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Original Article



# Influence of felling residue management on bark beetles and other insect diversity

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## Abstract

Bark beetle outbreaks have caused large-scale tree mortality and damage in recent decades, primarily following an increase in large-scale forest disturbances induced by climate change. After tree logging operations, leftover branches are traditionally piled to make the potential brood material less suitable for bark beetles, thereby lowering the risk of subsequent attacks on surrounding trees. On the other hand, the residues could prove valuable to biodiversity by supplementing important habitat, given the apparent decline in deadwood in European forests and its associated saproxylic fauna. Our aim was to identify the most successful method of logging residue management for both bark beetle management and biodiversity. We focussed on Norway spruce felling residues, their associated bark beetle pests and saproxylic insect orders, beetle families, and Cerambycidae species. We prepared four treatments: (i) logging residues in piles, (ii) scattered logging residues, (iii) logging residues removed, and (iv) a control plot with no felling activity. Five plots per treatment were established at each site. In total, three sites were selected: one at a high elevation and two at lower elevations in different parts of Slovenia. The catch was counted to the order level, the attracted beetles were identified to the family level, and Cerambycidae and Scolytinae to the species level. We found that the treatments with residues attracted the highest diversity of insect orders and the most beetles across different families, including Cerambycidae. Furthermore, we found that the species composition differed between control and residue treatments, although no difference was observed in species richness. More bark beetles and a higher number of bark beetle species were attracted to both piled and scattered residues. Thick branches were more frequently attacked in scattered residues. There was no difference in the number of attacked trees (within a plot) one month after treatment. Hence, leaving logging residues in the forest could represent an interesting compromise between pest management and biodiversity conservation. Conflicting aims, such as increasing biodiversity or controlling bark beetles, should be carefully considered in the management decisions.

*Keywords:* Scolytinae; forest management; Cerambycidae; Norway spruce; multipurpose forest management

## Introduction

Forests provide multiple ecosystem services (FAO 2020), including provisioning services such as wood production, regulating services such as protection against landslides and avalanches, cultural services such as recreation, and supporting services through forest biodiversity (Jenkins and Schaap 2018). These services often overlap, resulting in tensions when management priorities and measures need to be defined (Maes et al. 2021). Over the last decade, the effects of climate change on forests have become more pronounced, leading to large-scale disturbances and outbreaks of pests and diseases with negative consequences for wood production (Seidl et al. 2017, Hartmann et al. 2025). Consequently, pest management measures such as sanitation felling are frequently applied to reduce bark beetle populations, albeit with potential negative impacts on biodiversity (Hlásny et al. 2019, Hlásny et al. 2021). Meanwhile, there has been a steady decline in biodiversity in forests (Seibold et al. 2019). Therefore, it is crucial to find solutions that are beneficial for multiple forestry objectives, including both wood production and biodiversity conservation (e.g. Gazzea et al. 2024).

Forest pest management and conservation management are integral to maintaining the forest functions of wood production and biodiversity. However, these two management approaches often require opposing measures (Niemelä et al. 2005, Mikusiński et al. 2018, Blicharska et al. 2020). Due to the rising number of outbreaks caused by emerging and invasive pests, the urgency of action during these outbreaks usually results in reactive management. This includes destructive measures such as pesticide use or large-scale sanitation cutting and salvage logging (Thorn et al. 2018, Fettig et al. 2021, Hlásny et al. 2021, Boukouvala et al. 2022, Sweeney et al. 2023). These interventions can significantly impact forest biodiversity (Thorn et al. 2018, Hlásny et al. 2019). In contrast, proactive silvicultural measures can increase forest resistance to outbreaks (Waring and Bucholz 2023). For instance, high tree species diversity reduces the likelihood of damage caused by bark beetles and defoliators due to the lower abundance of host plants (Jactel et al. 2017, de Groot et al. 2023, Gazzea et al.

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2024) while also increasing biodiversity. Currently, most studies on the main effects of forest management focus on large spatial scales, although local-scale management also plays an important role in both nature conservation and pest management (Thorn et al. 2016, Hagge et al. 2019). It is important for forestry to apply measures that both benefit biodiversity and reduce the risk of outbreaks (Hagge et al. 2019, Gazzea et al. 2024).

One proactive measure that can impact both bark beetle pest management and biodiversity conservation is the management of leftover residues after logging. Leftover branches serve as brood material for bark beetles and other forest pests and therefore pose a risk of further outbreaks to surrounding trees (Bouget and Duelli 2004, Kacprzyk 2012). At the same time, these branches also form valuable deadwood habitat for saproxylic species, which may be of conservation importance given the widespread decline of deadwood in European forests (Nittérus et al. 2004, Johansson et al. 2007, Ranius et al. 2018). Currently, there are several approaches in forestry for dealing with logging residues. One approach involves piling the branches, with thicker branches covered by thinner branches; another involves scattering branches across the forest floor; and a third involves removing all branches from the forest (Foit 2015). The first two methods retain deadwood in the forest, whereas the third does not. Although there have been several studies examining the impact of residues on either pest management or biodiversity conservation (Kacprzyk 2012, Lassauce et al. 2012, Thorn et al. 2014), the combined effects of these two outcomes have not been studied.

In this study, we tested the effects of logging residue management on saproxylic insects. We used beetles (Insecta: Coleoptera) as an indicator group, due to their high relevance both for biodiversity conservation and pest management. Beetles are also an important indicator group for evaluating the effects of natural or anthropogenic disturbances, such as the impact of forest management measures on biodiversity, because of their high species diversity and specific habitat and environmental requirements (Ghannem et al. 2018). Additionally, beetle families exhibit a range of ecological roles important for forest production and pest dynamics (Fountain-Jones et al. 2015, Gossner et al. 2015), including predators, herbivores, decomposers, and species occupying more rare and specific saproxylic niches (Fountain-Jones et al. 2015, Gossner et al. 2015). Cerambycidae, in particular, are commonly used as indicators due to their multi-year development cycles, which make them vulnerable to forestry management practices such as the reduction of deadwood (Gibb et al. 2006, Lachat et al. 2012, Parisi et al. 2018). Many saproxylic species are now endangered due to their decline over the last century (Cálix et al. 2018).

Species that cause economic damage in forestry, and are therefore important for pest management, are mainly found within the bark beetle subfamily (Curculionidae: Scolytinae). Among these, the European spruce bark beetle (*Ips typographus* L.) is particularly notorious for its capacity to cause large-scale outbreaks and tree mortality (Wermelinger 2004, Vega and Hofstetter 2015, Hlásny et al. 2021), along with other species such as *Pityogenes chalcographus* (Kacprzyk 2012). Because of their significance as pests, Scolytinae were used in this study to estimate the effect of treatments on pest management.

The aim of this study was to investigate the effects of logging residue management on biodiversity conservation and pest management across different locations and elevations. To assess the impacts on biodiversity, we examined differences in the abundance of insect orders, beetle families, and the abundance and species composition of cerambycid beetles. To investigate the impacts on pest management, we compared the abundance of known bark beetle species between treatments. In addition, we monitored the number of bark beetle attacks on logging residues of different size classes within the treatment plots, as well as attacks on nearby trees. Finally, we explored whether the effects of residue management varied across locations and elevations.

# Materials and methods

## Area description

Slovenia is a relatively small Central European country with a geographically diverse landscape. It comprises the Alpine, Pre-alpine, Dinaric, Pre-Dinaric, Sub-Pannonian, and Sub-Mediterranean biogeographical regions, each with its own climatic conditions and forest habitat types (Zupančič et al. 1987). With 58% forest cover, Slovenia is one of the most forested countries in Europe. The most common tree species are European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.), which represent 33% and 30% of the total wood stock, respectively (ZGS 2023). Norway spruce occurs naturally only at higher elevations, but in the past, it was also planted outside of its natural range, often forming monoculture stands (Bončina et al. 2017). This has contributed to an increase in bark beetle outbreaks (de Groot et al. 2019). Additionally, damage to Slovenian forests caused by bark beetles has recently increased due to the impacts of climate change and related natural disasters.

The research was conducted in three areas in Slovenia: Jezersko, Šipek, and Kočevje. Jezersko is located in the Alpine biogeographical region, with research plots at altitudes of 1100–1290 m a.s.l. The main forest associations in these plots are *Homogyno sylvestris-Fagetum*, *Ranunculo platanifolii-Fagetum,* and *Luzulo-Fagetum sylvaticae* (Bončina et al. 2021). The Šipek area is in the Pre-alpine biogeographical region, where research plots dominated by *Blechno-Fagetum* and *Galio rotundifolii-Abietetum* forest associations were located at 740–900 m a.s.l. In Kočevje, the plots were located in the Dinaric and Pre-Dinaric biogeographical regions, with *Omphalodo-Fagetum* and *Hacquetio-Fagerum* forest associations at altitudes between 650 and 980 m a.s.l. All plots were located in mature forest stands dominated by Norway spruce (at least 70% of the total wood stock). In Šipek and Kočevje, European beech and silver fir (*Abies alba* Mill.) were the most abundant species, while in Jezersko, European beech and European larch (*Larix decidua* Mill.) were the most prevalent (ZGS 2024b).

## Experimental design

For the experiment, we established four treatments: (i) all residues removed, (ii) residues in piles, (iii) scattered residues, and (iv) a control where no logging took place. All areas had a similar stand structure and tree species composition, with 70% or more Norway spruce and a presence of populations of *I. typographus* and *P. chalcographus* in the endemic phase (Ogris 2022; ZGS 2024a). In the first three treatments, 20–30 $m^3$ of Norway spruce trees were removed, and the felling residues were left in the shade of tree crowns. For each plot, the volume of deadwood was measured in three $1 \times 1$ m subplots within a radius of 5 m of the plot centre and extrapolated to the entire plot area. A detailed description is provided in Annex 1. Furthermore, air temperature and relative humidity were measured at 20 cm and 2 m above the ground using a GM1365 automatic data logger (BENETECH), which includes an air humidity sensor (+ −2% accuracy between 20% and 80% RH; + −4% above 80%) and a temperature sensor (+ −0.3°C accuracy between 10°C and 60°C). Solar radiation shelters with data logger holders were manufactured at the Slovenian Forestry Institute and installed at each plot. In treatments with residues in piles or scattered, the lower logger was positioned within the residue at 20 cm above ground level, while the other data logger was placed at 2 m at all plots. Data were recorded every 10 min from deployment until trap collection. Each treatment per site had one replicate, totalling 12 logger pairs.

In the treatment where all residues were removed, only Norway spruce stumps remained. For the treatment with scattered residues, the residues were left without any specific arrangement. For the treatment with piled residues, the residues were arranged into small piles (average height = 1 m, average diameter = 2.02 m) following Slovenia Forest Service guidelines, with thinner branches on the outside and thicker ones inside. Control plots were located nearby, with similar topography and stand structure. No logging took place in the control plots during or in the year prior to the study.

There were five replicates per treatment across the three sites, totalling 15 plots per treatment and 60 plots in total. Each plot was 0.5 ha in size, and plots were spaced at least 200 m apart (average distance per site = 317 m).

## Sampling protocol

The effectiveness of each residue management method was assessed using three approaches. First, the presence and abundance of insects in each treatment were examined using passive traps. Second, we sampled felling residue branches from plots where residues were placed in piles or scattered. Third, bark beetle attacks on neighbouring trees around the traps were assessed through a survey.

After felling was completed and residues were managed according to the treatment, we assessed the presence and abundance of bark beetles by placing one cross-vane trap (deflector plate size: 80 × 40 cm, colour: black; distributor: Witasek) without an attractant in the forest stand near each treatment. At each of the three locations, 20 traps were set up (five repetitions of four treatments spaced at least 200 m apart, totalling 60 traps) for a 1-month period from the middle of July to August 2023 for the Kočevje and Šipek sites and from the end of June to the end of July in Jezersko. In plots with piled residues, the trap was placed on the south side, no >2 m from the treatment. In the treatment where residues were scattered, the trap was positioned in the middle of the dispersed branches. In the treatment where residues were removed, traps were positioned in the middle of the felling area, while in control plots, they were placed in the middle of the forest stand.

Traps were installed as close to the ground as possible and placed in an open area, avoiding thick vegetation or larger undergrowth that could obstruct them. The cross-vane traps were assembled on site and secured to two poles hammered into the ground with connecting tape. Once set, each trap was filled with 300 ml of 60% propylene glycol diluted with 150 ml of water (2:1 ratio) as a preservative. We sampled for 1 month, which is generally sufficient to collect a representative beetle sample without attractants. Because the sites were located at two different altitudes, trapping took place during two distinct phenological periods, allowing us to capture both early- and late-occurring species. The sampled beetles were those attracted to the treatments but not necessarily utilizing the residues. After 1 month, the catch was collected and taken to the Laboratory of Forest Protection for identification, which was conducted using an Olympus SZX12 stereo microscope. Insects were sorted to the order and beetle family levels, and Scolytinae and Cerambycidae were identified to the species level using standard identification keys (Grüne 1979, Bense 1995, Pfeffer 1995, Freude et al. 1999, Hurka 2005).

In plots with piled or scattered residues, two thick branches (diameter > 10 cm) and two thin branches (diameter < 2 cm), each ~50 cm in length, were randomly sampled to investigate bark beetle attacks. Large and small branches were collected 1 month after the treatment was applied. However, the small branches were initially unsuitable and were resampled at the end of October 2023 (18–26 October). Large branches were taken from the interior of piles, while small branches were collected from the top layer. For scattered residues, all branches were collected randomly from within the treatment. In total, four samples were collected per individual plot. The samples were placed in plastic bags and transported to the Laboratory of Forest Protection on the same day. There, they were examined for the number of small (< 1 mm) and large (>2 mm) entrance holes per branch, and hole density per square centimetre of bark surface was calculated. When possible, beetles found inside the branches were identified to the species level.

Following the 1-month trapping period, a visual survey was also conducted within each plot to assess attacks on Norway spruce by *I. typographus* and *P. chalcographus* within a distance of two average tree heights (~40 m) around each trap. All trees were healthy before the experiment. Up to 10 mature (height > 20 m) and up to 10 saplings (height < 1 m) closest to each trap were assessed for signs of infestation. The health status (alive or dead) of each tree was recorded, and any evidence of bark beetle attack was noted. This included the presence of entry holes, sawdust, or resin on the trunk; yellowing crowns; fallen green needles at the base; and any signs of mechanical damage due to logging.

## Analysis

Two types of analyses were performed: univariate and multivariate. The univariate analysis assessed differences between treatments, sites, or their interactions across different orders, families, or species. Initially, data were checked for outliers and skewness (Zuur et al. 2010). A general linear model (GLM) was used with a Poisson error distribution. For significantly skewed data, a GLM with a negative binomial error distribution was used. Due to excess zeros in species data and the data of Trogossitidae, a zero-inflated Poisson model from the 'pscl' package was used (Zeileis et al. 2008).

The species composition of Cerambycidae and Scolytinae, including the presence and absence of species caught in the traps, was analysed for treatment, location, and their interactions using a Permutational analysis of variance (PerMANOVA) with the adonis function in the 'vegan' package (Oksanen et al. 2013) with 999 permutations. When one of the independent variables was significant, a pairwise PerMANOVA was conducted using the 'pairwiseAdonis' package (Martinez Arbizu 2017). To visualize the data, nonmetric dimensional scaling (NMDS), a distance-based ordination technique, was carried out using a Bray–Curtis index with 999 permutations. This ordination method illustrates the relative distance between traps based on differences in species composition. We tested whether there were significant differences between plots across treatments or locations. Furthermore, indicator species for Cerambicidae and Scolytinae were identified for each treatment with the 'indicspecies' package (De Caceres and Legendre 2009). Based on these results, separate univariate analyses were conducted for the identified indicator species.

For the branch data, the number of holes was normalized to the surface area of the bark on the branches. A GLM with a Gaussian distribution was used to assess the differences

Table 1. Differences in deadwood volume, temperature, and humidity between different treatments.

| | No logging | | | Residues removed | | | Residues in piles | | | Scattered residues | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Avg | Min | Max | Avg | Min | Max | Avg | Min | Max | Avg | Min | Max |
| Deadwood (m^2) | 0.0850 | 0.0194 | 0.2263 | 0.1150 | 0.0195 | 0.2334 | 10.482 | 0.1316 | 39.152 | 0.4026 | 0.1545 | 11.357 |
| Temp (°C) FLOOR | 16.8 | 7.7 | 31.7 | 16.7 | 8 | 34 | 15.5 | 6.8 | 24.3 | 16.1 | 7.6 | 34.6 |
| Temp (°C) AIR | 17.0 | 7.5 | 30.3 | 17.0 | 8.4 | 30.7 | 17.0 | 7.6 | 30.1 | 16.6 | 7.6 | 29.4 |
| Humidity (%) FLOOR | 90.3 | 49.8 | 100 | 90.1 | 41.1 | 100 | 99.1 | 72.6 | 100 | 95.3 | 45.3 | 100 |
| Humidity (%) AIR | 86.1 | 46 | 100 | 85.9 | 42.2 | 100 | 85.1 | 44 | 100 | 87.6 | 46.7 | 100 |

between treatments with residues, locations, and their interactions.

Tree damage due to bark beetles was assessed by testing the proportion of attacked adult and young trees across different treatments and locations. A GLM with a binomial error distribution was used. The dependent variable was the proportion of attacked trees or saplings, and the model was weighted by the total number of trees assessed.

All analyses were conducted using the statistical program R (R Core Team 2022).

# Results

## Site conditions

For plots where residues were removed, the average deadwood volume within a 5 m radius from the centre of the plot was 0.12 $m^3$ (min = 0.02, max = 0.23) (Table 1). During the trapping period, humidity and temperature were measured. On average, ground-level temperatures were lower than air temperatures, while humidity at the ground level was higher than in the air (Table 1). In plots with scattered residues, the average deadwood volume was 0.4 $m^3$ (min = 0.15, max = 1.14) within a 5 m radius around the plot centre (Table 1). The temperature inside the residues was lower and had fewer extremes compared to the air temperature. Humidity inside the residues averaged 95.3%, which was higher than the air humidity (87.6%) and showed less fluctuation (Table 1). Plots with residues in piles had an average deadwood volume of 1.05 $m^3$ (min = 0.12, max = 3.92) within a 5 m radius from the centre of the plot (Table 1). Temperatures in the piles were lower than the air temperature and also lower than those recorded in the scattered residues (Table 1). Humidity in the piles was also higher than in the air (Table 1). In the control plots, the average deadwood volume was 0.09 $m^3$ (min = 0.02, max = 0.23), and the ground-level temperature and humidity values were similar to those measured in the air (Table 1). Each plot had a radius of 5 m, which did not cover the full extent of the scattered residues. Therefore, only a portion of the total deadwood volume was included in the measurement for that treatment. In contrast, the piles treatment always included a pile within the plot, which contributed to the higher recorded deadwood volume.

## Biodiversity and residue management

During the survey, a total of 4989 specimens across 18 orders were caught in traps. Coleoptera was the most dominant order, with 3159 individuals, followed by Diptera ($n$ = 923), Hymenoptera ($n$ = 235), and Hemiptera ($n$ = 204) (see Annex 2, Table S1). Coleoptera numbers were highest in the piles and scattered residue treatments, followed by the no logging and residue-removed treatments (Deviance Resid. = 67.83, df = 3, $P < .001$). Several families with the highest abundances ($n$ > 100 individuals) exhibited similar responses to the treatments (see Annex 2, Table S1, Annex 3): Cleridae, Curculionidae, Elateridae, Leiodidae, Staphylinidae, and Trogossitidae all displayed significantly higher abundances in plots where residues were left, either in piles or scattered, and the lowest in plots with no logging or where residues were removed (Fig. 1). Interestingly, plots with residues removed and residues in piles had significantly higher numbers of Cerambycidae compared to the no logging plots, while the number of specimens in the scattered residue treatment did not differ significantly from either of those two (Fig. 1). For Mordellidae, no significant differences were observed between any of the treatments (Fig. 1). Figure 1 provides more detail on the statistical significance between treatments.

The species composition of Cerambycidae was also significantly affected by treatment (df = 3, $R^2$ = 0.097, $F$ = 2.106, $P$ = .018) and location (df = 2, $R^2$ = 0.227, $F$ = 7.403, $P$ = .001) (Fig. 2, Table 2). Plots in the no logging treatment and those with either residues removed or residues in piles had significantly different species compositions (Table 2). Other treatment combinations showed no significant differences, indicating similar species compositions across these groups (Table 2). Regarding location, the plots at Šipek and Kočevje had similar species compositions, while both differed significantly from the plots at Jezersko (Table 2). There were no interactions observed between location and treatment for the species composition of Cerambycidae. The number of Cerambycidae species did not differ significantly between treatments (Deviance Resid. = 5.34, df = 3, $P$ = .15), with average values per treatment as follows: no logging = 0.87, residues removed = 1.4, residues in piles = 1.67, residues scattered = 1.73. Species richness did not differ between locations (Deviance Resid. = 12.2207, df = 2, $P$ = .002), with Jezersko showing higher species richness compared to Kočevje and Šipek (Annex 2, Table S4).

No Cerambycid species were indicative for any of the treatments. However, *Tetropium castaneum*, *T. fuscum*, *T. gabrieli*, and *Monochamus sartor* were more commonly found in Jezersko, while *Corymbia rubra* was more commonly found in Kočevje and Šipek (Table 3).

## Bark beetles and residue management

The abundance of Scolytinae in traps was highest in the scattered residues treatment and was significantly different from the residues removed treatment. At the same time, the scattered residues treatment was not significantly different from the residues in piles treatment and the residues removed treatment. The lowest abundance of Scolytinae was found in the no logging treatment (Fig. 3). The number of species of bark beetles followed a similar pattern to total abundance, with significant differences among treatments (Deviance Resid. = 65.041, df = 3, $P$ = 4.915e-14), but not among locations (Deviance Resid. = 4.222, df = 2, $P$ = .1211). The scattered residues and residues in piles treatments had the

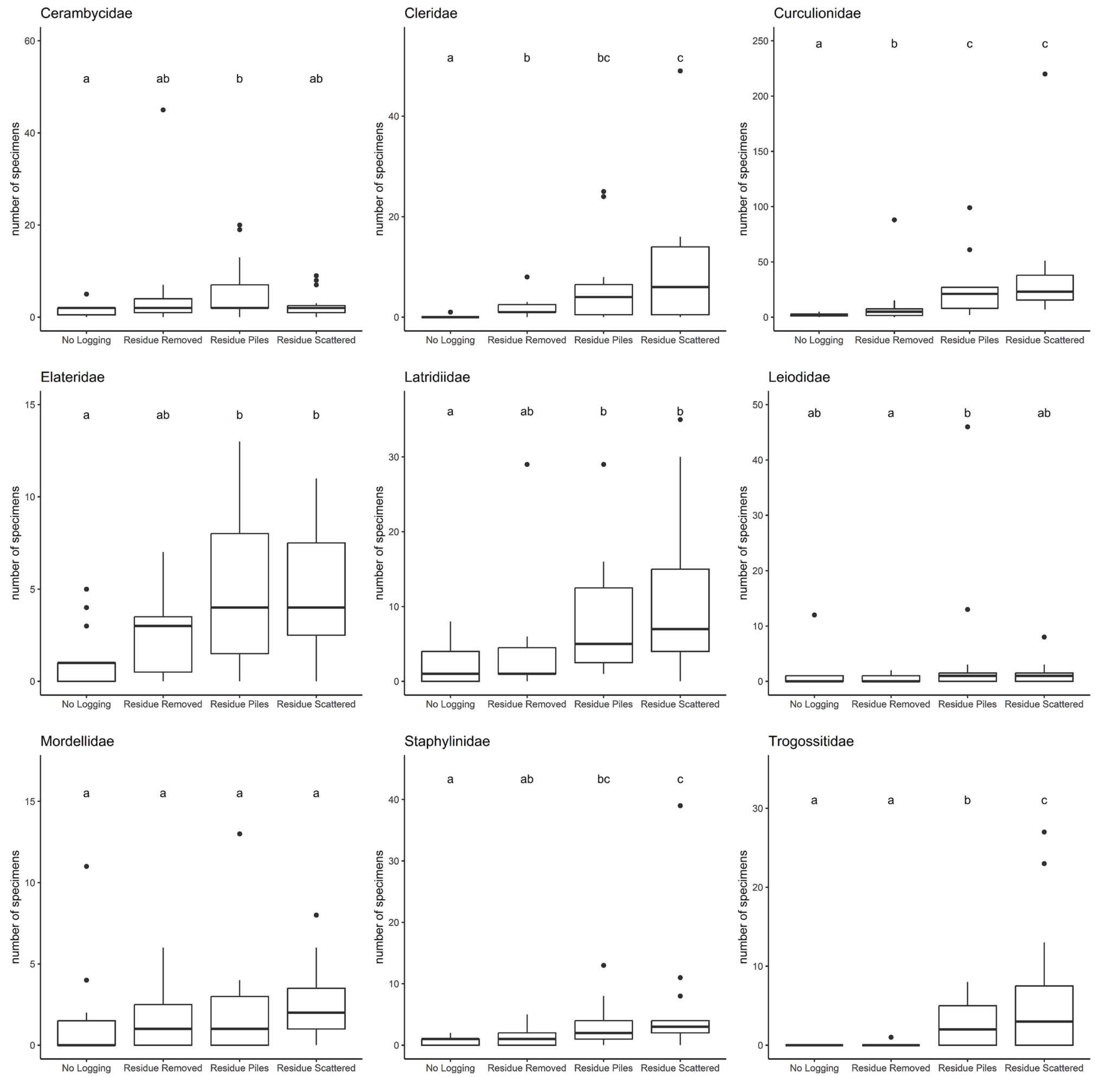


**Figure 1.** Influence of treatment on the total number of individuals per trap for Coleoptera families: Cerambycidae (*N* = 226), Cleridae (*N* = 258), Curculionidae (*N* = 1140), Elateridae (*N* = 202), Latridiidae (*N* = 376), Leiodidae (*N* = 113), Mordellidae (*N* = 121), Staphylinidae (*N* = 168), and Trogossitidae (*N* = 138). Letters indicate significantly different groups ($P < .05$). Statistical tests are detailed in Annex 3. Note: Y-axis scales differ between panels.

highest species numbers, with no significant differences between them (4.93 and 3.6 species on average, respectively). The residues removed treatment had significantly fewer species (average = 2 species), while the no logging treatment had the fewest (average = 0.6 species) (Annex 2, Table S3).

The species composition of Scolytinae was significantly influenced by treatment (df = 3, $R^2$ = 0.191, $F$ = 3.841, $P$ = .001) and location (df = 2, $R^2$ = 0.111, $F$ = 3.322, $P$ = .001) (Fig. 2). Species composition was similar between the residues in piles and scattered residues treatments (Table 2). Significant differences were observed between most other treatment combinations. Regarding location, Šipek and Kočevje had similar Scolytinae compositions, while Jezersko differed significantly from both (Table 2).

*Pityophthorus pityographus* was most indicative of the scattered residues treatment (Table 3). *Polygraphus poligraphus* and *I. typographus* were indicative of both the residues in piles and scattered residues treatments. *Pityogenes chalcographus* was indicative of the residues in piles, scattered residues, and residues removed treatments. *Hylastes cunicularius* was most commonly found in Jezersko, while *Dryocoetes autographus* was most indicative of the Jezersko and Šipek locations. *Hylastes cunicularius* was significantly more abundant in the residues removed and residues in piles treatments compared to the scattered residues and no logging treatments (Fig. 4). The abundance of *I. typographus* was significantly higher in the scattered residues and residues in piles treatments compared to the residues removed and no logging treatments (Fig. 4). The abundance of *P. chalcographus* was also divided into three significantly different groups, with the highest abundance in the scattered residues treatment, lowest in the residues removed and no logging treatments, and intermediate

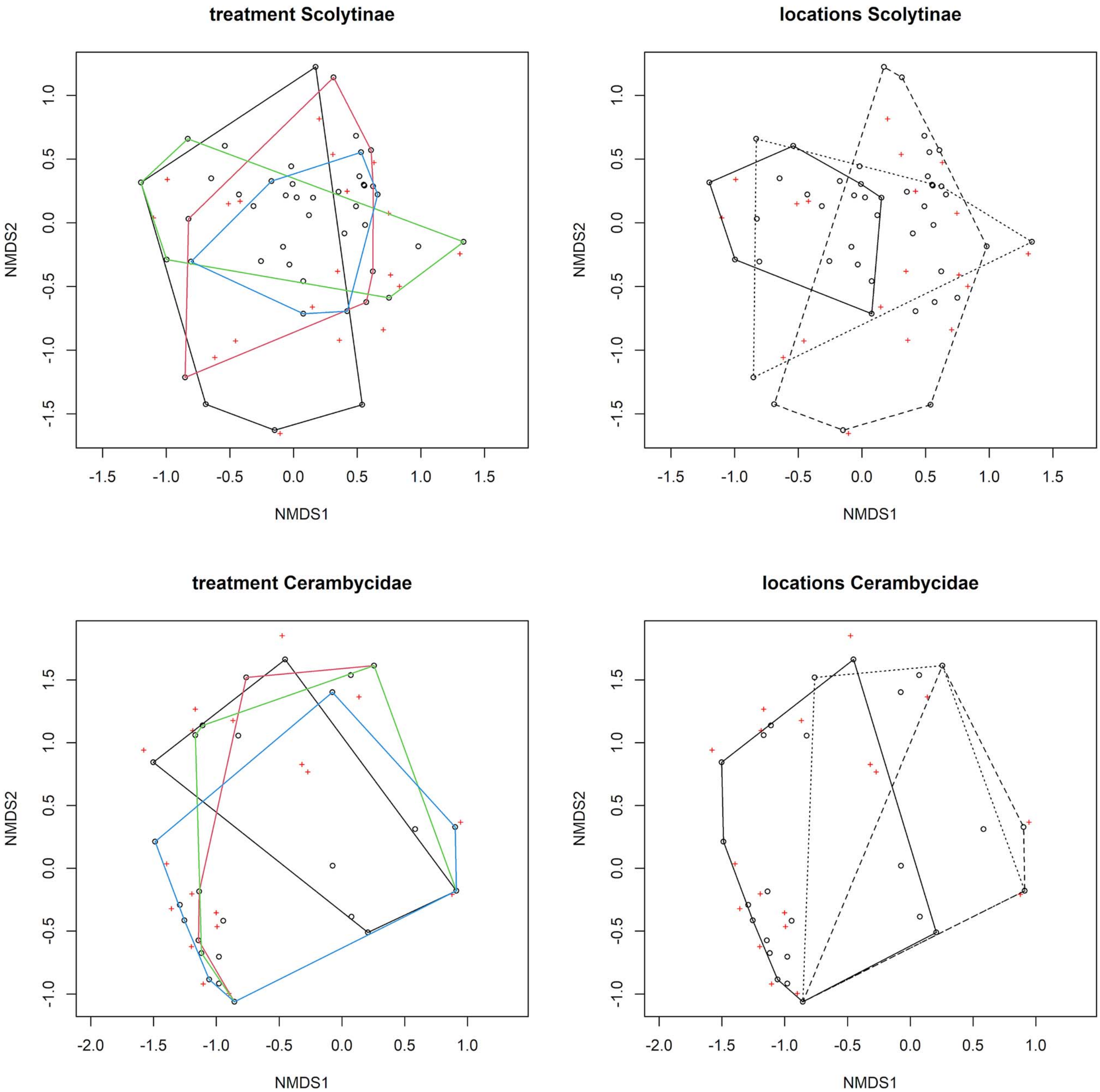


**Figure 2.** NMDS plots of the species composition of Scolytinae and Cerambycidae, showing differences between locations and residue management treatments. Treatments are indicated as follows: black line for no logging treatment, green line for residues removed, red line for scattered residues, and blue line for residues in piles. Locations: continuous line for Jezersko, dashed line for Kočevje, and stippled line for Šipek. Circles show the plots, and crosses show the species.

in the residues in piles and residues removed treatments (Fig. 4). However, the residues removed treatment was not significantly different from the no logging and residues in piles treatments. Similarly, the abundance of *P. poligraphus* also showed three significantly different groups, with the highest abundance in the scattered residues treatment, intermediate abundance in the residues in piles treatment, and the lowest abundance in the no logging and residues removed treatments. For both *D. autographus* and *P. pityographus*, there were no significant differences in abundance between the treatments.

Branch analysis showed that thicker branches in the scattered residues treatment had more large holes than those in the residues in piles treatment (Fig. 5A). For small holes in thicker branches, there was no difference between the residues in piles and scattered residues treatments (Fig. 5B). The abundance of small holes in thin branches were location dependent: there was no difference in Jezersko, while in Kočevje and Šipek, there were more small holes in scattered residues compared to residues in piles, although compared to Jezersko, this was not significant for Kočevje ($t = 1.461$; $P = .15$), it was for Šipek ($t = 2.35$; $P = .02$) (Fig. 5C). Large holes were associated with *I. typographus* and *D. autographus*, while small holes were associated with *P. chalcographus*, *P. pityographus,* and *P. poligraphus*.

On average, 5.38 adult trees and 1.42 saplings per 10 trees per plot showed signs of bark beetle attack. One month after the treatment started, there were no differences in attack rates between treatments for either saplings or mature trees (attacked saplings: Likelihood ratio (LR) $\chi^2 = 3.09$, $df = 3$, $P = .377$; attacked

**Table 2.** Statistics showing differences in the species composition of Scolytinae and Cerambycidae across treatments and locations and their interactions using a PerMANOVA.

| Taxa | | Combinations | df | $R^2$ | F | P |
|---|---|---|---|---|---|---|
| Scolytinae | Treatment | **Residues in piles** vs scattered residues | 1 | 0.022 | 0.630 | .778 |
| | | **Residues in piles vs residues removed** | **1** | **0.128** | **3.379** | **.001** |
| | | **Residues in piles vs no logging** | **1** | **0.177** | **4.534** | **.001** |
| | | **Scattered residues vs residues removed** | **1** | **0.176** | **4.911** | **.001** |
| | | **Scattered residues vs no logging** | **1** | **0.217** | **5.848** | **.001** |
| | | **Residues removed vs no logging** | **1** | **0.101** | **1.8011** | **.049** |
| | Location | Šipek and Kočevje | 1 | 0.045 | 1.285 | .179 |
| | | **Jezersko vs Kočevje** | **1** | **0.14** | **5.32** | **.001** |
| | | **Jezersko vs Šipek** | **1** | **0.067** | **2.15** | **.05** |
| Cerambycidae | Treatment | **Residues in piles vs no logging** | **1** | **0.122** | **3.055** | **.019** |
| | | **Residues removed vs no logging** | **1** | **0.115** | **2.727** | **.023** |
| | | Residues in piles vs scattered residues | 1 | 0.015 | 0.369 | .916 |
| | | Residues in piles vs residues removed | 1 | 0.042 | 1.008 | .428 |
| | | Scattered residues vs residues removed | 1 | 0.046 | 1.154 | .293 |
| | | Scattered residues vs no logging | 1 | 0.095 | 2.427 | .06 |
| | Location | Kočevje vs Šipek | 1 | 0. 034 | 1.046 | .364 |
| | | Jezersko vs Kočevje | 1 | 0.284 | 12.673 | .001 |
| | | Jezersko vs Šipek | 1 | 0.194 | 7.681 | .001 |

**Table 3.** Indicator species analysis for the taxonomic groups Cerambycidae and Scolytinae across different locations and treatments by assessing the strength and statistical significance of the relationship between species abundance and groups of site with the package 'indicspecies' using a permutation test.

| Group | Family | Treatment/Location | Species | stat | P-value |
|---|---|---|---|---|---|
| Location | Cerambycidae | Jezersko | *Tetropium castaneum* | 0.789 | .001 |
| | | | *Tetropium fuscum* | 0.527 | .009 |
| | | | *Monochamus sartor* | 0.489 | .032 |
| | | | *Tetropium gabrieli* | 0.471 | .029 |
| | | Kočevje + Šipek | *Corymbia rubra* | 0.876 | .001 |
| | Scolytinae | Jezersko | *Hylastes cunicularius* | 0.903 | .001 |
| | | Jezersko + Šipek | *Dryocoetes autographus* | 0.661 | .009 |
| Treatment | Scolytinae | Scattered residues | *Pityophthorus pityographus* | 0.532 | .043 |
| | | Residues in piles + scattered residues | *Polygraphus poligraphus* | 0.938 | .001 |
| | | | *Ips typographus* | 0.871 | .001 |
| | | Residues in piles + residues removed + scattered residues | *Pityogenes chalcographus* | 0.742 | .028 |

mature trees: LR $\chi^2 = 2.38$, df = 3, $P = .50$). However, there was a difference in mature tree attack rates between locations (attacked mature trees: LR $\chi^2 = 6.024$, df = 2, $P = .049$), while no difference was observed for saplings (attacked saplings: LR $\chi^2 = 1.002$, df = 2, $P = .605$).

## Discussion

We found a higher abundance of beetles in plots with increased deadwood due to leftover felling residues, both in plots where residues were left scattered across the forest floor and where residues were placed in piles. Higher abundances were recorded across a wide range of beetle families belonging to different feeding guilds, including Cleridae, Curculionidae (including Scolytinae), Elateridae, Leiodidae, Staphylinidae, Trogossitidae, and Cerambycidae. Although Cerambycidae are often used as an indicator group, and their numbers were higher in plots with residues, no species was found to be an indicator for a specific treatment. For the bark beetles, which include many economically important pest species, we generally found higher abundances in plots with residues, both in the residues in piles and scattered treatments. Notably, the more economically problematic bark beetles, such as *I. typographus*, showed increased abundance when residues were left in the forest. However, the number of attacks by smaller bark beetles on logging residues depended on location. In Jezersko, residues in the scattered and piles treatments had a similar number of entry holes, while in Kočevje and Šipek, more holes were found in the scattered residues treatment. Larger bark beetles attacked thick branches in the residues in piles treatment less frequently than in the scattered residues treatment. Despite these differences in attack rates on residues, no treatment effect was observed on the attack rate on saplings and mature trees 1 month after treatment.

The interpretation of these results must be considered in the context of the specific timeframe of the experiment, which ran from the end of June to the middle of August. Several studies have suggested that the impact of residue treatment on bark beetles depends on the time of year (Foit 2015). Our study coincided with much of the flight period of species such as *I. typographus* and *P. chalcographus*. However, we did not record the spring flight associated with the initiation of the first brood. In addition, other species may have different peak flight periods throughout the year. Furthermore, the experiment was conducted at varying altitudes. Combined with the earlier sampling dates, this meant that the higher-elevation plots were likely still in an earlier stage of the flight season of the main bark beetles due to the

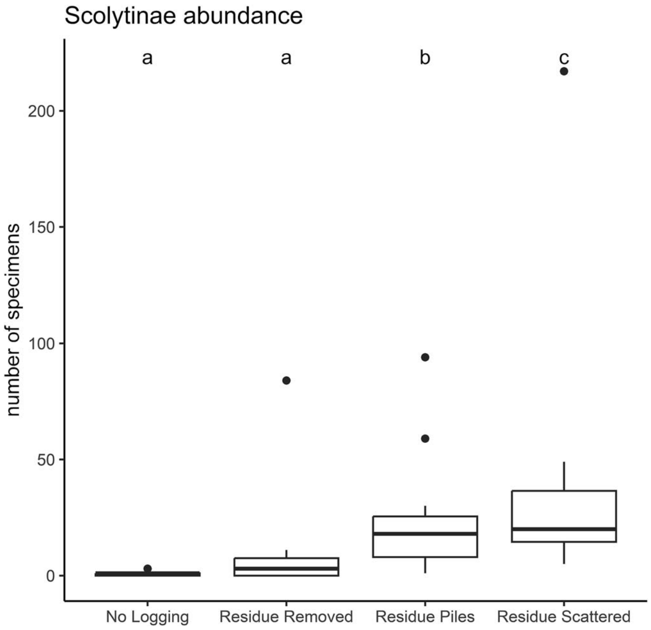


**Figure 3.** Influence of treatment on the total number of individuals per trap for Scolytinae ($N = 1038$). Letters indicate significantly different groups ($P < .05$).

influence of lower temperatures on phenology (Hodkinson 2005). This variation in timing and temperature may have contributed to differences in the species abundances of Scolytinae and/or Cerambycidae across locations, as our results suggest. The 1-month sampling period during mid-summer provides a useful initial indication of broader trends, but sampling over a longer duration, both within and across seasons, would provide a more complete understanding. Results may vary over time due to the varying flight periods among species and changes in the suitability of branch residues as they dry out (e.g. Jonsell et al. 2019). Initially, branches may offer favourable conditions for beetle development, but later in the season, they may become less suitable, potentially acting as an ecological trap. In this case, drying branches could kill larvae that had already colonized them (Ranius et al. 2018). Therefore, the long-term influence of residue treatments on beetle communities warrants further research.

Another limitation of this study is that, except for Scolytinae, beetles were generally only trapped and not sampled directly from the branches. As a result, we cannot say with certainty whether the captured beetles were merely attracted to the treatment, possibly by volatiles emitted by the residues, or whether they were also feeding and breeding in the material. However, for Scolytinae, both our findings and those of previous studies have demonstrated that many species do indeed feed and lay their eggs in branches (Gibb et al. 2006, Kacprzyk 2012). Although our results do not show whether the offspring completed their development, other studies have confirmed this (Kacprzyk 2012). Furthermore, Cerambycidae have also been found developing in branch residues in other research (Foit 2015, Sandström et al. 2019). Thus, it is reasonable to infer that the beetles caught in this study were not only attracted to the residues but that at least some species were also actively using them as a breeding or feeding habitat during the study period.

## Biodiversity assessment of residue management

Interestingly, we found that a wide variety of feeding guilds were attracted to the treatments with residues. As expected, primarily bark- and wood-boring species such as Scolytinae and Cerambycidae were attracted. However, we also observed that beetles from families such as Cleridae, Trogossitidae, and Staphylinidae, which belong to other feeding guilds, were also attracted to the treatments with residues. In this study, Cleridae were predominately represented by *Thanasimus formicarius,* while Trogossitidae were represented by *Nemosoma elongatum*, both of which are known to respond to the volatiles emitted by damaged trees and branches, as well as to the pheromones of their prey (Hulcr et al. 2006, Wegensteiner et al. 2015). *Thanasimus formicarius* mainly preys on Scolytinae larvae, while *N. elongatum* feeds on Scolytinae larvae and adults, which were present in greater numbers in plots with residues. Staphylinidae, on the other hand, display a wide range of feeding behaviours, including predation, mycophagy, and saprophagy (Thayer 2005). Although we did not identify species in this family and therefore could not determine their specific feeding guilds, this relatively understudied group warrants further investigation to assess whether residues provide resources for multiple feeding guilds (Johansson et al. 2007). Latridiidae and Leiodidae also exhibited a preference for treatments with residues, despite many species in these groups being mycophagous (Bangay et al. 2022). This attraction may be related to fungal development following branch cutting or to the introduction of fungal communities by ambrosia beetles. Elateridae, whose adults are phytophagous (Costa et al. 2010), may have been attracted by freshly cut wood or branches with fresh needles. These results indicate that felling residues are important for a variety of species across different feeding guilds.

The family of Cerambycidae is known to serve as an indicator for deadwood, meaning that the presence of species within this family can provide insights into the properties and conditions of the deadwood (Lachat et al. 2012). However, in our study, no species was found to be an indicator for any of the residue treatments. Instead, they were only found to be indicators for study locations. This likely reflects the rarity of Cerambycid beetles in the sample, as individuals were often captured only once (i.e. as singletons). The altitudinal difference between the Jezersko location and the combined areas of Kočevje and Šipek illustrates the influence of phenology on early- and late-season species (Hodkinson 2005). It was also noteworthy that the species assemblage differed only between the control and the other treatments, including the treatment in which residues were removed. Moreover, we found no differences in the number of species between treatments. This could be due to the fact that the larvae of many species develop in stumps, which were present even in the residues removed treatment but not in the no logging treatment. However, in order to assess whether and how residue management affects the long-term population dynamics and survival of Cerambycidae, continued trapping in the years following treatment is necessary.

## Bark beetles and residue management for pests

Scolytinae are among the most diverse groups of Coleoptera in forests and include many species considered to be pests (Vega and Hofstetter 2015). Our results showed that Scolytinae were predominantly attracted to plots with residues. Interestingly, differences between assemblages could be attributed to the availability of brood material. In the treatment where residues were removed, only stumps were available, while the treatments that attracted Scolytinae included branches (e.g. Schroeder et al. 1999, Kacprzyk 2012). *Hylastes cunicularius* is an early-season species that attacks saplings (Lindelöw 1992) and shows a preference for stumps (Rahman et al. 2018). This preference likely explains its higher abundance in the residues removed

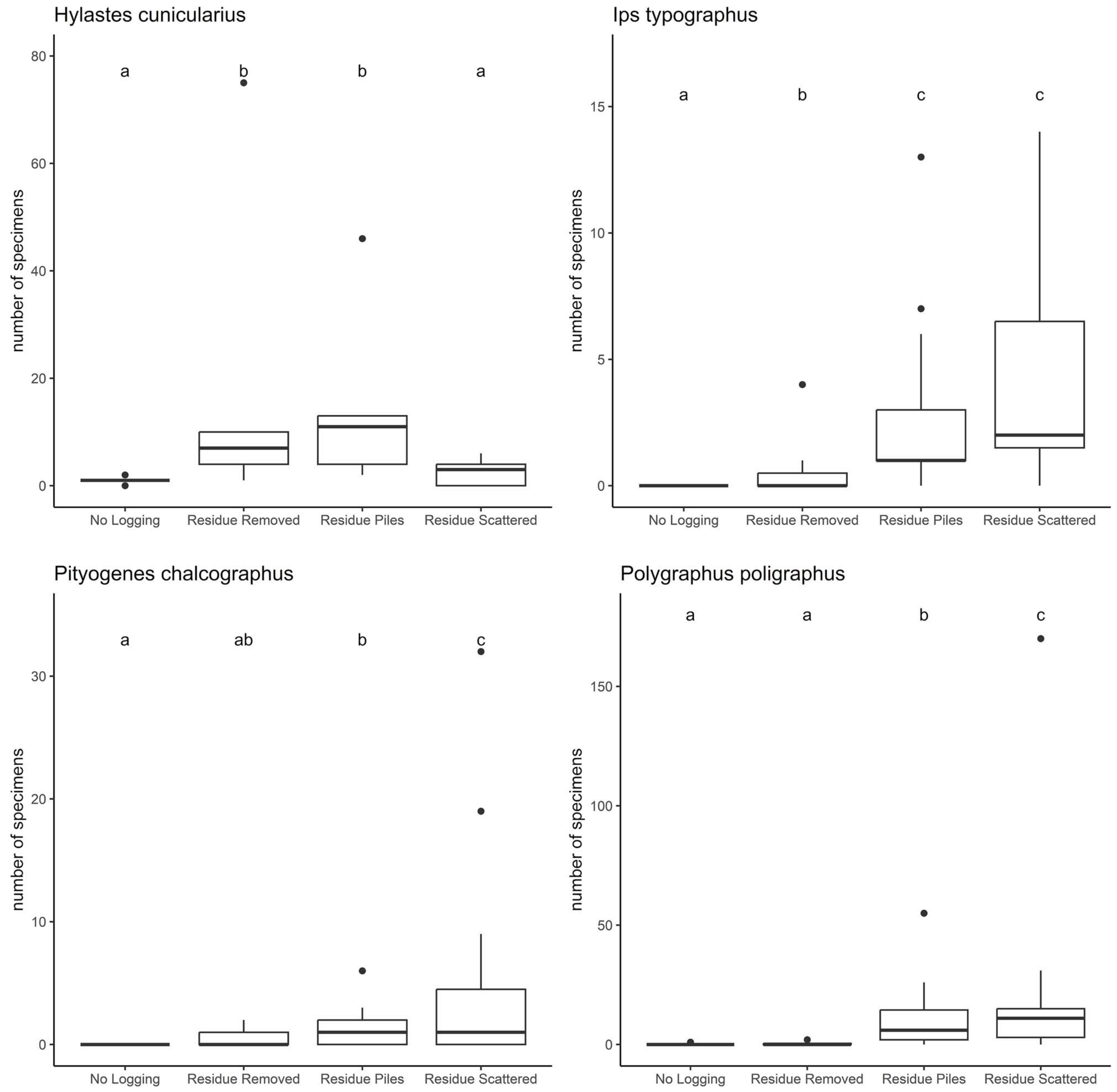


**Figure 4.** Difference in the total number of specimens per trap for *Hylastes cunicularius* (*N* = 204), *Ips typographus* (*N* = 216, *Pityogenes chalcographus* (*N* = 99), and *Polygraphus poligraphus* (*N* = 483). Letters indicate significantly different groups ($P < .05$).

and residues in piles treatments, where stumps were more accessible. In contrast, in scattered residues treatment, stumps were often covered by residues. *Hylastes cunicularius* is regarded as a pest due to the damage caused by adult maturation feeding on the bark of young conifers. *Ips typographus*, *P. poligraphus,* and *P. chalcographus* are species that are attracted to branches (Kacprzyk and Bednarz 2015), with *I. typographus* preferring thicker branches and the latter two species preferring thinner ones. Therefore, it is not surprising that they were attracted only to treatments with residues, *I. typographus* and *P. poligraphus* more clearly so, and *P. chalcographus* along a gradient from the scattered treatment to the control. All of these species are known pests, affecting either saplings and the thinner bark of mature trees (*P. poligraphus* and *P. chalcographus*) or the trunks of mature trees (*I. typographus*). Our results demonstrate that leaving residues in the forest increases the attractiveness of the site to Scolytinae, particularly to species that pose a threat to surrounding trees.

Although both the residues in piles and scattered residues treatments attracted a relatively similar number of Scolytinae, differences were observed in attack rates on the residues of both treatments. Thicker branches in the residues in piles treatment were attacked less frequently than those in the scattered residues treatment. This may be because thicker branches within piles were more concealed and therefore more difficult for beetles to access. Moreover, branches in piles retain more moisture, while *I. typographus* prefers drier wood. Nevertheless, we still observed an average attack density of 0.005 holes/cm$^2$ in residues in piles (compared to an average 0.011 holes/cm$^2$ in the scattered residues treatment), indicating a substantial colonization of breeding material, which could lead to increased offspring number and fitness (e.g. Botterweg 1983, Anderbrant et al. 1985).

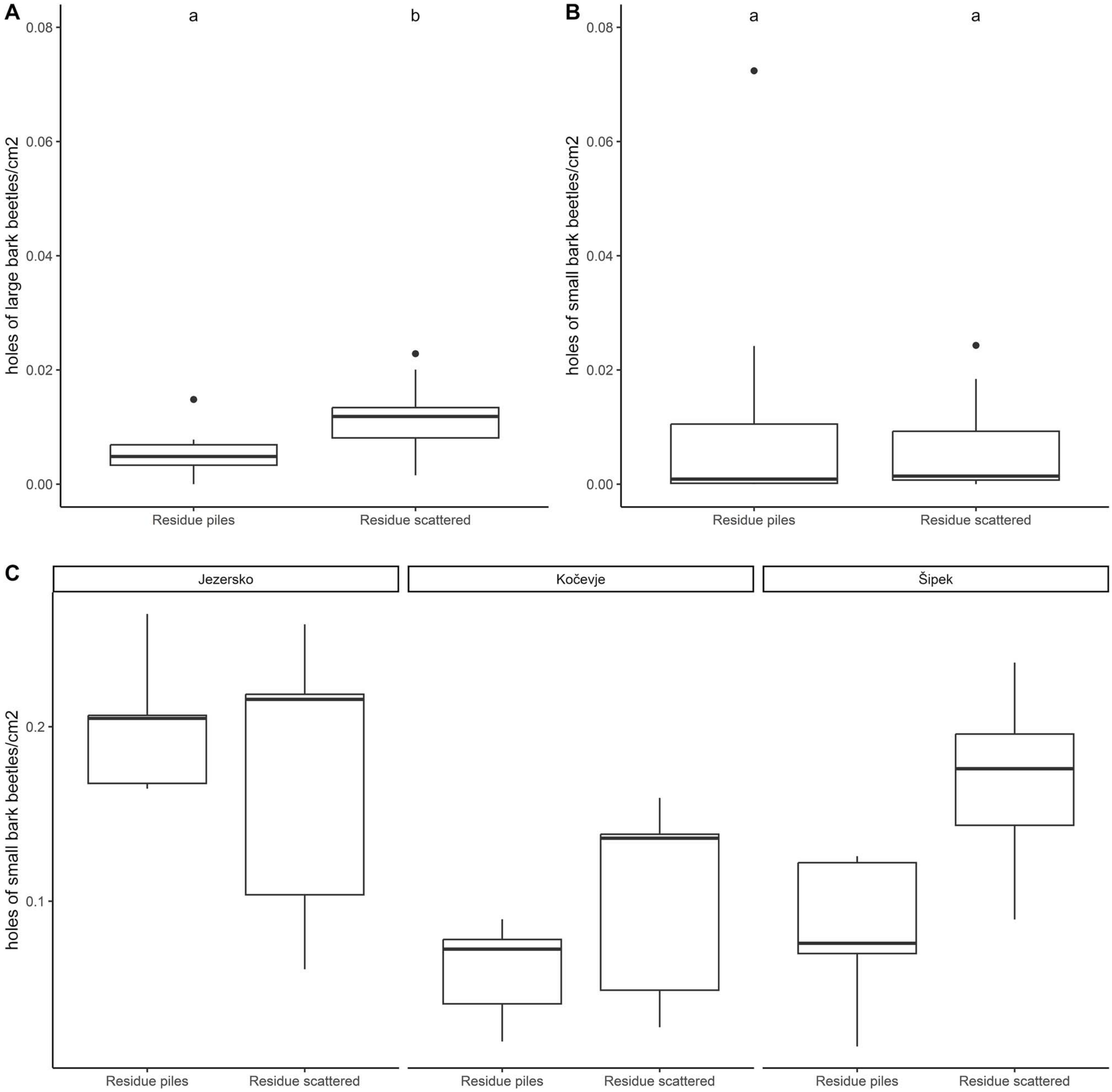


**Figure 5.** Number of small and large holes in thick (A, B) and thin branch residues (C). Letters indicate significantly different groups ($P < .05$). Species such as *Ips typographus* and *D. autographus* are referred to as large bark beetles (>2 mm), while *P. chalcographus*, *P. pityographus*, and Polygraphus *P. poligraphus* are classified as small bark beetles (<1 mm). *N* large holes in thick branches = 997, *N* small holes in thick branches = 800, *N* small holes in thin branches = 995.

Furthermore, smaller branches were more frequently attacked by *P. chalcographus* (Kacprzyk and Bednarz 2015) and *P. poligraphus*. Interestingly, we observed an interaction between treatment and location: lower-elevation sites experienced higher attack rates on thin branches in the scattered residues treatment than in the residues in piles treatment. This was unexpected, as the thin branches in the residues in piles treatment where consistently taken from the top layer of the piles and therefore had similar exposure to bark beetles as those taken in the scattered residues treatment. Moreover, other results showed no differences between these two treatments in terms of small entry hole density (presumably *P. chalcographus* and *P. poligraphus*; Fig. 5B) or in the abundance of *I. typographus*, *P. chalcographus,* and *P. poligraphus* in trap catches (Figs 3 and 4), all of which are pest species.

The higher number of Scolytinae attracted to and attacking the branch material in treatments with residues might suggest an increased risk of attacks on surrounding trees. However, we found no evidence that mature trees or saplings experienced a higher attack rate in these treatments. One explanation could be that the assessment occurred too early and that damage would become more apparent later. Nevertheless, we accounted for early detection signs (Kautz et al. 2023), such as the presence of entry holes and resin flows, making it unlikely that mass attacks on surrounding trees were overlooked. Many of the specimens found in branches were adults nearing maturity, indicating that development may not have been fully complete within the 1-month study period. The attacks observed were therefore likely not caused by offspring that had developed in the residues. Although

*I. typographus* can develop within that timeframe, it still requires an additional period of maturation feeding before emergence and would not have left the wood during the experiment (Wermelinger 2004). However, it is possible that adults attracted to the piles initiated attacks on mature trees and saplings in the process of hatching a sister generation (Wermelinger 2004). An analysis of sanitary felling at the plot sites later in the year also showed no difference in the number of attacked trees between treatments, suggesting that, in the timeframe of our experiment, felling residues did not pose a risk to surrounding trees. After the experiment ended, all felling residues were placed into piles to reduce any potential future risk.

### Implications for forest management

Sustainable forest management should take multiple functions into account in order to support resilient forest ecosystems. Our study addressed both biodiversity conservation and pest management, testing whether certain logging residue management treatments could benefit both objectives. We found that treatments leaving residues in the forest generally attracted a diverse array of saproxylic beetle species and families, suggesting that retaining logging residues can support forest biodiversity. While we found no significant differences in beetle abundance or species richness between the residues in piles and the scattered residues treatments, we did observe fewer attacks on thick branches in piles by economically problematic bark beetle species. Therefore, placing residues in piles could reduce the amount of available brood material for bark beetles. As a result, our findings suggest that collecting logging residues in piles could offer a compromise solution, supporting both biodiversity conservation and pest management.

In recent decades, the volume of deadwood in forests has declined considerably due to intensive forest management (Fridman and Walheim 2000). This loss of deadwood has led to a corresponding decline in deadwood-associated species, many of which are now listed as threatened (Cálix et al. 2018). To maintain viable populations of deadwood-associated insects, an average of 30–40 $m^3$ of deadwood per hectare should remain in the forest (Müller and Bütler 2010). Recent studies have indicated that manipulating deadwood can increase the number of saproxylic species in forests (Sandström et al. 2019). Likewise, our results suggest that retaining felling residues in forests could contribute to the total volume of deadwood and thereby support a higher diversity of saproxylic beetles and other taxa. However, it should be noted that logging residues typically have a small diameter and thus represent only one type of deadwood. Many saproxylic species depend on deadwood of larger dimensions, a mix of tree species or standing deadwood. Both scattered and piled residues are created at the felling site and contribute relatively small amounts of deadwood spread across the forest. Forest management practices vary by country (e.g. single-tree selection vs clear cutting), affecting the spatial distribution of deadwood in the forest. Haeler et al. (2024) emphasized the importance of heterogeneity in both the amount and dispersion of deadwood for maintaining diverse saproxylic communities. This suggests that varied management approaches and timing could foster a more robust saproxylic community.

In integrated forest management, no single forest function should undermine another. Although our study indicated that the availability of fresh deadwood could potentially increase the risk of bark beetle outbreaks, it also demonstrated that thicker branches in residues in piles were attacked less frequently than those in scattered treatments. While our study did not assess risk to surrounding trees directly, this reduced attack rate on thick branches may indicate lower overall risk when residues are piled. Our results suggest that placing residues in piles could help reduce bark beetle infestations by large bark beetle species while still promoting a high diversity of saproxylic beetle species. However, our experiment was conducted in small gaps with a lot of shadow and results may differ in large gaps, where increased sunlight can alter microclimatic conditions within the residues. Further research is needed to evaluate outcomes in such conditions.

## Conclusions

We tested three methods of felling residue management in the context of pest management and biodiversity conservation. Our results showed that leaving residues in the forest attracted higher beetle biodiversity to the felling residuals, particularly among saproxylic species that can utilize this resource. However, we also found an increased abundance of bark beetle pest species in both the residues in piles and scattered residues treatments. Therefore, complete removal of residues appears most effective for bark beetle control, while piling or scattering residues provides a compromise between pest management and biodiversity conservation. Forest management decisions should carefully consider these potentially conflicting objectives. As climate change and other pressures continue to affect forest resilience and biodiversity, it is essential to develop and apply sustainable management practices that support multiple forest ecosystem services.

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## Author contributions

Maarten de Groot (Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Writing—original draft), Luka Capuder (Investigation, Writing—original draft, Writing—review & editing), Farah Kootstra (Formal analysis, Investigation, Methodology, Writing—original draft), Martin Križaj (Investigation, Writing—review & editing), Marija Kolšek (Conceptualization, Methodology, Writing—review & editing), and Mitja Ferlan (Investigation, Methodology, Writing—review & editing)

## Supplementary data

Supplementary data are available at *FORESJ Journal* online.

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## Data availability

The data underlying this article are available in DIRROS (https://dirros.openscience.si/info/index.php/eng/), at https://dx.doi.org/10.20315/Data.0003.

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