific competitors are likely unable to prevent outbreak initiation (Marini et al., 2013; Weslien & Schroeder, 2023). Nevertheless, since studies indicate that natural enemies and interspecific competitors are involved in reducing *I. typographus* population size, it is suggested that they can contribute to limiting outbreak extent and duration by reducing the number of bark beetles capable of exploiting disturbances during the non-outbreak phase (Raffa et al., 2015; Weslien & Schroeder, 2023). To understand if biodiversity enhancement in managed forests will be an effective preventative measure of *I. typographus* outbreaks, the question of how and to what extent natural enemies and competitors limit bark beetle outbreaks requires further studies.

In summary, although results are divided, predators and competitors can have strong negative effects on *I. typographus*, and near-natural unmanaged forests have been found to host larger populations of natural enemies and interspecific competitors than managed forests. Together, this suggests that *I. typographus* population regulation could be stronger in unmanaged forests (Hlásny et al., 2019). Whether intraspecific competition varies between management types remains to be investigated but could theoretically be higher in unmanaged forests. Overall, this suggests that control of *I. typographus* by natural enemies and competitors in managed forests could be enhanced through preventative measures that alter forest conditions and increase forest diversity (Hlásny et al., 2019; Kenis et al., 2004), which could decrease the likelihood of large-scale outbreaks in managed forests (Hlásny et al., 2021).

In this thesis, I explored how competition and predation affects *I. typographus* reproductive output in two different forest management types: previously clear-cut and near-natural stands. This study aims to investigate whether forest management practices that promote forest diversity, including natural enemy and interspecific competitor populations, suppresses bark beetle reproductive output and thus has the potential to reduce bark beetle outbreak risk. I aim to test two hypotheses: **(i)** near-natural forests support a higher diversity and abundance of predatory beetles, more interspecific competitors, and lower attack rates (less intraspecific competition) of *I. typographus*, than previously clear-cut forests, and **(ii)** this correlates with lower *I. typographus* reproductive success in near-natural forests.

2. Materials and methods

2.1. Study area

This master thesis is a part of the EcoForest project, which aims to investigate the long-term effects of forestry on biodiversity, carbon storage, and ecosystem functions in mature boreal forests by comparing near-natural Norway spruce stands with previously clear-cut forest stands. Near-natural stands are characterized as being minimally impacted by human activity and have never been clear-cut, whereas clear-cut stands were planted with spruce 60-70 years ago and are now mature.

Ten site pairs were established by the project in SE Norway (Figure 1, Table 1). Each pair consisted of one mature previously clear-cut forest stand and one near-natural forest stand. A 15 x 15 m study plot was established in each of the forest stands. Apart from the different management history, the sites were chosen to be otherwise similar concerning site productivity, soil profile, bedrock, vegetation type, elevation, topography, and aspect. For further details on site selection, see Asplund et al. (2024). The sites were all dominated by Norway spruce and bilberry (*Vaccinium myrtillus*) and ranged from the hemiboreal zone (Halden) to the south boreal (Blåfjell, Särkilampi) and middle boreal zones (all other sites) (Asplund et al., 2024) (Figure 1). The intra-pair distance between near-natural and previously clear-cut stands was 1270 m on average, with a minimum distance of 540 m and a maximum distance of 3140 m. The age of the dominant trees in near-natural and previously clear-cut stands were 130 and 65 years, respectively.

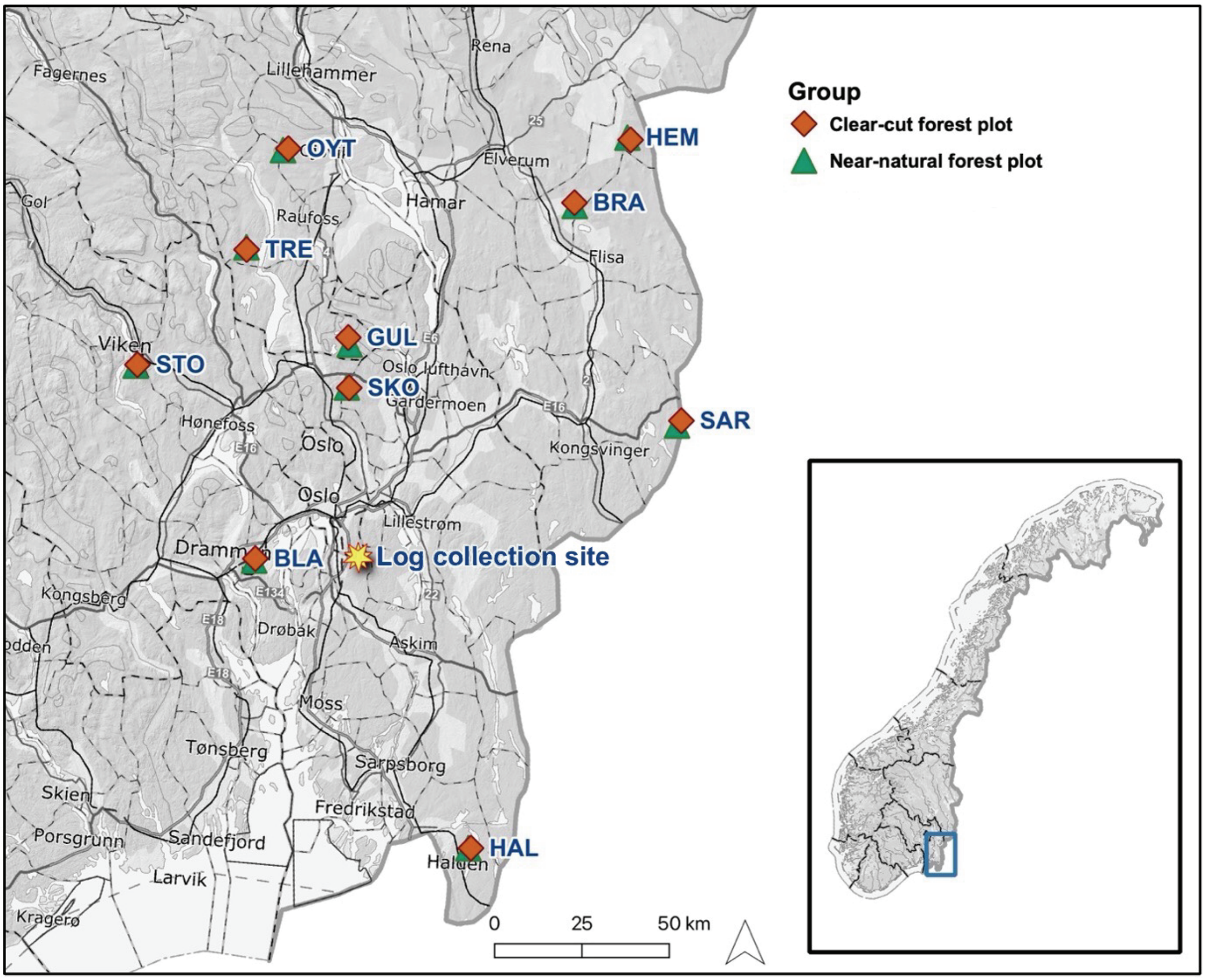

Figure 1. The 10 paired sites used in this study, each consisting of one previously clear-cut forest stand and one near-natural forest stand. The sites are Skotjernfjell (SKO), Gullenhaugen (GUL), Hemberget (HEM), Braskereidfoss (BRA), Särkilampi (SAR), Øytjern (OYT), Tretjerna (TRE), Halden (HAL), Blåfjell (BLA) and Storås (STO). Star indicates the origin of the experimental spruce logs.

Data on forest stand microclimate and characteristics was collected by Asplund et al. (2024) and is summarized in Table 1. Mean summer air temperature (June-September) was measured by repeated registrations every 15 minutes in the air (15 cm) by six temperature loggers (TMS-4, Tomst) at each forest plot for 2023 and then the mean temperature across all six sensors was calculated. Precipitation in the warmest quarter was modeled at 100 m resolution from 2004 to 2014 using monthly data from seNorge on a 1 km grid (Asplund et al., 2024). The volume of living spruce was estimated by measuring diameter at breast height and height in each study plot. The percentage of forested area within a 10 km radius of each stand was derived from the national land resource map AR50 on a 1:50 000 scale (NIBIO).

Table 1. The 10 paired sites used in this study, ordered from southernmost to northernmost. Management types at the different sites were mature previously clear-cut (CC) or near-natural (NN) forest stands. Environmental variables are elevation, mean summer air temperature (June-September; TEMP), precipitation in the warmest quarter (June-August; PREC), volume of spruce, and forested area around each site.

Site	Management type	Elevation (m.a.s.l.)	TEMP (°C)	PREC (mm)	Volume spruce (m^3 ha^{-1})	Forested area (% of total area within 10 km radius)
Halden	CC	197	14.6	295.5	467	72.7
	NN	211	14.9	297.0	459	73.9
Blåfjell	CC	322	14.0	350.0	384	47.5
	NN	264	14.1	346.9	591	48.0
Särkilampi	CC	388	13.5	274.8	292	77.1
	NN	368	13.4	274.3	111	77.3
Skotjernfjell	CC	571	12.4	321.5	353	88.5
	NN	610	12.4	322.6	269	88.4
Storås	CC	432	12.6	335.8	301	81.0
	NN	483	12.5	338.6	309	81.9
Gullenhaugen	CC	591	11.9	300.6	385	84.9
	NN	668	11.9	302.8	325	85.0
Tretjerna	CC	520	12.4	319.9	245	81.4
	NN	472	12.4	320.3	207	81.9
Braskereidfoss	CC	332	13.1	246.5	642	71.1
	NN	427	13.1	246.2	288	72.5
Øytjern	CC	663	11.5	311.0	247	75.9
	NN	640	11.5	311.2	451	75.2
Hemberget	CC	584	12.2	286.2	166	76.4
	NN	581	12.1	286.2	174	78.2

2.2. Study species

The European spruce bark beetle *Ips typographus* is endemic to the spruce forests of Eurasia (Biedermann et al., 2019). It has the typical morphological characteristics of bark beetles; it is small (5 mm) with a cylindrical body in cross-section, has an enlarged head with sizeable mandibles and chewing muscles, and short legs and antennae (Hulcr et al., 2015). *I. typographus* prefers host trees that are older than 60 years with a breast height diameter over 20 cm, but younger and smaller trees can also be chosen if population levels are high (Hlásny et al., 2021). Typically, the number of offspring is positively correlated with bark thickness and tree diameter.

In Norway, *I. typographus* is univoltine, meaning it has one generation per year (Økland et al., 2022). Therefore, the beetles usually stay in the host tree until the weather turns colder in fall, and seek for the forest floor to start hibernation. In S Norway, *I. typographus* normally emerges from hibernation in mid-May, when the maximum temperatures reach 18-20 °C (Økland et al., 2022). The males are the first to arrive at the host tree (Cognato, 2015), where they produce pheromones to attract conspecific males and females, and construct mating chambers in the tree (Raffa et al., 2015). The beetle is polygynous, and each male mates with 1-3 females (Ehnström, 2002). If a host tree has a high density of beetle attacks, the females can re-emerge after mating and form sister broods in less crowded trees (Hlásny et al., 2019). From the mating chamber, the females construct maternal galleries that are up to 10 cm long and 2 mm wide. Each female deposits up to 80 eggs in niches along both sides of the gallery (Wermelinger, 2004). When the eggs hatch, the larvae begin feeding on the phloem tissue (Ehnström, 2002). The larvae pupate in oval chambers at the end of these larval mines. After pupal development, the teneral beetles feed on phloem tissues until maturity and then emerge through 2-3 mm wide, circular emergence holes.

As previously mentioned, outbreaks of *I. typographus* are usually initiated by widespread abiotic disturbances that provide large amounts of damaged or weakened trees that increases the population size of the beetles, which allow them to exhaust the defenses of healthy trees through mass attacks (Hlásny et al., 2019). Beetle aggregation and subsequent mass attacks on suitable host trees and other social interactions in *I. typographus* depends on effective intra-specific communication by pheromones (Raffa et al., 2015). One downside of using pheromones is that they can be exploited by competitors and natural enemies to locate the bark beetles and their host trees (Wegensteiner et al., 2015).

2.3 Study design

To investigate *I. typographus* reproductive output in the two management types, an experiment was established. A total of 80 logs 0.5 m long and about 40 cm in diameter were cut from 13 healthy spruce trees felled in Nordre Follo in late February 2022 (Figure 1). The ends of the logs were sealed with paraffin wax, to prevent excessive drying of the bark. Four logs were randomly assigned to each of the 20 forest stands and transported there by helicopter from 11-15 March.

The experiment was set up from 12 April to 19 May 2022. The four logs were arranged in a 2 x 2 square formation on a white fiber sheet towards the center of each forest stand (Figure 2a). A 60cm square wooden stick was placed in the middle of the logs, and four strips of 2 x 5 cm pheromone dispenser tape were stapled on each edge of the stick and covered by a protective paper cup (Figure 2b, Figure 3). The tape was Hercon type releasing methylbutenol, cis-verbenol, and ipsdienol at a ratio of about 160:7:1 (Hercon Environmental, Emigsville, PA, USA) (Bakke et al., 1983; Mageroy et al., 2020). The pheromone dispensers and logs were left throughout the summer, to allow for bark beetle attack. One IBL2 window trap was hung from the trees nearest to the log group, at approximately 1.5 m height (CHEMIPAN, Warsaw, Poland) (Figure 2a, Figure 3). Flying insects collide with the trap and fall into a collection bottle with conservating liquid (70% glycol and 30% alcohol).

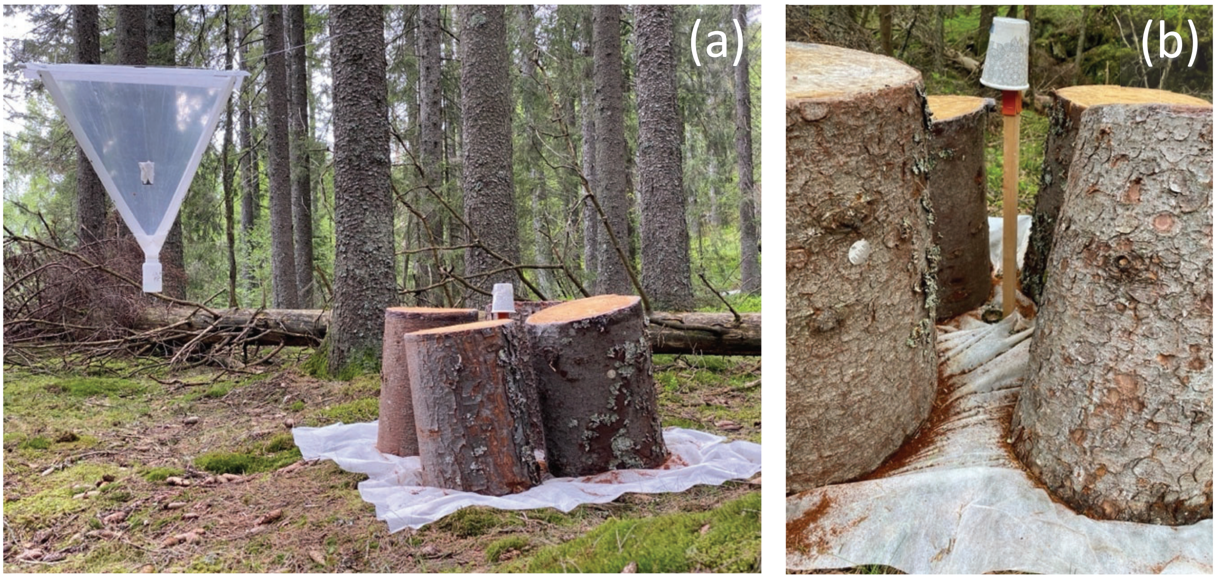

Figure 2. Experiment setup. (a) The logs were placed on level ground in a 2 x 2 formation and a window trap was hung nearby the logs. (b) A square wooden stick with pheromone dispenser tape covered by a protective paper cup was placed between the logs. Photos: Milda Norkute.

To follow the ongoing larval development in the logs, the *I. typographus* generation development map by NIBIO was used (*Kilden*, 2022). This map was created by NIBIO to estimate bark beetle populations and the risk of outbreaks in Norway. The map utilizes a temperature model to estimate the extent of beetle development. When the map indicated that the larval development was nearing completion (between 15-27 July 2022) at the different sites, emergence traps were installed (Figure 3). These traps were designed to collect the beetles and their associates emerging from the logs. Before installation, the number of bark beetle entrance holes was counted and marked with an acrylic pen. Then the logs were hung on a handle to a strap stretched between two trees. Each log was placed in a fine mesh net, and a round plexiglass roof was mounted to maintain the net's shape. A funnel attached to a bottle with conservating liquid (70% glycol and 30% alcohol) was hung beneath the log. Two small holes were punctured in the upper part of the bottles to release rainwater.

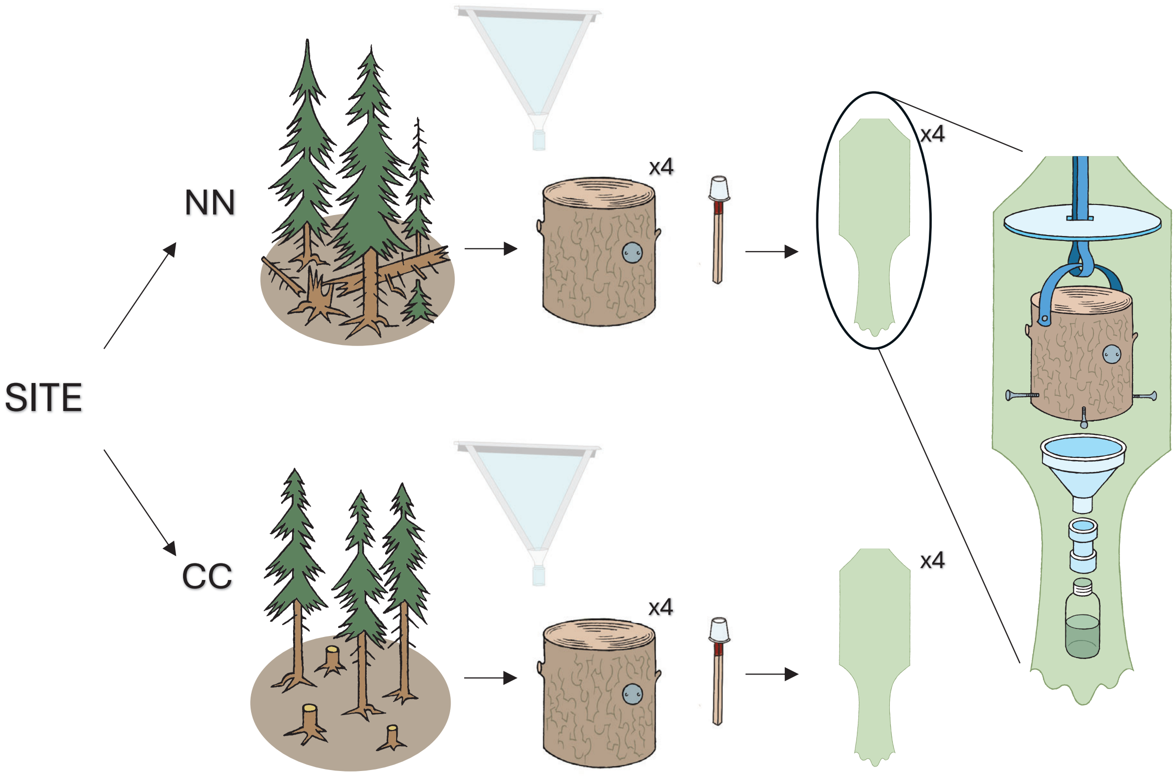

Figure 3. The experiment setup. At all 10 paired sites, four logs were placed in each management type (near-natural (NN) and previously clear-cut (CC) forest stands), along with a stick with pheromone dispenser tape and a window trap (Figure 2). The logs were later hung in emergence traps. Illustrations: Lars Fiske and Vera Fiske.

2.4. Data collection

The bark was collected from the logs from 20-28 June 2023. First, the emergence traps were dismantled, and the logs were lowered to the ground and laid on a white PVC cloth. A vertical incision was made in the bark with a knife, and it was pried away from the wood. The bark for each log was divided into three to four pieces, which were then labeled and put in plastic bags. The bags were placed in a -21°C freezer within 1-4 days. Emergence trap bottles were collected, but are not a part of this thesis.

2.5. Data processing

Photographs of all the collected bark pieces and different gallery systems were taken using a iPhone XS camera in August 2023, and then digitally cataloged by site and management type. To outline the ensuing bark area analysis, the surface area of the bark was examined. Areas with interspecific competitors were noted and later included as separate area categories in addition to *I.* the *typographus* galleries A selection of the gallery systems that had an atypical structure compared to typical *I. typographus* galleries, was sent to experienced field entomologist Jozef Vakula, to confirm that the galleries were created by *I. typographus*. The data processing consisted of two main procedures in the lab: a bark area analysis and an analysis of *I. typographus* reproductive output.

2.5.1. Bark area analysis

To collect data on bark surface area occupied by *I. typographus* and its interspecific competitors, plastic cover sheets (0.1 mm) cut into A3 size were used. The sheets were pinned onto the individual bark pieces, flush with the inner bark surface and completely covering the bark area. Five different area categories that together made up about 99% of the bark area on most logs were chosen: *Ips typographus,* other bark beetles, cerambycids, fungi and unoccupied bark (Table 2, Figure 4).

Table 2. Criteria used to identify five different bark area categories used during the bark area analysis.

Area category	**Criteria**
Ips typographus	Any activity of *Ips typographus;* maternal and larval galleries and maturation feeding
Other bark beetles	Galleries of other bark beetles than *Ips typographus*
Cerambycids	Any activity of cerambycids, particularly species of *Tetropium*. Characterized by the presence of larvae, distinct pupal chambers, and wider undulating tunnels with grainy and often tightly packed frass
Fungi	Bark dominated by fungal hyphae. Lighter, yellowish bark color, often accompanied by wood decomposition and white hyphae
Unoccupied bark	Intact bark with no signs of biotic damage

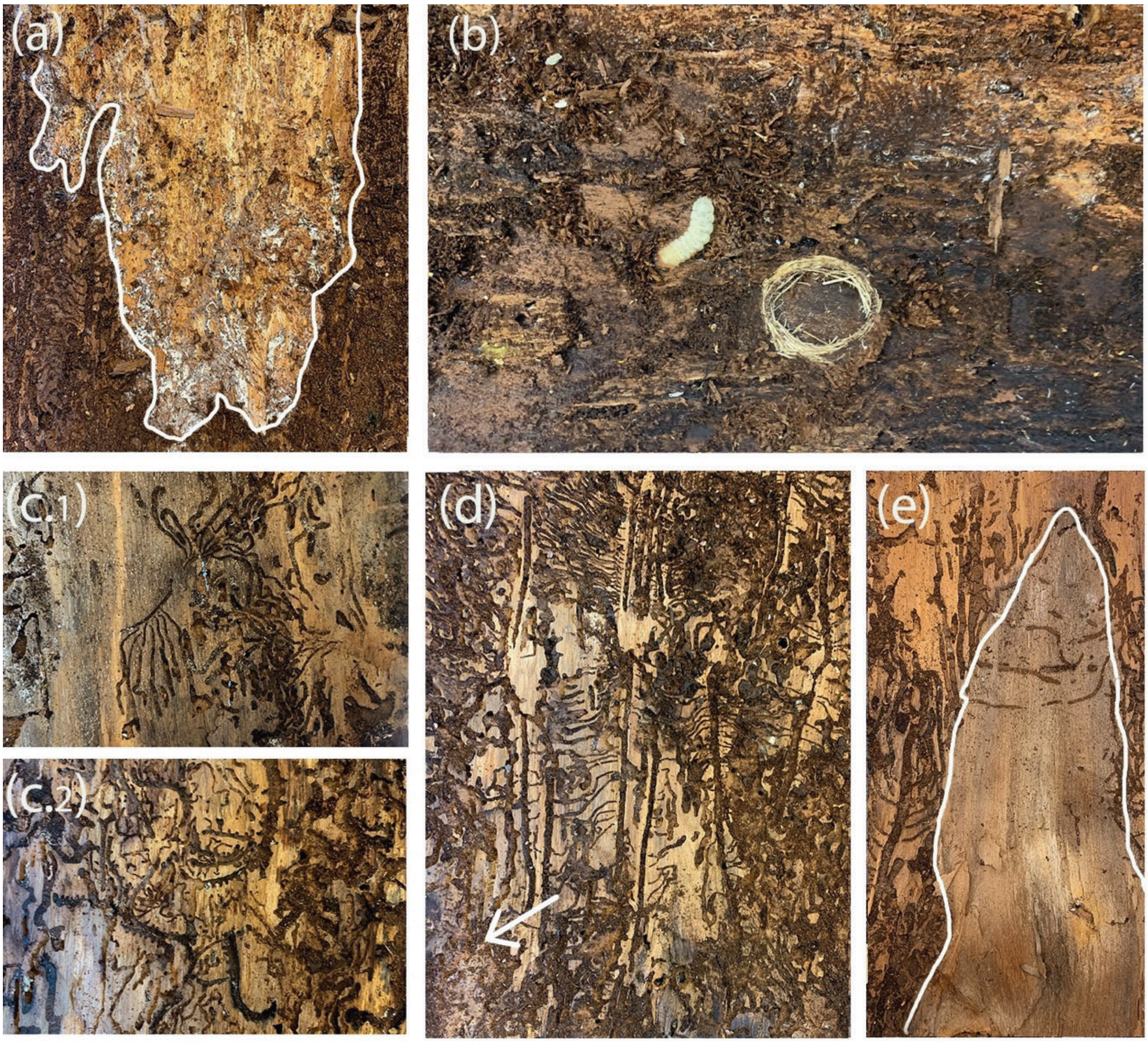

Figure 4. Examples of five different categories used for the bark area analysis: (a) fungi, (b) cerambycids (here larvae and pupal chamber of *Rhagium inquisitor*), (c.1, c.2) other bark beetles, (d) *Ips typographus* galleries and maturation feeding (arrow), and (e) unoccupied bark.

The outline of the bark piece and the outline of the five different categories were drawn on the plastic sheets in permanent marker, along with a 5 cm reference line for scale (Figure 5). The sheets were then scanned separately and joined together again digitally in Photoshop version 25.0.0. The area measurements were done in ImageJ version 1.53 K (Rasband, 1997). Here, the scale was set according to the reference line, and the entire bark area and the different category sections were traced and outlined to extract the surface area in m^2. This area was later joined to represent each log.

Figure 5. Examples of the bark area analysis process, from original bark samples to scanned and digitally re-assembled tracings of the five different bark area categories that were analyzed (numbers represent: 1 = *Ips typographus*, 2 = cerambycids, 3 = other bark beetles, 4 = fungi, and 5 = unoccupied bark. X = missing bark).

2.5.2. Analysis of *Ips typographus* reproductive success

To estimate the reproductive success of *I. typographus* (Hedgren & Schroeder, 2004), exit holes that had the typical shape and size for *I. typographus* were counted on the outer surface of the bark pieces (Ehnström, 2002) (Figure 6a). Maternal galleries on the inner surface were also counted and measured (Figure 6b). Unusually short maternal galleries (less than 2.5 cm) were excluded, to reduce workload and because they would not contribute significantly to the data. The prominence and intactness of the maternal galleries varied; bark from five logs (two from Halden, two from Blåfjell, one from Gullenhaugen) could not be analyzed due to a high degree of maturation feeding or feeding by cerambycids. Also, 17 logs had 1-2 bark pieces that could not be analyzed while the remaining pieces had intact galleries. Therefore, to avoid disregarding these logs, the analysis was reduced to only examining 1-3 pieces per log.

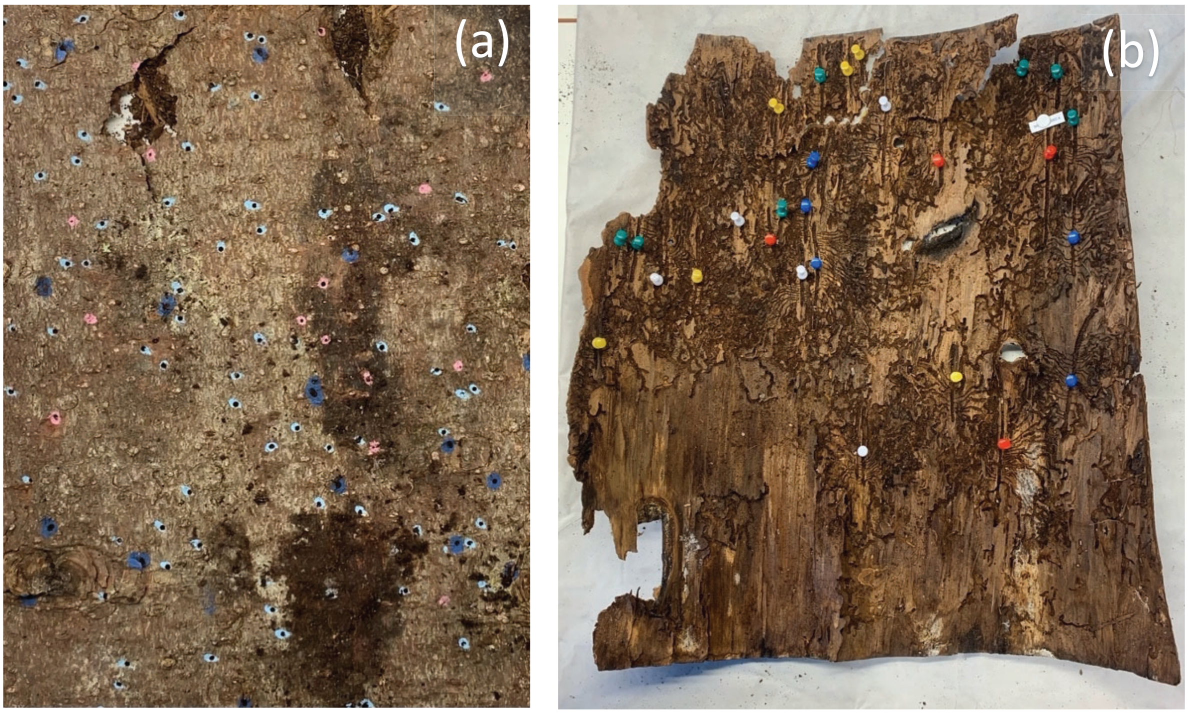

Figure 6. Analysis of *Ips typographus* reproductive success. (a) Exit holes were counted by marking them with a light blue acrylic marker (dark blue is *Ips typographus* entrance holes, pink is entry holes by smaller bark beetles. They are not used in this thesis). (b) Each maternal gallery was counted and measured. The pins were placed to keep track of the counting.

Reproductive success of *I. typographus* is the average number of daughters produced per mother beetle. This was calculated for each log as: [number of emerged individuals × 0.5]/[number of maternal galleries] (Hedgren & Schroeder, 2004). Attack density for each log was calculated as [number of maternal galleries]/[total bark area in m^2] (Andersson, 2023). The total bark area per log (in m^2) was extracted during the ImageJ analysis.

2.5.3. Predatory beetles of *Ips typographus* in the window traps

The insects caught in the window traps were kept in a freezer at -20°C after collection. All beetles were picked out from the collected material and sent to experienced beetle taxonomist Sindre Ligaard for species identification. They were then sorted into feeding groups, based on data from Seibold et al. (2015) and SLU artdatabanken (2023). Then, beetles that are known predators of *I. typographus* were selected from the general predators group (Table C-1). The selection of predatory beetles of *I. typographus* was based on a literary study (Bakke & Kvamme, 1993; Kenis et al., 2004; Wegensteiner et al., 2015) (Table C-1).

2.6. Statistical analysis

To account for the missing data on *I. typographus* reproductive output for the five logs in Halden, Blåfjell, and Gullenhaugen, the mean of the remaining logs in each forest stand was used for variables daughters per mother, maternal gallery length, and attack density. I assessed the comparability of results for the 17 logs with limited data on reproductive success to the logs with complete data by ensuring that using a reduced number of bark samples provided relatively equal results to using the whole bark area. Additionally, I verified that the mean and sum of total bark area were similar between the two management types.

All subsequent data analysis was done in RStudio version 4.3.2 and R version 2023.12.1 (RStudio Team, 2020). All figures were made with the ggplot2 package (Wickham, 2016), except for Venn-diagrams which were made using the VennDiagram package (Chen, 2022). To investigate the relationship and correlation between the variables, and to determine which variables to use as covariates in my analyses, a correlation matrix was fitted with the "corplot" function using the corrplot package (Wei & Simko, 2021) (Figure A-1). The correlation coefficients $|r|$ were interpreted from a categorization by Taylor (1990), stating that values $|r| \leq 0.35$ are weak correlations, $|r| = 0.36$ to 0.67 are modest correlations and $|r| = 0.68$ to 1 are strong to high correlations. To avoid including strongly correlated variables in the same model, a correlation threshold of |r| = 0.7 was used (Dormann et al., 2013). For further visualization of the relationships between the variables, a principal component analysis (PCA) was plotted with the ggplot2, MASS (Venables & Ripley, 2002), and factoextra (Kassambara & Mundt, 2020) packages (Figure B-1).

To investigate how response variables abundance and richness of predatory beetles, the five bark area categories (*Ips typographus*, other bark beetles, fungi, cerambycids, unoccupied bark), daughters per mother, and attack density differed between the two management types, paired t-tests were performed. Assumptions of the t-test were tested with a Shapiro-Wilks test (Shapiro & Wilk, 1965) within the moments package (Komsta & Novomestky, 2022) for normality, and the performance package for outliers. If non-normality was too severe or outliers were detected, the variables were either sqrt- or log-transformed before the t-test, depending on the degree of skewness. For all the area data except the area of fungi, zeros were accounted for by adding a constant before log-transforming (log + 1).

To investigate the different effects of predation, interspecific competition, and intraspecific competition on *I. typographus* reproductive success, linear mixed models (LMM) were used. Daughters per mother was the response variable in all models, and it was transformed using the square-root (sqrt) function for all models to make the data more normally distributed and improve linearity between the response variable and the explanatory variable(s). I predicted the effect of richness and abundance of *I. typographus* predatory beetles in separate models, as the correlation between the variables was too high (Pearson's correlation coefficient, $|r| = 0.80$, df = 78, $p < 0.001$) (Figure A-1). I also predicted the effect of interspecific competition (m^2 of area occupied by fungi, cerambycids, other bark beetles, and unoccupied bark) in separate models due to strong correlations between the variables. To ensure that the variables for intraspecific competition (attack density and maternal gallery length) were not too strongly correlated, the variance inflation factor (VIF) was calculated for the model using the car package (Fox, 2019). A VIF of 1.30 revealed no significant collinearity issues between the variables and they were used in the same model. The variables forested area, precipitation in the warmest quarter and mean annual summer temperature had low correlation with daughters per mother (Figure A-1, Figure B-1), and the relationships were not significant in single-variable models, therefore these variables were not included in subsequent models.

To find the best model fit and select the highest preforming models, AIC weights and marginal and conditional R^2 were investigated with the aid of the “compare_performance” function from the performance package (Lüdecke et al., 2021), and residual variance plots were investigated using the DHARMa package (Hartig, 2022). Functions from the performance package were used to test model assumptions. Model predictions were extracted from the LMMs with the ggeffects package (Lüdecke, 2018), and plotted with ggplot2.

3. Results

3.1. Reproductive success of *Ips typographus* in unmanaged vs. managed forests

The number of daughters produced per mother was close to significantly higher in previously clear-cut stands than near-natural stands (Paired t-test, t = 1.803, df = 39, p-value = 0.079). An average of 48% more daughters were produced per mother in previous clear-cuts compared to near-natural stands (Figure 7).

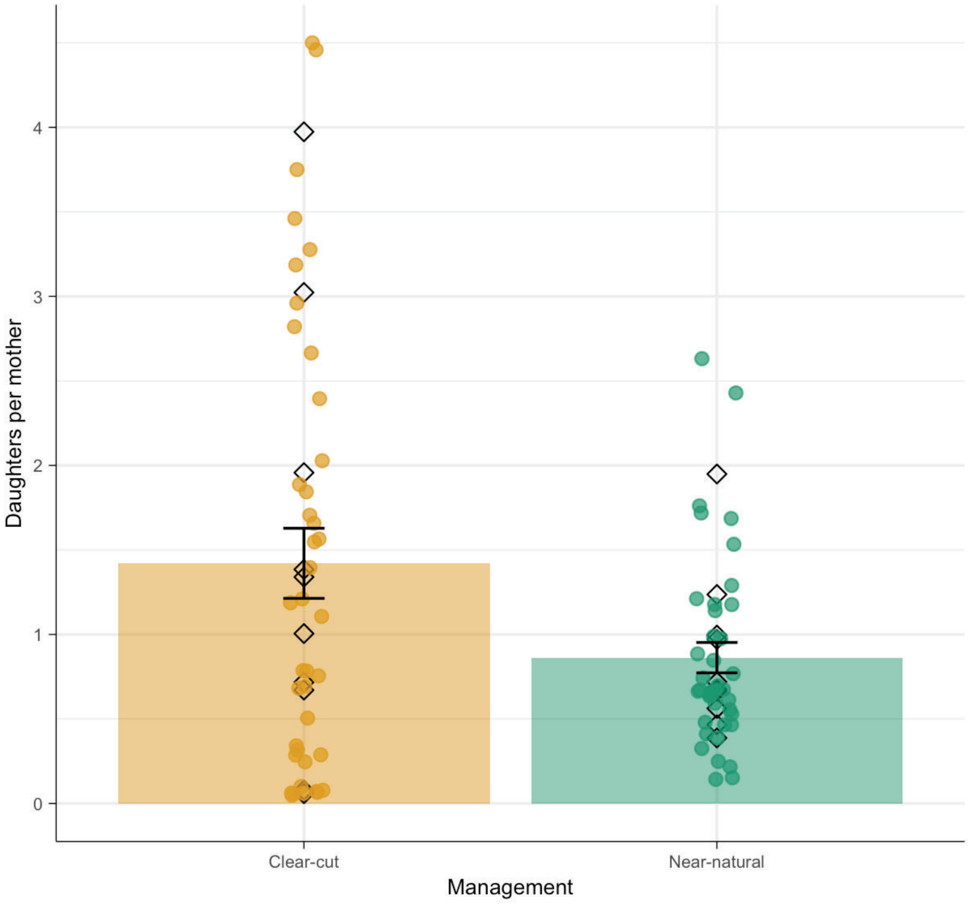

Figure 7. Mean (± SE) daughters per mother in the two forest management types. The dots represent daughters per mother for individual logs, while the diamonds represent the mean daughters per mother for each of the 10 sites.

3.2. Predation by beetles

3.2.1. Predatory beetles in unmanaged vs. managed forests

A total of 1054 individuals of 42 beetle species that are known predators of *I. typographus* were caught in the window traps (Table C-1). Out of these, 642 individuals representing 35 species were caught in near-natural stands, while 412 individuals representing 38 species were caught in the previously clear-cut stands (Figure 8). A total of 42 species were captured, where seven were only caught in previous clear-cuts and four were only caught in near-natural stands (Figure 8b).

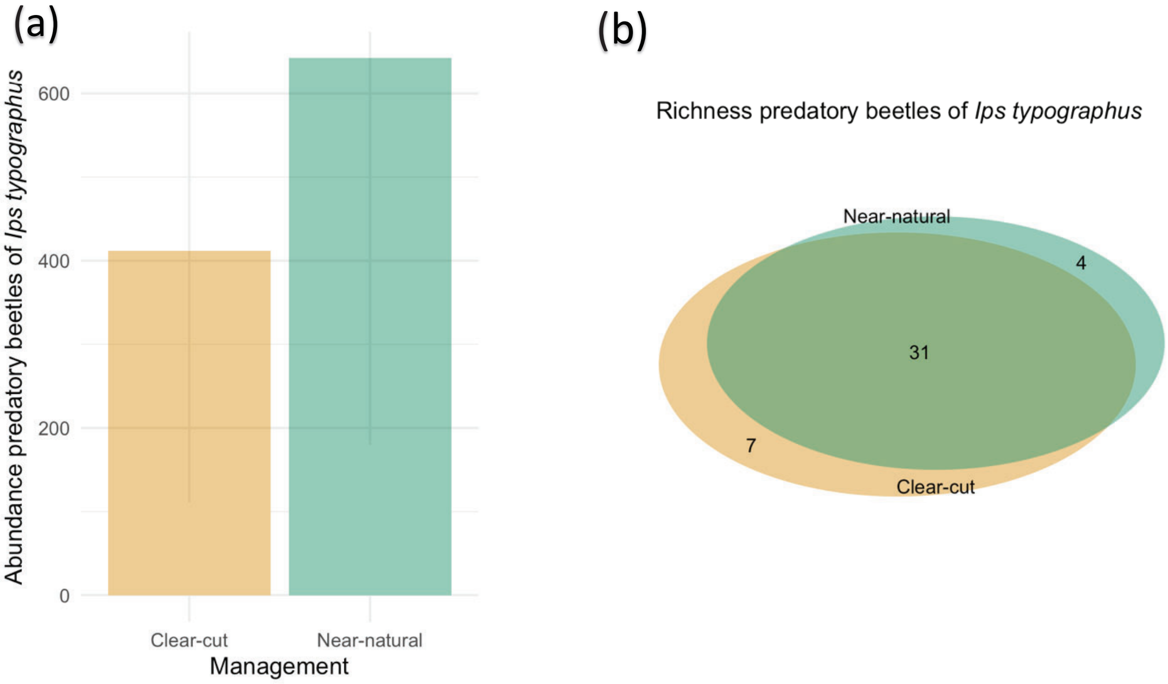

Figure 8. Total abundance (a) and number of unique and shared species (b) of predatory beetles of *Ips typographus* caught in window traps in the two forest management types.

The abundance of predatory beetles was not significantly different between the two management types (Paired t-test, t = -1.375, df = 9, p = 0.202), although mean abundance and variation was higher in near-natural forest stands (Figure 9a). Species richness was similar between management types (Paired t-test, t = 0, df = 9, p = 1.000) (Figure 9b).

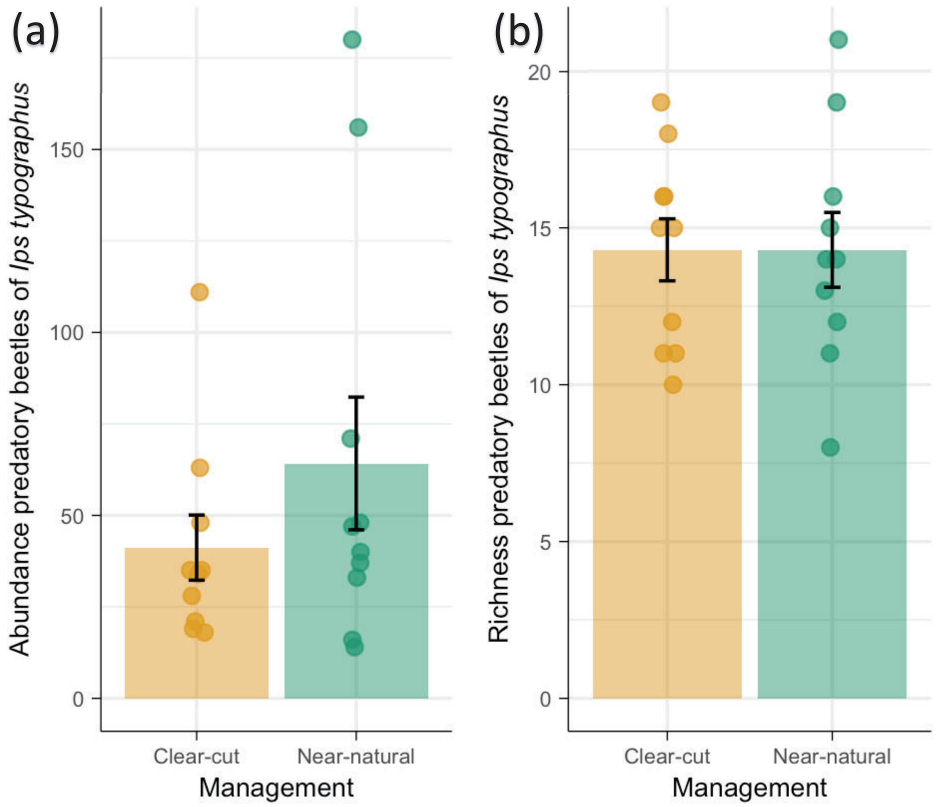

Figure 9. Mean (± SE) abundance (a) and species richness (b) of predatory beetles of *Ips typographus* captured in window traps the two forest management types. The dots represent the number of beetles captured in each of the 10 sites.

3.2.2. Effect of predatory beetles on *Ips typographus* reproductive success

The highest performing model revealed that richness of predatory beetle species had no effect on the reproductive output of *I. typographus* ($p = 0.117$) (Table 3). Candidate explanatory variable abundance of predatory beetles also had no effect on daughters per mother.

Table 3. Summary of the linear mixed model that was used to predict daughters per mother as the response variable (square-root-transformed) with richness of predatory beetles of *Ips typographus* as the explanatory variable. Site was added as random effect.

Variable	*Estimate*	*SE*	*Df*	*t-value*	*Pr(>|t)*
Fixed effects					
(Intercept)	1.414	0.304	7.573	4.659	< 0.001
Richness predatory beetles of *Ips typographus*	-0.032	0.020	62.124	-1.592	0.117
Random effect	*Variance*	*SD*			
Site ID	0.105	0.324	Cond. $R^2 = 0.513$, Marg. $R^2 = 0.048$		

3.3. Interspecific competition

3.3.1. Interspecific competitors in unmanaged vs. managed forests

I. typographus galleries occupied the greatest proportion of the bark area of the logs, taking up 69% of the total area in near-natural stands and 73% in former clear-cut stands (Figure 10). The second largest area was fungi, which made up 13% and 16% in previous clear-cuts and near-natural stands, respectively. The surface area occupied by cerambycids, other bark beetles and unoccupied bark all made up less than 10% in both near-natural and previous clear-cuts, with other bark beetles occupying the smallest area (2% of the total area) in each management type (Table 4). The area occupied by interspecific competitors (cerambycids, other bark beetles, and fungi) was not significantly different between near-natural and previously clear-cut stands (Table 4). The only area category that differed between management types was area of unoccupied bark, with an average of 42% more in previous clear-cuts ($p < 0.05$) (Table 4; Figure 10).

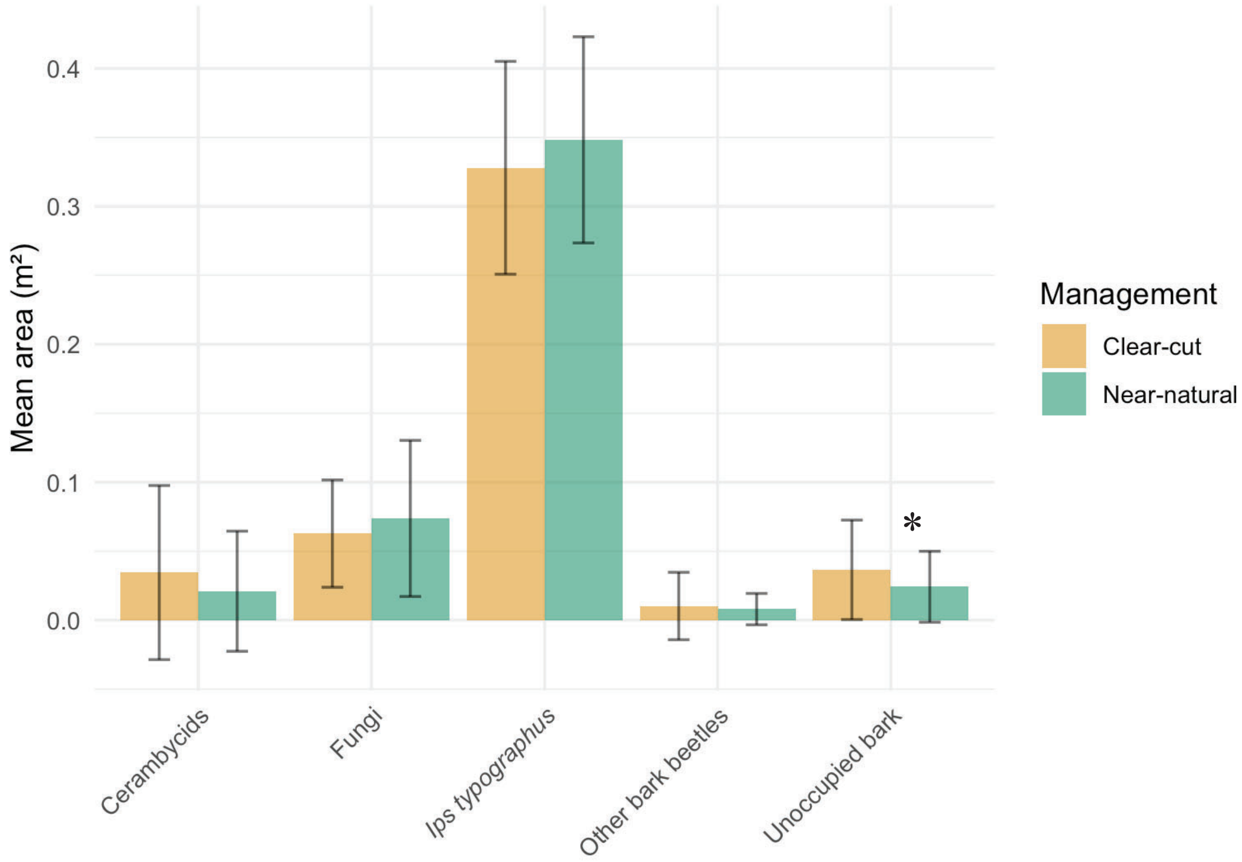

Figure 10. Mean (± SE) area in m^2 of the five different area categories on the bark in the two management types. Area categories that differed significantly between management types are marked with an asterisk.

Table 4. Summary of the results from paired t-tests for the five area categories investigating the difference between clear-cut and near-natural management types. Significant ($p < 0.05$) results are given in bold.

Area category	**% of total area in NN**	**% of total area in CC**	***t-value***	***Df***	***Pr(>|t)***
Ips typographus	73%	69%	-1.422	39	0.163
Fungi	16%	13%	-0.011	39	0.991
Cerambycids	4%	7%	1.420	39	0.164
Other bark beetles	2%	2%	-1.649	39	0.107
Unoccupied bark	5%	8%	2.060	39	**< 0.05**

3.3.2. Effect of interspecific competition on *Ips typographus* reproductive success

The analyses revealed that bark area occupied by other bark beetles had a significant positive effect on the reproductive output of *I. typographus* ($p < 0.05$) (Model 1, Table 5). An increase in the area occupied by other bark beetles resulted in an increase in the number of daughters per mother (Figure 11a). However, the area occupied by other bark beetles explained a small ratio of variation (Marg. $R^2 = 0.072$), indicating a limited effect on reproductive success overall.

The area of unoccupied bark also had a significant positive effect on reproductive output of *I. typographus* ($p < 0.05$) (Model 2, Table 5), where increasing area of unoccupied bark led to an increase in daughters per mother (Figure 11b). Also, the marginal R^2 for unoccupied bark was moderate, indicating that the variable explains a moderate ratio of variation (Marg, $R^2 = 0.124$). Candidate explanatory variables bark area occupied by fungi and cerambycids had no significant effect on daughters per mother.

Table 5. Summary of the linear mixed models that were used to predict daughters per mother as the response variable (square-root-transformed) with area of other bark beetles and area of unoccupied bark (in m^2) as explanatory variables. Site was added as random effect. Significant ($p < 0.05$) results are given in bold.

Variable	*Estimate*	*SE*	*Df*	*t-value*	*Pr(>|t)*
Model 1: Fixed effects					
(Intercept)	0.896	0.115	9.607	7.811	< 0.001
Area of other bark beetles	7.052	2.216	71.223	73.260	**< 0.05**
Model 1: Random effect	*Variance*	*SD*			
Site ID	0.115	0.339	Cond. $R^2 = 0.572$, Marg. $R^2 = 0.072$		
Model 2: Fixed effects					
(Intercept)	0.808	0.106	12.317	7.634	< 0.001
Area of unoccupied bark	5.003	1.447	77.959	3.45	**< 0.05**
Model 2: Random effect	*Variance*	*SD*			
Site ID	0.079	0.282	Cond. $R^2 = 0.510$, Marg. $R^2 = 0.124$		

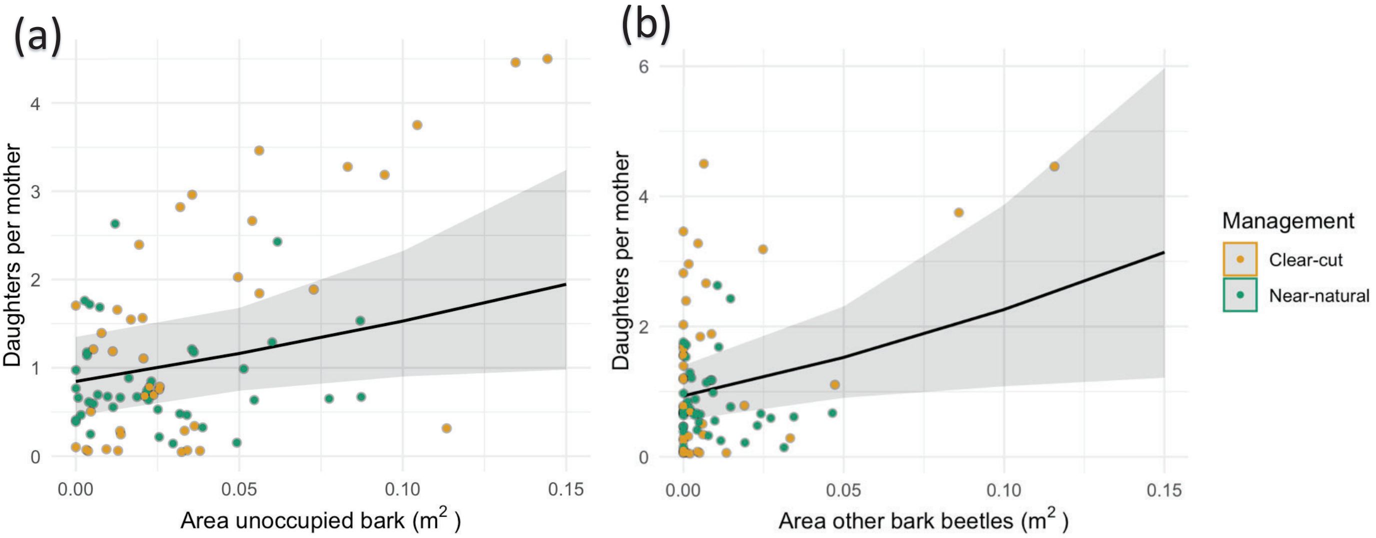

Figure 11. The relationship between area of unoccupied bark (m^2) (a) and area occupied by other bark beetles (m^2) (b) and the reproductive output of *Ips typographus* as daughters per mother. The predicted regression lines are plotted with associated 95% confidence interval. Both slopes are significantly different from zero.

3.4. Intraspecific competition

3.4.1. Intraspecific competition in unmanaged vs. managed forests

Attack density of *I. typographus* was close to significantly different between management types (Paired t-test, t = -1.762, df = 39, p = 0.085). Attacks by *I. typographus* were on average 12% more dense in near-natural compared to previously clear-cut stands (Figure 12).

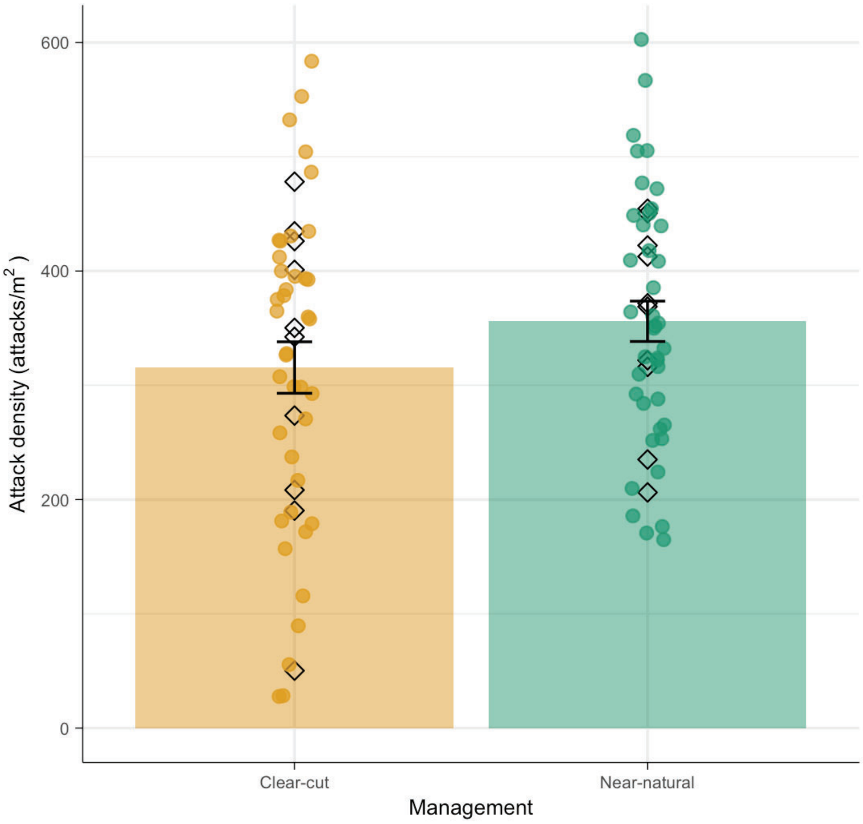

Figure 12. Mean (± SE) attack density in the two forest management types. The dots represent attack density for individual logs, while the diamonds represent the mean attack density for each of the 10 sites.

3.4.2. Effect of intraspecific competition on *Ips typographus* reproductive success

The top model investigating the effect of intraspecific competition included both explanatory variables attack density and maternal gallery length (Table 6). Analysis results showed evidence for a decrease in the number of daughters per mother with increasing attack density ($p < 0.05$) (Figure 13a), and contrastingly an increase with increasing maternal gallery length ($p < 0.05$)

(Figure 13b). The marginal R^2 for the model is high, indicating that both attack density and maternal gallery length explain a big proportion of variation in the model.

Table 6. Summary of the linear mixed model that was used to predict daughters per mother as response variable (square-root-transformed) with attack density and maternal gallery length explanatory variables. Site was added as random effect. Significant ($p < 0.05$) results are given in bold.

Variable	***Estimate***	***SE***	***Df***	***t-value***	***Pr(>|t)***
Fixed effects					
(Intercept)	0.602	0.135	64.912	1.901	0.062
Attack density	-0.001	0.001	59.960	-3.779	**< 0.001**
Maternal gallery length	0.144	0.041	64.320	3.530	**< 0.001**
Random effect	***Variance***	***SD***			
Site ID	0.0176	0.132	Cond. R^2 = 0.549, Marg. R^2 = 0.460		

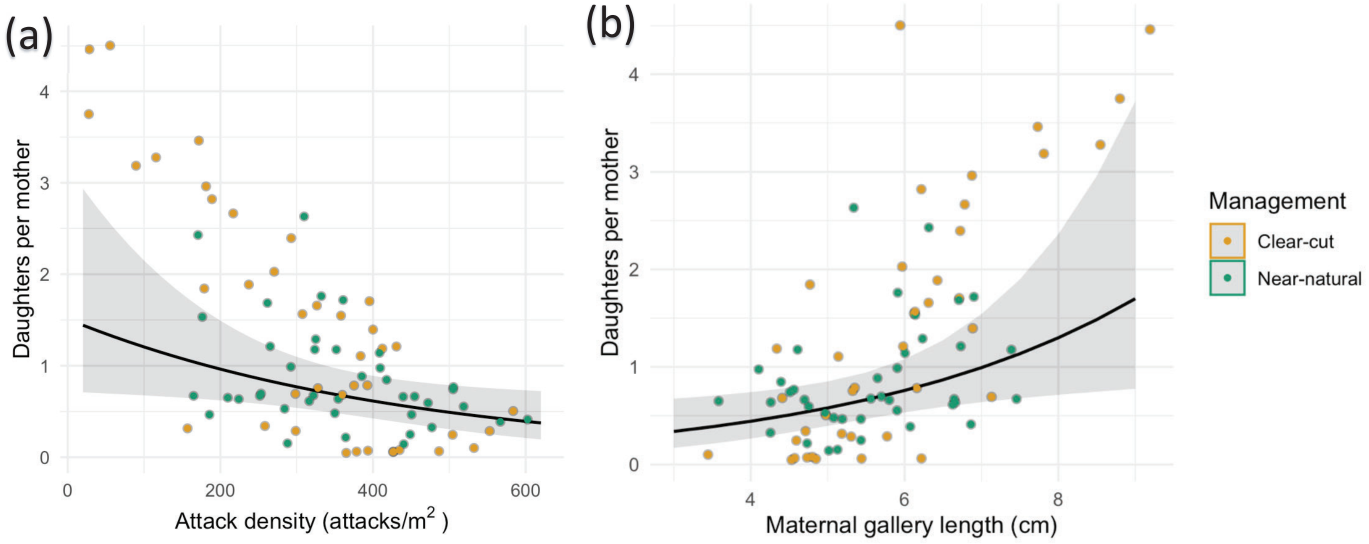

Figure 13. The relationship between attack density (a) and maternal gallery length (b) and the reproductive output of *Ips typographus* as daughters per mother. The predicted regression lines are plotted with associated 95% confidence interval. Both slopes are significantly different from zero.

4. Discussion

4.1. Reproductive success of *Ips typographus* in. unmanaged vs. managed forests

The reproductive success of *I. typographus* tended to be higher in previously clear-cut forests than in near-natural forests, which gives partial support for my hypothesis (ii) that reproductive success would be higher in managed stands. However, my results were not strongly significant, which is supported by previous studies finding similar reproductive success between different management types (Andersson, 2023; Weslien & Schroeder, 1999). On the other hand, the nearly significant findings and average of 48% higher reproductive success in managed forests suggest greater control of *I. typographus* in unmanaged forests in my study. Additionally, the average number of daughters per mother was slightly below 1 in near-natural stands and about 1.5 in previously clear-cut stands, which is generally considered low (Weslien & Regnander, 1990), but common under natural conditions due to mortality factors such as predation and competition (Anderbrant et al., 1985). This suggests that, although the non-outbreak populations of *I. typographus* were kept at lower levels in both management types, the effect was somewhat more pronounced in unmanaged forests. I will further discuss the potential contributions of predation by beetles, interspecific competition, and intraspecific competition to the observed lower reproductive success of *I. typographus* in unmanaged forests in this study.

4.2. Effect of predation by beetles in unmanaged vs. managed forests

Species richness and abundance of predatory beetles of *I. typographus* were similar between management types, contradicting my hypothesis (i) that unmanaged forests would support higher predatory beetle richness and abundance. These findings align with previous studies that also found no significant difference in the abundance of common predatory beetles of *I. typographus* in unmanaged forests (Hilszczański et al., 2007; Johansson et al., 2007; Schroeder, 2007). However, the contradictory nature of the literature, with both higher (Weslien & Schroeder, 1999) and lower (Feicht, 2006; Schlyter & Lundgren, 1993) densities of natural enemies reported in unmanaged forests, makes it difficult to draw any conclusions on whether forest management affects *I. typographus* predator beetle assemblages.

However, possible explanations for the discrepancies could be the habitat requirements and dispersal abilities of the studied enemy species. Although managed forests might be less diverse than unmanaged forests, they may still possess the necessary habitat qualities to support similar abundances of most predators of bark beetles. Johansson et al. (2007) suggest that finding slightly higher, but non-significant, abundances of saproxylic predatory beetles in unmanaged forests, could be explained by managed forests sufficiently meeting predatory beetle habitat demands. Moreover, some important predatory beetles are found to be more abundant in managed forests, due to a preference for the sunnier and more open conditions (Schlyter & Lundgren, 1993). This suggests that species-specific habitat preferences might influence the results when investigating predatory beetles as a group. Also, the dispersal abilities of predatory beetles could lead to more even distributions between management types. Although the general dispersal abilities of *I. typographus* predatory beetles are unknown, studies show that beetles connected to dead wood in early decay stages are generally good dispersers (Johansson et al., 2007; Valeria et al., 2016). Additionally, predatory beetle species of other bark beetles are found to be able to disperse up to several kilometers and to have greater long-distance dispersal abilities than their prey (Cronin et al., 2000; Fielding et al., 1991). The abundance of prey and attraction to prey habitat are also suggested to be important factors in explaining predatory beetle assemblages (Johansson et al., 2007; Weslien & Schroeder, 1999), and could also affect predatory beetle distributions between management types. Thus, the effect of habitat preferences and dispersal abilities of predatory beetles may have led them to be more evenly distributed between management types in this study.

No significant effect of predatory beetle abundance or species richness on the reproductive output of *I. typographus* was found in this study. Although previous studies show that predatory beetles can greatly reduce rates of bark beetle reproductive output (Wermelinger, 2002; Weslien & Schroeder, 1999), there is a large variation in findings overall (Weslien & Schroeder, 2023). These inconsistencies could potentially be attributed to the mortality inflicted by predatory beetles greatly depending on the outbreak phase of *I. typographus* (Wermelinger, 2002). Evidence suggests that natural enemies of *I. typographus*, many of which are generalists and non-specific on bark beetles, do not focus on *I. typographus* during non-outbreak population stages (Hilszczański et al., 2007; Martikainen et al., 1999). Some of the highest impacts of predatory beetles on *I. typographus* have been observed following the onset of outbreaks, when numbers of *I. typographus* in the forest stand increase (Weslien, 1992; Weslien & Schroeder, 1999). This suggests that, even though pheromones may have attracted predatory beetles in this study, the non-outbreak conditions of *I. typographus* in the forest stands could have limited their effect on *I.*

typographus reproductive output. As a result, predatory beetle assemblages do not seem to explain the tendency for lower reproductive success of *I. typographus* in unmanaged forests in this study.

However, the conclusions about predator beetle effect and assemblages in management types are made uncertain by the low sampling effort of predatory beetles in this study. Using only one window trap per forest stand, along with possible issues with species-specific probabilities of catches affected by factors such as height and flight duration of species, might influence the results (Martikainen et al., 1999). The higher mean abundance and greater variability in near-natural stands might indicate that results might be different with higher sampling effort. Therefore, whether the captures of predatory beetles are representative of the population and the distribution between management types is somewhat uncertain. It is also worth mentioning that other important natural enemy groups, such as parasites of *I. typographus*, were not studied, which could also influence the estimated effect.

4.3. Effect of Interspecific competition in unmanaged vs. managed forests

The bark area occupied by interspecific competitors did not differ between management types, which contradicts my hypothesis (i) that they would be more prevalent in near-natural stands. In support of my findings, other studies have also found that other bark beetles (Martikainen et al., 1999), cerambycids (Karpiński et al., 2021; Similä et al., 2003), and saproxylic fungi (Stokland & Larsson, 2011) were not more common in unmanaged forests than managed forests. However, the significantly bigger surface area of unoccupied bark in previously clear-cut forests than in near-natural forests, suggests less competition for this resource in managed forests. The effect of forest type on the interspecific competitor area categories might have disappeared due to high variability within the categories, and less unoccupied bark in near-natural forest stands could indicate that there was more occupied surface area for all the interspecific competitor categories combined. This may suggest that there were fewer interspecific competitors in previously clear-cut forests, leading to more bark being left untouched.

However, the mean area occupied by interspecific competitors was not larger in near-natural stands, which does not indicate that they had a greater influence on *I. typographus* reproductive success there. Also, they occupied a relatively small surface area compared to *I. typographus* in both management types, indicating they had limited impact on the beetle. This is supported by analysis results showing that neither area occupied by other bark beetles, cerambycids, or fungi had any important effect on the reproductive success of *I. typographus*. This contradicts studies that found strong negative effects of these groups on *I. typographus* (Cardoza et al., 2006; Ray et al., 2019; Schlyter & Anderbrant, 1993). However, other studies have found that interspecific competitors have a reduced effect on *I. typographus* in natural conditions, due to limited impact in newly dead spruce logs and different occupation of host trees in space and time (Johansson et al., 2007; Weslien, 1992). Also, consistent with my findings, Pelto-Arvo (2020) found that potential interspecific competitors were almost absent from pheromone-baited log emergence traps. This suggests that interspecific competitors may struggle to compete for space in logs already inhabited by early *I. typographus*.

The usage of pheromones might have given *I. typographus* a competitive advantage in this study (Pelto-Arvo, 2020), potentially causing the effect and occurrence of interspecific competitors in the logs to deviate somewhat from natural conditions. Using *I. typographus* pheromones would naturally lead to higher proportions of the beetle, and it has been found that *I. typographus* easily colonizes pheromone-baited substrate even when the abundance of the local population is very low (Weslien & Schroeder, 1999). The significantly greater area of unoccupied bark in previously clear-cut forests may also suggest lower occurrence of *I. typographus*, and thereby, less intraspecific competition. This interpretation is supported by studies indicating *I. typographus* to be more affected by intraspecific competition than interspecific competition (Marini et al., 2013; Schlyter & Anderbrant, 1993), and by *I. typographus* occupying the greatest proportion of the bark area in this study. In general, the results for interspecific competition point to intraspecific competition explaining more of the significant difference in area of unoccupied bark.

4.4. Effect of Intraspecific competition in unmanaged vs. managed forests

The results revealed that attack density tended to be higher in near-natural than previously clear-cut forests, which contradicts my hypothesis (i) that intraspecific competition would be higher in previously clear-cut forests. Few studies have investigated the difference in attack densities between forest management types. However, Andersson (2023) and Eriksson (2021) also found no significant difference in attack density between managed and unmanaged forests in their master's and bachelor's theses. These findings are consistent with studies reporting no difference in abundance of *I. typographus* between management types, which is related to attack density (Schlyter & Lundgren, 1993; Weslien & Schroeder, 1999). However, the observation that attack density tended to be higher in unmanaged forests in my study, might be explained by higher availability of breeding substrate in unmanaged forests (Marini et al., 2013), along with the dispersal abilities of *I. typographus* (Weslien & Schroeder, 1999). In general, the availability of breeding substrate is one of the main regulators of *I. typographus* (Marini et al., 2013), and unmanaged forests likely offer a more constant supply of dying trees (Martikainen et al., 1999). It is suggested that, due to the increased host availability in unmanaged forests, immigration of *I. typographus* is higher from managed to unmanaged forests (Martikainen et al., 1999). Valeria et al. (2016) investigated *I. typographus* dispersal and found that managed forests had more emigrants and received fewer immigrants than unmanaged forests, concluding that less intensive management in unmanaged stands causes less attacks in nearby managed stands. Thus, the tendency for attack density to be higher in unmanaged stands in my study could be explained by a more constant availability of breeding substrate, leading to immigration from managed stands and a larger local *I. typographus* population.

Analysis results revealed significantly lower reproductive success of *I. typographus* with higher attack rate and reduced maternal gallery length, and the relationship between these variables was one of the strongest findings of this study. The mean attack density in previously clear-cut forests was around 300 galleries per m^2 and around 350 galleries per m^2 in near-natural forests, which is estimated to be the upper limit of attack density during non-outbreak conditions (Furuta, 1989). Additionally, the significant positive effect of the area of unoccupied bark on daughters per mother, and the seemingly limited effect of interspecific competition and predation, indicates that less intraspecific competition led to higher reproductive success in unmanaged forests in this study. However, the number of daughters per mother was low and attack density was relatively high in both management types, indicating an important effect of intraspecific competition in each. Also, previous research has suggested that at lower densities of enemies, some of the mortality caused by natural enemies can be replaced by mortality due to intraspecific competition (Schroeder, 2007). Overall, the negative effect of attack density and the positive effect of maternal gallery length on reproductive success is in accordance with previous findings and further highlights the important impact of intraspecific competition on *I. typographus* (Anderbrant et al., 1985; Byers, 1989; Marini et al., 2013; Økland & Berryman, 2004). As a result, more intraspecific competition seems to best explain the lower reproductive success of *I. typographus* in unmanaged forests than managed forests in this study.

However, the usage of pheromones in this study might affect the results for intraspecific competition. As discussed earlier, the baiting effect of pheromones is strong and can attract *I. typographus* from a large radius even when local abundances are very low (Weslien & Schroeder, 1999). Also, the pheromones in this study were left in situ during the summer, which might cause conditions to differ from natural ones. Once a tree's resistance is overcome by *I. typographus*, the beetle will cease production of attractive pheromones and start production of repellant pheromones, limiting the arrival of more beetles of the same species (Raffa et al., 2008). This implies that the attack density could be higher in this study than in natural conditions because pheromone production would cease earlier, and because pheromones might give *I. typographus* a competitive advantage. Also, the exclusion of the five logs that could not be analyzed due to maturation feeding, along with the 17 logs that were reduced in analysis area, might lead to an under/overestimation of reproductive success for some sites. Although the number of samples that were difficult to analyze was relatively similar between management types, and only specific sites stood out overall.

4.5. Limitations and further studies

The relatively small number of study sites is an important limitation of this study. Inclusion of more study sites would lead to higher data resolution and might have provided stronger and more significant results. Also, the low sampling effort for predatory beetles with window traps means that results should be interpreted more carefully. Another important limitation was that the data on emerging *I. typographus* and its associates from the log emergence traps was not available yet. Future studies could benefit from using both data from emergence trap captures and employing multiple window traps per site to enhance data resolution for predators. Additionally, investigating species of predators individually may provide more pertinent insights into their effects on *I. typographus*, as species-specific window trap captures and different habitat requirements among species might lead to more uncertain results when grouping predatory beetles. Future studies investigating bark area occupied by interspecific competitors might also benefit from supplementing results with abundances of emerged and captured individuals in the forest stands. It would also be interesting to compare data from *I. typographus* reproductive success analysis with emerging beetles and with abundance of *I. typographus* captured in the forest stand, to get a more nuanced picture of *I. typographus* population dynamics between the management types.

5. Conclusions – Implications for *Ips typographus* management

The hypothesis (i) that there would be more predatory beetles and interspecific competitors of *I. typographus* in near-natural forests than previously clear-cut forests was not confirmed in this study, as assemblages of both groups were similar between management types. Also, contrary to my hypothesis (i), intraspecific competition tended to be higher in unmanaged forests. However, there was some support for the hypothesis (ii) that there would be lower *I. typographus* reproductive success in unmanaged forests, as reproductive success tended to be higher in managed forests. Intraspecific competition had a strong negative influence on *I. typographus* reproductive success, while predatory beetles and interspecific competitors had no apparent effect. Overall, the findings do not support the theory that forest management practices that promote forest diversity by increasing predator and interspecific competitor populations can help reduce bark beetle outbreak risks. However, questions arise regarding whether sampling effort, species-specific effects, and the usage of *I. typographus* pheromones influenced the estimations of impact and distributions of predatory beetles and competitors in management types. Still, higher intraspecific competition in unmanaged forests seems to best explain the lower reproductive success in unmanaged forests in this study.

This thesis contributes to filling the gap in knowledge on the effect of forest management on *I. typographus* reproductive success and how assemblages of predatory beetles and competitors fit into this picture and into the complex population dynamics of *I. typographus*. Results indicate that preventative measures that promote forest diversity do not increase predatory beetle or interspecific competitor populations or their impact on *I. typographus* reproductive success, and thereby might not mitigate bark beetle outbreak risks. Instead, it appears that the qualities of near-natural forests decrease reproductive success of *I. typographus* through increased intraspecific competition for resources, underscoring the existing consensus that intraspecific competition is one of the main drivers of *I. typographus* population dynamics.

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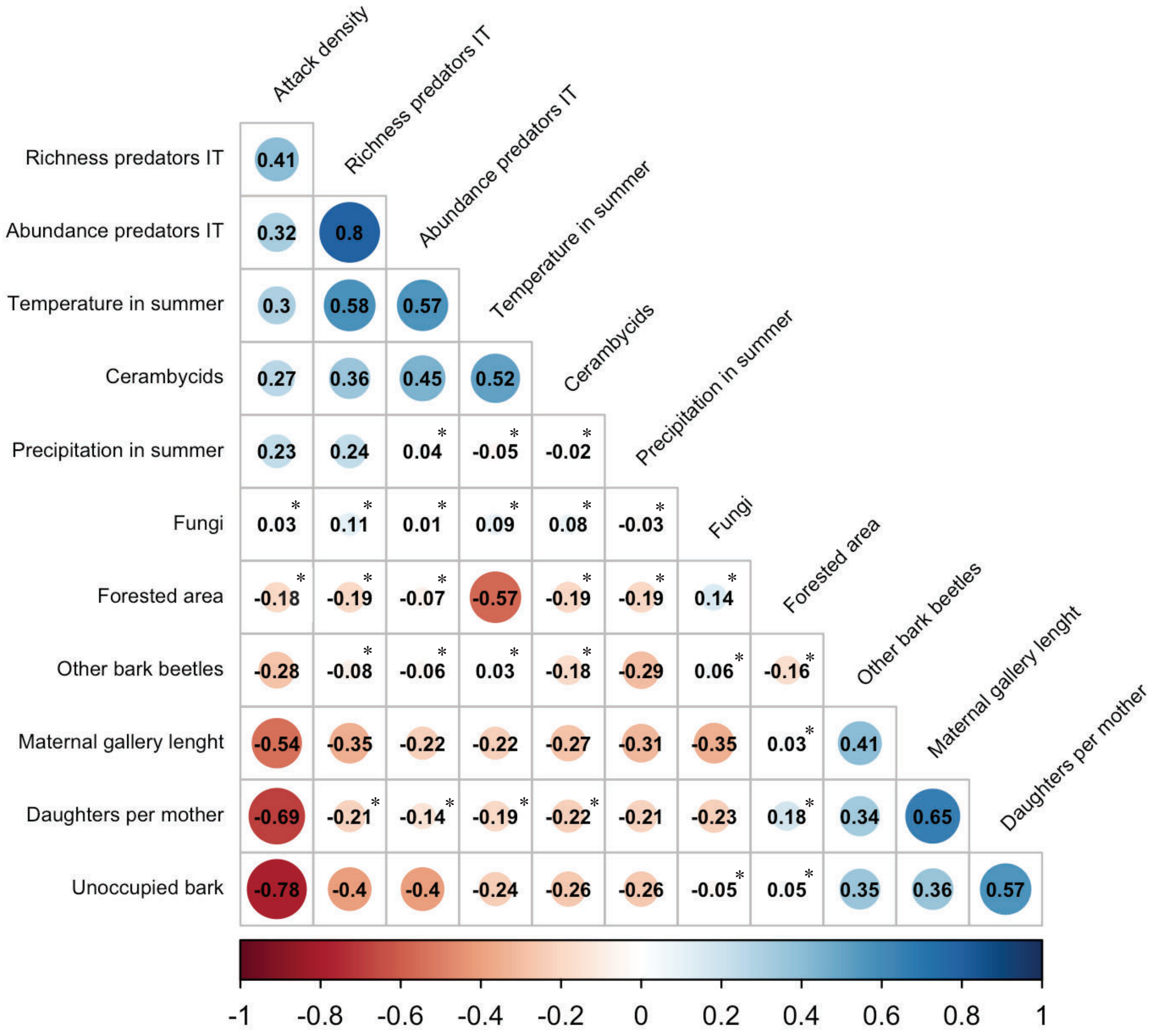
7. Appendix

Appendix A: Correlation matrix



	Attack density	Richness predators IT	Abundance predators IT	Temperature in summer	Cerambycids	Precipitation in summer	Fungi	Forested area	Other bark beetles	Maternal gallery lenght	Daughters per mother
Richness predators IT	0.41										
Abundance predators IT	0.32	0.8									
Temperature in summer	0.3	0.58	0.57								
Cerambycids	0.27	0.36	0.45	0.52							
Precipitation in summer	0.23	0.24	0.04*	-0.05*	-0.02*						
Fungi	0.03*	0.11*	0.01*	0.09*	0.08*	-0.03*					
Forested area	-0.18*	-0.19*	-0.07*	-0.57	-0.19*	-0.19*	0.14*				
Other bark beetles	-0.28	-0.08*	-0.06*	0.03*	-0.18*	-0.29	0.06*	-0.16*			
Maternal gallery lenght	-0.54	-0.35	-0.22	-0.22	-0.27	-0.31	-0.35	0.03*	0.41		
Daughters per mother	-0.69	-0.21*	-0.14*	-0.19*	-0.22*	-0.21	-0.23	0.18*	0.34	0.65	
Unoccupied bark	-0.78	-0.4	-0.4	-0.24	-0.26	-0.26	-0.05*	0.05*	0.35	0.36	0.57

Figure A-1. A correlation matrix showing correlation values for all variables used in this thesis. The values lie on a scale between +1 and -1, where a correlation of zero indicates no association between variables, and the closer to ±1 the stronger the relationship is. The size and color of the circles visualize the strength of the correlation and whether it is positive or negative. Non-significant coefficients are marked with an asterisk.

Appendix B: Principal component analysis

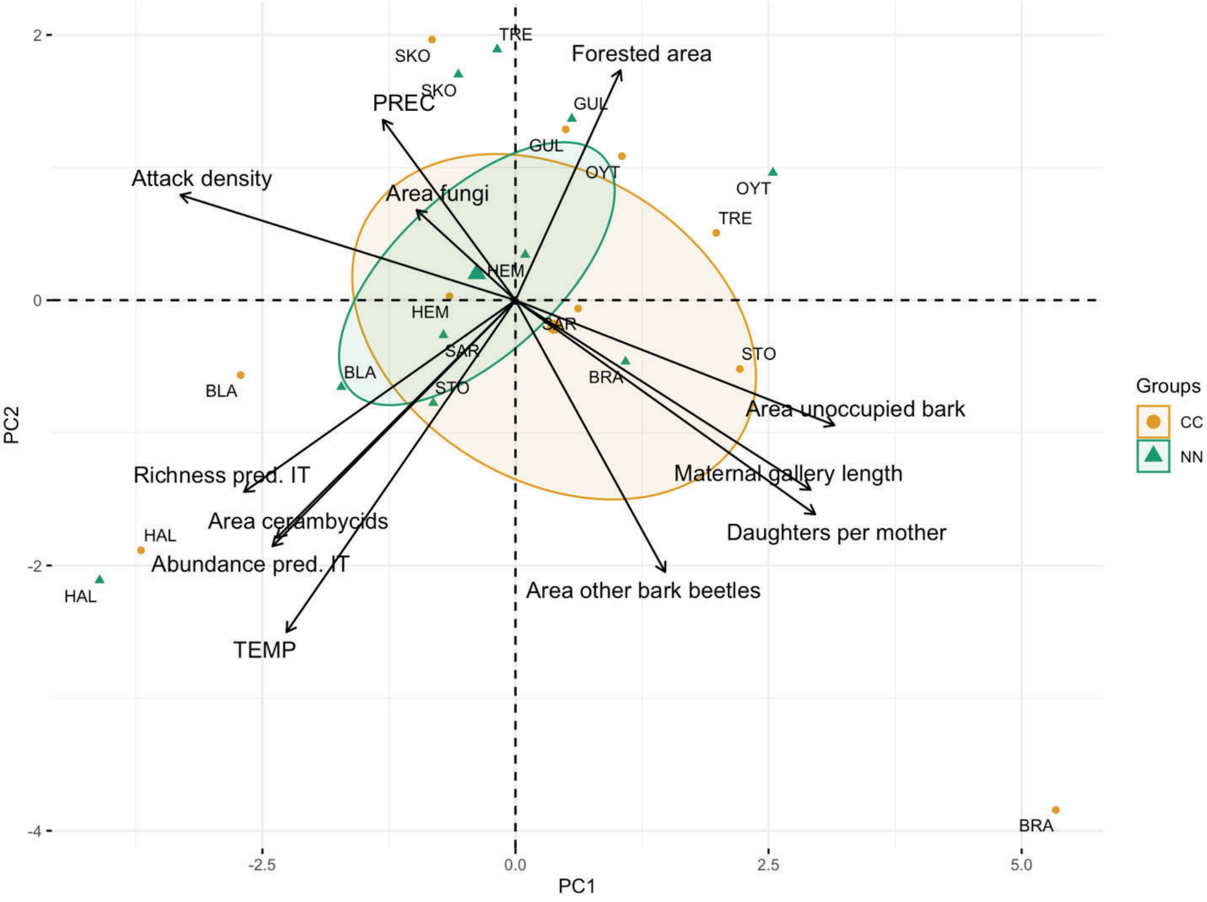


Figure B-1. Principal component analysis of variables used in this thesis. Confidence ellipses are given for each management type (previously clear-cut (CC) and near-natural (NN) forest stands) at the 10 study sites are represented as points. Abbreviations are Mean summer air temperate (TEMP), precipitation in the warmest quarter (PREC) and *Ips typographus* (IT). Site abbreviations are given in figure 1.

Appendix C: Predatory beetles of *Ips typographus*

Table C-1. Overview of abundance of predatory beetles of *Ips typographus* collected from window traps in near-natural (NN) and previously clear-cut (CC) forest management types.

Family	Species	Total individuals captured	Individuals captured in NN	Individuals captured in CC
Staphylinidae	*Nudobius lentus*[1]	6	4	2
	Phloeonomus spp. [1,3]			
	P. planus	1	0	1
	P. punctipennis	5	3	2
	P. lapponicus	6	3	3
	P. pusillus	44	20	24
	Phloeopora Testacea[1,3]	33	18	15
	Placusa spp. [1,2,3]			
	P. tachyporoides	36	20	16
	P. depressa	73	61	12
	P. incompleta	1	0	1
	Quedius plagiatus[1,3]	38	17	21
Tenebrionidae	*Corticeus linearis*[1,3]	2	2	0
Histeridae	*Plegaderus vulneratus*[1,2,3]	44	22	22
Trogossitidae	*Nemozoma elongatum*[1,2]	1	1	0
Cleridae	*Thanasimus formicarius*[1,2,3]	36	24	12
	Thanasimus femoralis[1,2,3]	4	3	1
Nitidulidae	*Epuraea* spp. [1,2,3]			
	E. laeviuscula (not ips?)	7	0	7
	E. pygmaea	119	68	51
	E. marseuli	26	12	14
	E. rufomarginata	16	8	8
	E. silacea	9	4	5
	E. thoracica	1	0	1
	E. placida (detri, fjerne)	2	2	0
	E. boreella	3	2	1
	E. pallescens	4	3	1
	E. melina (detri, fjerne)	5	3	2
	E. aestiva (detri, fjerne)	6	4	2
	E. terminalis	6	3	3
	E. unicolor (not Ips, fjerne)	7	5	2
	E. binotata	22	20	2
	E. muehli	171	109	62

	Glischrochilus hortensis[1]	35	19	16
	Pityophagus ferrugineus[1,2,3]	68	55	13
Monotomidae	*Rhizophagus depressus*[1,2,3]	1	1	0
	Rhizophagus ferrugineus[1,2,3]	121	86	35
	Rhizophagus cribratus[1,3]	4	3	1
	Rhizophagus dispar[1,3]	49	23	26
Laemophloeidae	*Cryptolestes abietis*[2]	3	0	3
Salpingidae	*Rabocerus foveolatus*[1]	2	0	2
	Salpingus planirostris[1,3]	7	4	3
	Salpingus ruficollis[1,3]	24	9	15
	Sphaeriestes castaneus[1,3]	1	0	1

The sources used for the predator species selection are specified in the table: [1](Kenis et al., 2004) ,[2](Bakke & Kvamme, 1993), [3](Wegensteiner et al., 2015).

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