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# How does debarking of bark-beetle-colonised spruces affect the saproxylic beetle species richness and composition?

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## 1 Abstract

In many natural forests, forest managers fell and debark spruces (*Picea abies*) colonised by the European spruce bark beetle (*Ips typographus*) to prevent the beetle from spreading to other tree stands. The aim of this study was to examine how this method affects the biodiversity of other saproxylic beetle species. Elector traps were installed on debarked and non-debarked dead spruces of four different ages in four nature reserves to compare the richness and composition of saproxylic beetles. The results indicated that a significantly higher number of species and individuals emerged from standing dead trees with bark compared to debarked logs. The highest emergence of species and individuals occurred in one-year-old standing trees with bark. There was a significant interaction between the type and the age of wood, suggesting that the richness declined with the aging of wood with bark, while it remained constantly low in debarked logs. The species composition varied greatly between standing trees with bark and debarked logs, as well as between standing trees with bark of different ages. This study demonstrated that debarking spruces as a pest control method reduces the diversity of non-target saproxylic beetle species. Potential reasons behind that could be the hardening and drying of consumable parts of the wood, rendering it inhabitable for many saproxylic organisms, as well as the presence of the European spruce bark beetle itself, which is associated with many other species.

Key words: dead wood, debarking, *Ips typographus*, *Picea abies*, saproxylic beetles

## 2 Introduction

The Fennoscandian boreal forests span from 58°N in Sweden to 69°N in Norway. These forests are predominantly composed of Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), birches (*Betula pendula* and *B. pubescens*), and aspen (*Populus tremula*) (Kuuluvainen & Aakala, 2011). The natural dynamics of these forests are influenced by a complex interplay of succession patterns and disturbances occurring in Fennoscandia. Key natural disturbances in Fennoscandian boreal forests include windstorms, fires (prevalent until the 1920's), floods, snow and ice damage, and insect outbreaks (Engelmark, 1999; Rouvinen et al., 2002; Chapin et al., 2007; Kuuluvainen & Aakala, 2011). Some of the disturbances can be expected to increase due to climate change and global warming, leading to more frequent extreme weather events and pest outbreaks (Kattsov et al., 2005; Chapin et al., 2007; Jactel et al., 2019). These changes pose significant threats on both the economy and biodiversity.

In European boreal forests, Norway spruce provides vital ecosystem services, e.g., the provision of timber and pulpwood (Hansen & Malmaeus, 2016), and because of that, it is an economically significant species. Apart from that, as Sweden's most common tree species (SLU, 2022), Norway spruce plays a crucial role in maintaining high forest biodiversity, hosting the highest number of host-dependent species among other indigenous trees. It is a fundamental host to approximately 1100 species from various kingdoms (animals, fungi, and plants) and can support an additional 600 species. Notably, around 300 of them are beetles (Sundberg et al., 2019). In some regions of Sweden, the spruce has been planted on dry, lean soils (Skogsstyrelsen, 2020; Länsstyrelsen Östergötland, 2023; Skogsstyrelsen, n.d.), making it susceptible to drought and weak (Rehschuh et al., 2017). In turn, weakened spruces are more prone to insect colonisations (Seidl et al., 2016; Wulff & Roberge, 2021).

The European spruce bark beetle (*Ips typographus*) is a significant coloniser of spruces. In Europe, it is one of the most common species that can substantially impact forest dynamics, especially when it comes to tree mortality (Seidl et al., 2016; Kortmann et al., 2021). Typically, this beetle species colonises newly dead, wind-felled, or weakened trees. The situation changes during large-scale outbreaks, when the species, after growing into large population densities, spreads to living, healthy trees (Jönsson et al., 2007; Kärvmemo et al., 2016). The primary causes of these outbreaks and greater propagation of the European spruce bark beetle include storms and drought (Wermelinger, 2004; Jönsson et al., 2007). In the summer of 2018, Sweden experienced a major drought, which stressed many Norway spruce stands (Länsstyrelsen Östergötland, 2023). This event led to the historically largest spruce bark beetle outbreaks in Sweden and the subsequent high mortality of trees. This impacted not only production forests but also nature reserves (Schroeder & Kärvmemo, 2022; Länsstyrelsen Östergötland, 2023). Consequently, forest managers are actively developing strategies to combat the spruce bark beetle infestations.

In production forests, one of the most straightforward and economically beneficial solutions is removing the bark beetle colonised trees from plantations. This practice reduces the risk of new outbreaks that could kill other trees within the affected or neighbouring stands (Hlásny et al., 2021). However, finding an appropriate solution for reserves is more complex, as the primary purpose of protected areas is to support biodiversity. Some conservationists and forest managers opt to actively manage the colonised forest stands for several reasons. One of them is that large-scale insect disturbances can lead to the loss of mature trees, which other species depend on (Koprowski et al., 2005). Another argument for active fighting with bark beetle outbreaks is

that owners of production forests fear that unmanaged reserves will serve as sources of “infestation” in their forest stands, causing significant economic losses (McFarlane & Witson, 2008; Skogsaktuellt, 2019). Conversely, an argument for leaving colonised forest stands in the protected areas is that insect outbreaks are a natural phenomenon and a disturbance that creates habitats for other species. By killing trees, bark beetles create new habitats by increasing the quantity of dead wood in the forests, as well as open conditions in more sun-exposed habitats (Weslien, 1992; Bässler & Müller, 2010; Lehnert et al., 2013; Busse et al., 2022). This enhances biodiversity in the attacked forests, including the increase in the abundance of bark beetles’ natural enemies that reduce bark beetle productivity. In some cases, it also facilitate the return of rare or locally extinct species (Weslien, 1992; Bässler & Müller, 2010; Lehnert et al., 2013; Busse et al., 2022).

One of the common methods of active fighting spruce bark beetle outbreaks is debarking of colonised trees (Wermelinger, 2004). Newly colonised spruces displaying early signs of bark beetle attack (e.g., falling needles, loosened bark, and bore dust under the tree) are felled, debranched, and the bark is sawed off (Knížek & Zahradník, 2004; Mellanskog, 2023). Debarking is ineffective once the needles turn brown; it is then too late for intervention. The debarked logs are then left in the forest as dead wood. Trees that were colonised and killed long ago typically no longer host European spruce bark beetles, but their natural enemies may still inhabit the wood (Länsstyrelsen Östergötland, 2023). The County Administration Board of Östergötland (Swedish: *Länsstyrelsen Östergötland*) also frequently employs debarking as a to manage the bark beetle outbreaks. Since 2019, debarking has been conducted almost 50 times in Östergötland’s reserves; in 2022 alone, there were 19 nature reserves in the county managed this way (Länsstyrelsen Östergötland, 2023). This creates an excellent opportunity to study the impact of debarking on saproxylic beetle communities. Is there any difference between debarked and non-debarked spruces infested by the European spruce bark beetle?

The aim of this study was to evaluate if and how the debarking of spruces colonised by the European spruce bark beetle impacts the richness and species composition of other saproxylic beetles. Specifically, the comparison was made regarding the differences in number of individuals, number of species, and species composition of saproxylic beetles that may inhabit spruces colonised by the European spruce bark beetle that were left unmanaged compared to those subjected to debarking. My first hypothesis is that debarked trees harbour fewer beetle species than those that were not debarked. My second hypothesis is that the age of debarked logs (how many years since the debarking was conducted) may affect the beetle communities,

and the densities of caught beetles will differ between the different years of management. Furthermore, the potential effects of some ecological factors (canopy openness, diameter at breast height, and bark coverage) were tested to determine if they could provide a better explanation for the observed results.

### 3 Materials and methods

This research required a multi-step approach. Initially, it was necessary to find suitable sites to conduct tests. Next, the study required the installation of traps of the right type to obtain samples. Following collection, the samples were sorted, counted, and statistically analysed.

#### 3.1 Study sites

The study sites consisted of four nature reserves in Östergötland: Loreberg, Ösbyskogen, Storskogen, and Hälla (Figure 1). All these sites predominantly featured coniferous forests or mixed forests dominated by coniferous species (Länstyrelsen Östergötland, 2023a–d). Notably, several spruce-dominated locations in the reserves experienced large-scale colonisation of European spruce bark beetle, first documented in 2019 in Loreberg. Since then, forest managers from the County Administration Board of Östergötland have taken measures

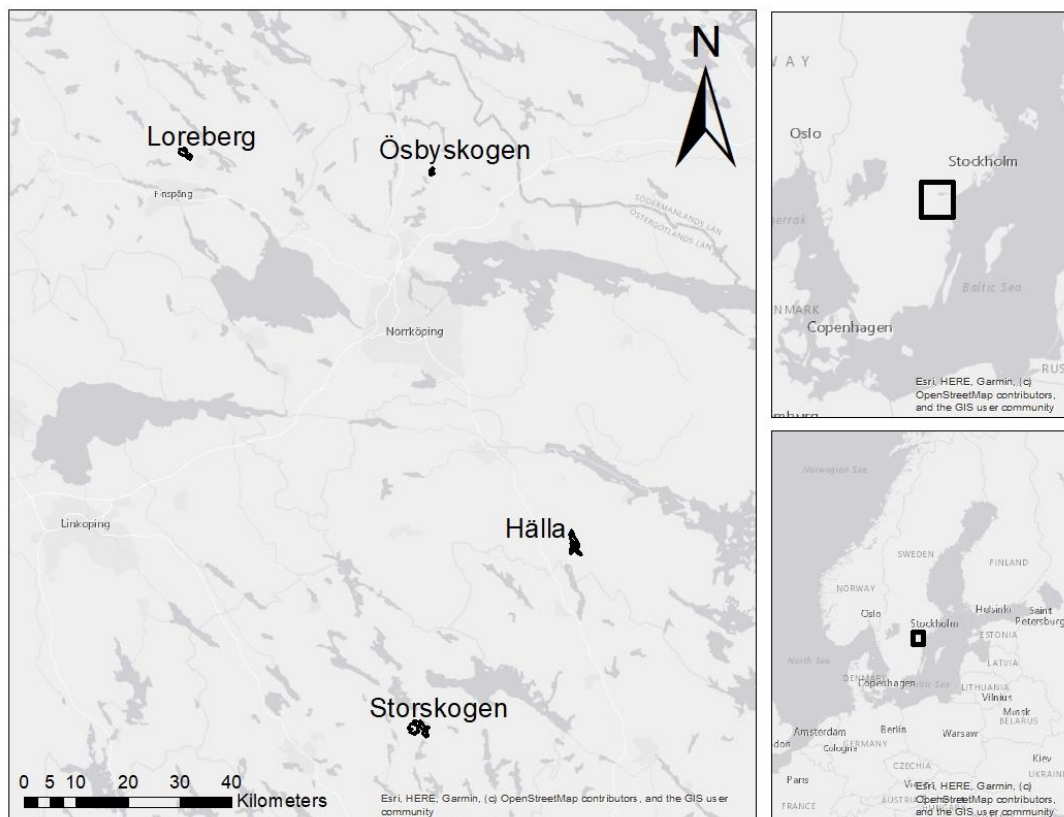


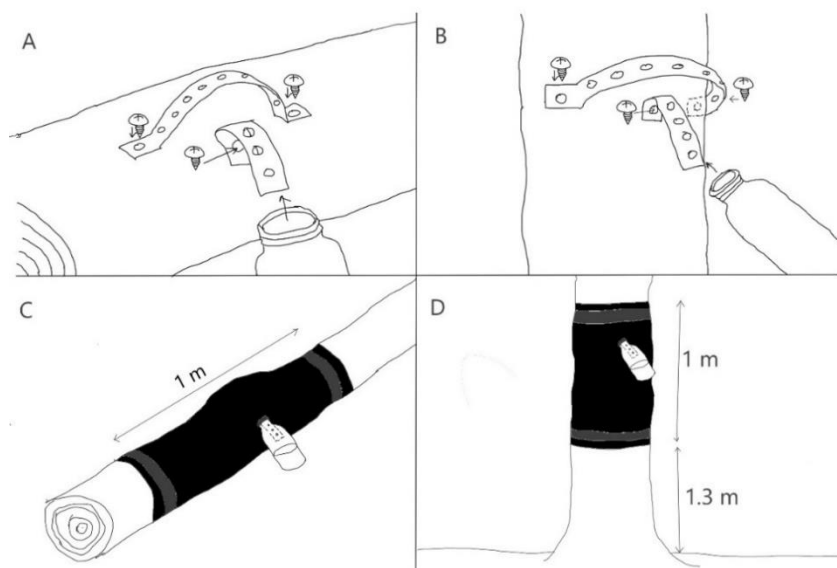
Figure 1. Locations of the reserves I visited for the study: Loreberg (54,97 ha; X: 58.7449, Y: 15.7956), Ösbyskogen (18,98 ha; X: 58.7289, Y: 16.2251), Storskogen (130,13 ha; X: 58.2258, Y: 16.1899) and Hälla (97,43 ha; X: 58.3995, Y: 16.4642).

to prevent the beetle's further expansion to new locations. One of the main methods in all four reserves is the debarking of colonised trees.

In March, the study sites were visited together with the forest managers responsible for the reserves. The objective was to find and identify locations where debarking took place in previous years: 2019 (only Loreberg), 2020, 2021, and 2022. In three to six locations per reserve, suitable dead wood of ages between one and four years was identified and chosen for further study.

### 3.2 Sampling

To sample saproxylic beetles, eclector traps were used (Figure 2A–D). Traps of this type consist of a piece of fabric tightly encircling a tree trunk, coupled with a container into which insects emerging from the tree are to be caught. Accordingly, each trap used in this study consisted of  $1.0 \times 1.5$  m of dark fabric that was put around trunks. A small hole was cut into the fabric, to which a bottle cap with a hole was attached. The cap was secured with a metal wire and sticky tape to attach a sample bottle for catching beetles. A steel band was attached to the stem or log to secure the placement of the bottle. The bottle was filled with a solution of propylene glycol, water, and dish soap to preserve the collected insects. A bow of steel band was installed on the stem and under the fabric above the bottle to create a space to make it easier for insects to find the false "exit". The dark fabric prevented light penetration, and the only way out was the way to the bottle. To assure maximum possible light exposure for "exits" in the bottles in each trap, the bottles were oriented in southern, south-eastern, and south-western directions. The fabric was tightly attached to the stem utilizing a combination of adhesive silver tape, staples, and/or metal wire to make sure there was no way for the insects to escape the trap except through the



*Figure 2. A) Installation of steel band to create a big bow that would create space under the fabric and a small bow to secure the placement of the bottle on a log. B) Installation of steel band to create a big bow that would create space under the fabric and a small bow to secure the placement of the bottle on a standing tree. C) The eclector trap installed on a log. D) The eclector trap installed on a standing tree. Black color show fabric, grey color shows tape.*

bottle. Where necessary, the tree stem was cleared of twigs and branches so that the trap could be tightly adhered to the stem.

Within each reserve, 6 traps for each year of debarking (2019, 2020, 2021, and 2022) were installed, giving 18 or 24 traps per reserve, 50% of which were installed on debarked spruce logs and 50% on standing dead spruces with bark. Additionally, one to three reference traps were also built on fallen logs of trees that were spared from debarking in 2019 and 2020 across the reserves. The number of reference traps depended on the number of available suitable fallen trees; in Ösbyskogen and Hälla, there was only one tree found that met the requirements. A total of 89 traps were installed (Table 1).

*Table 1. The number of installed traps (corresponding to the years of debarking) in the four reserves in Östergötland. L = debarked logs, S = standing dead trees with bark, and R = logs with bark, reference.*

Nature reserve	Year	L	S	R
Loreberg	2019	3	3	3
	2020	3	3	3
	2021	3	3	0
	2022	3	3	0
Ösbyskogen	2019	0	0	0
	2020	3	3	1
	2021	3	3	0
	2022	3	3	0
Storskogen	2019	0	0	0
	2020	3	3	3
	2021	3	3	0
	2022	3	3	0
Hälla	2019	0	0	0
	2020	3	3	1
	2021	3	3	0
	2022	3	3	0

All traps were set up between 3<sup>rd</sup> and 20<sup>th</sup> April 2023. They were emptied and all the insects collected for the first time between 13<sup>th</sup> and 19<sup>th</sup> May 2023, for the second time between 17<sup>th</sup> and 19<sup>th</sup> June 2023, and for the third time between 11<sup>th</sup> and 16<sup>th</sup> July. This resulted in 267 samples being gathered.



### **3.3 Sorting and identification of species**

After collecting all the samples, all adult beetles caught in the traps were sorted and counted. Afterwards, they were identified to species level, and in rare cases only to genus level (one individual of the genus *Malthodes* (Fam. Cantheridae) and most of the caught individuals of the genus *Crypturgus* (Fam. Curculionidae)) (Appendix 1). Those beetles (families or genera) that raised uncertainty in identification were sent to a professional coleopterologist (Acknowledgements).

### **3.4 Ecological variables**

A few additional measurements were taken in the field. The circumference of each standing tree at breast height and of every log in the middle of the area where the trap was installed was measured using measuring tape.

Using a Samsung Galaxy A52s smartphone and an Apexel Fisheye 205° lens, hemispherical photographs of the forest canopy were taken. Each picture was processed and analysed using RStudio software – the package hemisphere (Chianucci & Macek, 2023). The value of canopy openness for each individual photograph was extracted separately for each trap.

Each trunk and log were photographed in such a way as to capture the same degree of bark coverage on both the front and back sides. Areas of trunks and logs that were under the fabric of the traps were edited to have contrasting colours of patches covered in bark and without bark. Then, the percentage of bark covered areas was calculated. Every photograph was analysed in the program ImageJ.

### **3.5 Statistical analysis**

To handle the non-normal distribution of the data, and to incorporate both fixed and random effects, generalised linear mixed models (GLMM) were used to examine the effects of debarking (type of wood), and years since debarking (age of wood) on the abundance and diversity of collected saproxylic beetles, following several steps of analysis. First, the type and age of wood were set as fixed (explaining) factors in separate tests, and the “reserve ID” (Loreberg, Ösbyskogen, Storskogen, or Hälla) as a random effect to account for the non-independence of observations. The number of individuals and the number of species were separately set as dependent (response) variables. Further, the effect of the interaction between the type and age of wood on the response variables was included in the GLMM as an explanatory variable. In this test, data covering logs with bark (reference, type R) and all four-year-old wood (debarked or left with bark in 2019) was removed. Subsequently, the ecological

factors were added to the tests as fixed factors to examine their effects on the response variables. All GLMM-tests were done with negative binomial distribution, due to the character of the data that was an over dispersed count data (with the variance greater than the mean).

To test species composition, three PERMANOVA tests were conducted. Firstly, only standing dead wood with bark (type S) and debarked logs (type L) were tested against each other. Secondly, all three types of one- and two-year-old wood (debarked or left with bark during years 2020 and 2019, respectively) were tested against each other. Thirdly, standing dead wood with bark (type S) and debarked logs (type L) of each age were tested within the type. The results were presented using Non-metric MultiDimensional Scaling (NMDS), which is a visualisation technique that enables showing similarities and dissimilarities in multivariate data sets.

#### 4 Results

In total, 47 818 individuals belonging to 124 saproxylic beetle species were collected. Within this assemblage, 99 species were identified as obligate saproxylic, 25 species as facultative saproxylic, 9 were classified as red-listed, and 19 were designated as nature value indicators (Appendix 1). The majority of the caught individuals belonged to the genus *Crypturgus*. Notably, 31 species were highly abundant in standing trees with bark, while absent or present only in low numbers in debarked logs (Appendix 1). The most common species in the study were those associated with standing trees with bark, such as bark borers *Ips typographus*, *Trypodendron lineatum/laeve*, *Polygraphus poligraphus*, and the genus *Crypturgus*. Debarking proved to be an effective method for eliminating bark beetles, particularly the European spruce bark beetles, which emerged almost exclusively from standing wood with bark (Appendix 1). Besides bark borers, other species such as, e.g., *Corticium fraxini*, *Plegaderus vulneratus*, *Phloeonomus pusillus*, *Paromalus parallelepipedus*, and some beetles from the family Cerambycidae were also found (Appendix 1). A few species (eg., *Stenichnus bicolor*, *Stenichnus godarti*, and *Diaperis boleti*) were more abundant in debarked logs than in standing trees with bark, although their numbers were generally low (usually no more than five individuals) (Appendix 1). The most common species found in debarked logs were *Corticaria longicornis*, *Enicmus rugosus*, *Phloeonomus pusillus*, and *Crypturgus spp.* (Appendix 1).

#### 4.1 Differences within and between the type and age of wood

The highest number of species and individuals were recorded in standing trees with bark, whereas debarked logs exhibited the lowest counts (Table 2). Specifically, the greatest diversity of obligate, facultative, red-listed, and nature-value-indicating saproxylic beetles was observed in samples from standing trees with bark, while the lowest numbers of those beetles were found in traps on debarked logs (Table 2). Notably, all the red-listed species except one (*Buprestis heamorrhoidelis*) were found exclusively on standing wood with bark (Appendix 1).

In terms of wood age, the greatest abundance of both individuals and species was observed in one-year-old wood (debarked or left with bark in 2022), while the lowest counts were documented in four-year-old wood (debarked or left with bark in 2019) (Table 2). No single age of the wood simultaneously exhibited the highest number of species across all categories of saproxylic beetles: red-listed, nature value indicators, obligate, and facultative.

*Table 2. Total number of individuals, species, red-listed species, nature value indicators, obligate, and facultative saproxylic beetles on standing wood with bark (S), debarked logs (L), and logs with bark (reference, R), as well as on four-, three-, two-, and one-year-old wood (debarked or left with bark in 2019, 2020, 2021 and 2022, respectively).*

	S	L	R	2019	2020	2021	2022
Number of individuals	45 512	141	2165	62	3197	6529	38 030
Number of species	102	43	50	19	76	69	77
Red-listed species	8	1	0	0	4	7	4
Nature value indicators	16	4	4	1	10	11	11
Obligate saproxylic species	86	36	37	16	58	59	65
Facultative saproxylic species	16	7	13	3	18	10	12

Both the number of species and individuals differed significantly across the three types of wood, with the most pronounced difference observed between standing trees with bark and debarked logs (Figure 3). On average, the number of individuals was 367 times higher in standing wood with bark than in debarked logs. Additionally, the species richness was 4.3 times greater in standing wood with bark than in debarked logs.

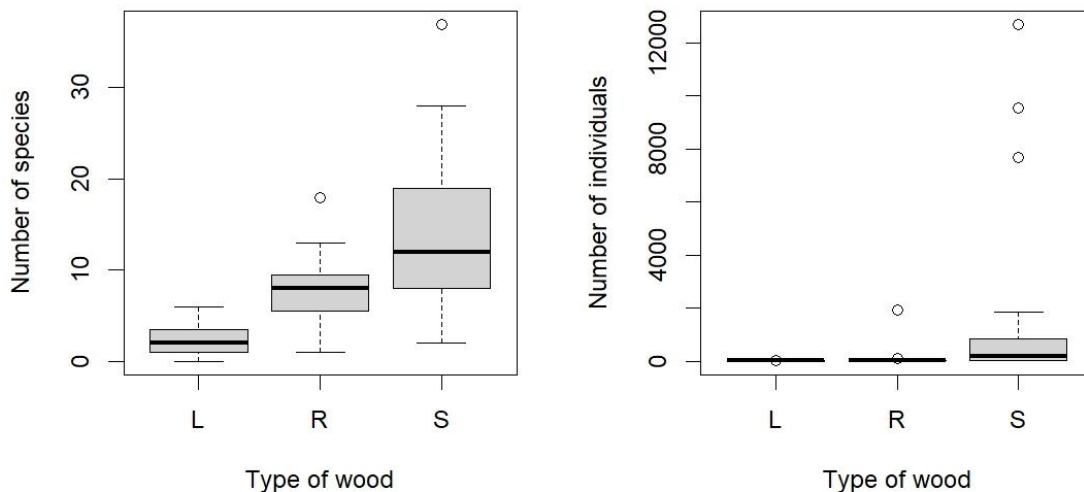


Figure 3. To the left: Number of species found in traps installed on different type of wood. To the right: Number of individuals caught in traps installed on the three types of wood. L = debarked logs. R = reference, logs with bark. S = standing trees with bark. All types of wood were significantly different from each other.

The age of wood (years since debarking) had a significant effect both on the number of species and individuals, with the exception of two-year-old wood, which showed no significant effect on the number of species ( $p < 0.2037$ ). The most substantial differences were observed between one-year-old wood (debarked or left with bark in the area in 2022) and four-year-old wood (debarked or left with bark in the area in 2019). There was a significant difference only between one- and four-year-old wood regarding the number of species, but no significant difference only between two- and three-year-old wood when it comes to the number of individuals (Figure 4). On average, one-year-old wood yielded 307 times more individuals than four-year-old wood, and the species richness was 2.5 times higher in one-year-old wood compared to four-year-old wood.

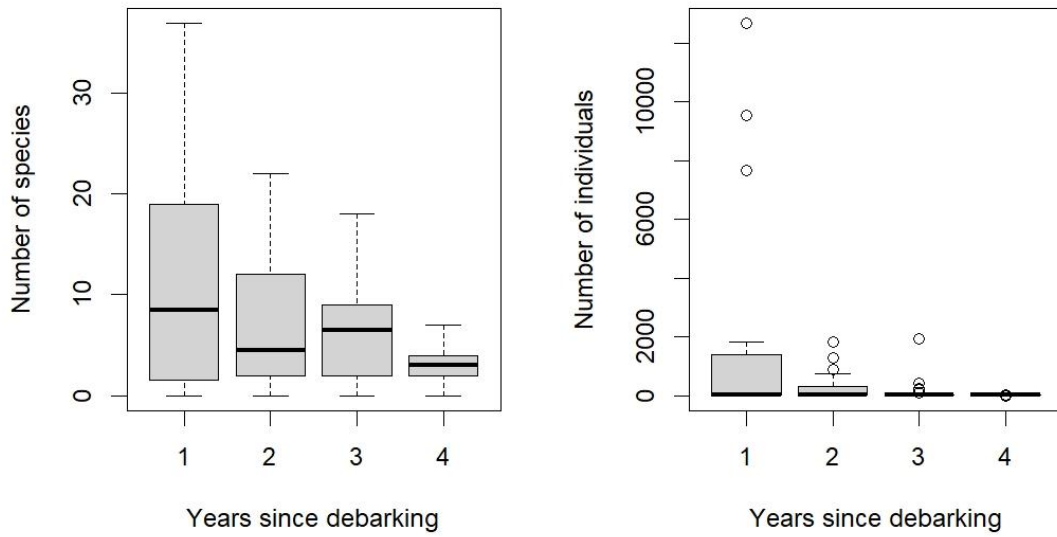


Figure 4. To the left: Number of species found in traps installed on wood of different ages. To the right: Number of individuals caught in traps installed on wood of different ages. 4 years since debarking (4-year-old wood) = debarking (or leaving with bark in this area) took place in 2019, 3 years since debarking (3-year-old wood) = debarking (or leaving with bark in this area) took place in 2020, and so on.

There was a significant interaction between age and type of wood (Est. = -0.465,  $p < 0.008$ ), indicating species richness in standing trees with bark declined with age, whereas debarked logs consistently maintained low numbers of species over time. However, after four years, standing wood with bark still had significantly more species than debarked logs (Figure 5; Figure 6).

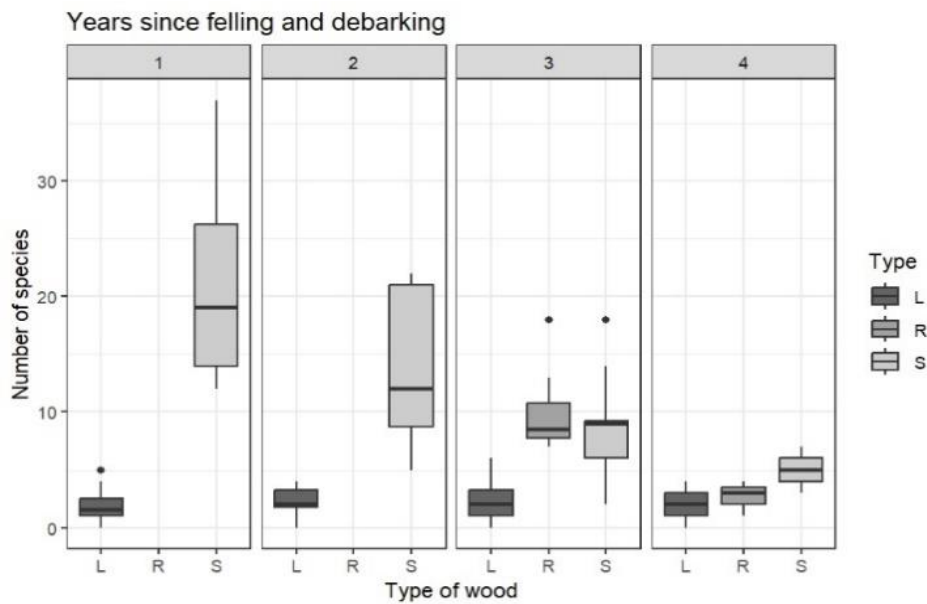


Figure 5. Differences in number of species depending on years since debarking and type of wood. There were no traps installed on logs with bark (reference, R) from years 2021 and 2022 (2 and 1 year since debarking).

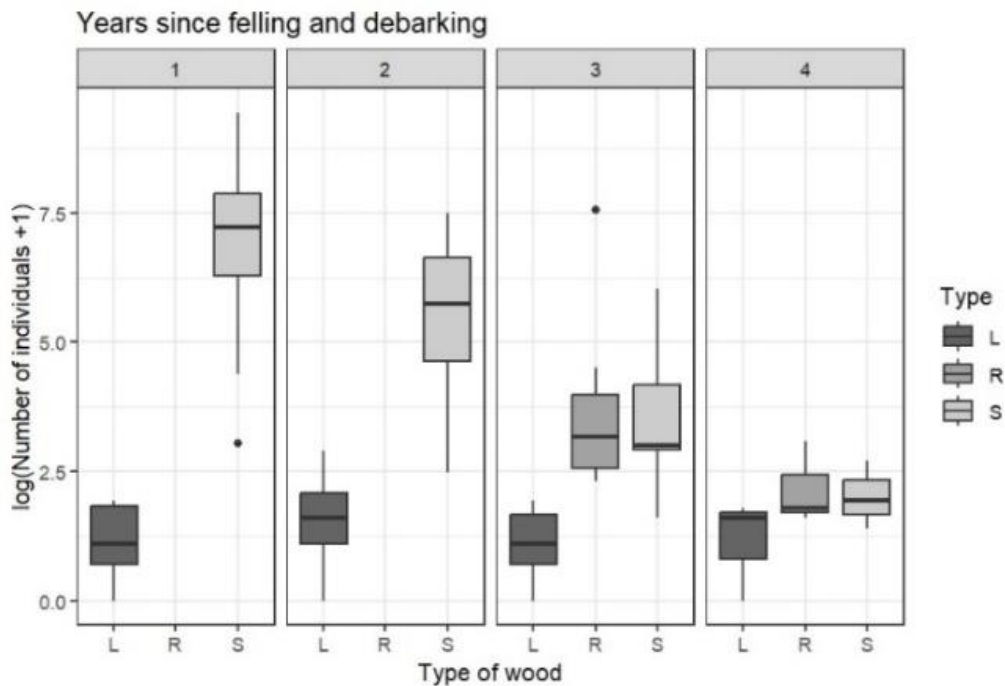


Figure 6. Differences in number of individuals ( $\log(N+1)$ ) depending on years since debarking and type of wood. There were no traps installed on logs with bark (reference, R) from years 2021 and 2022 (2 and 1 year since debarking).

#### 4.2 Environmental factors vs type and age of wood

Measurements of diameter at breast height, canopy openness, and bark coverage for each trap were recorded and compiled into a table (Appendix 2). The diameter at breast height was relatively evenly distributed between the types of wood (Figure 7). Canopy openness was generally greater over traps placed on debarked logs and more closed over traps on standing wood with bark, due to the felling and debarking of trees (or lack of them) and of the

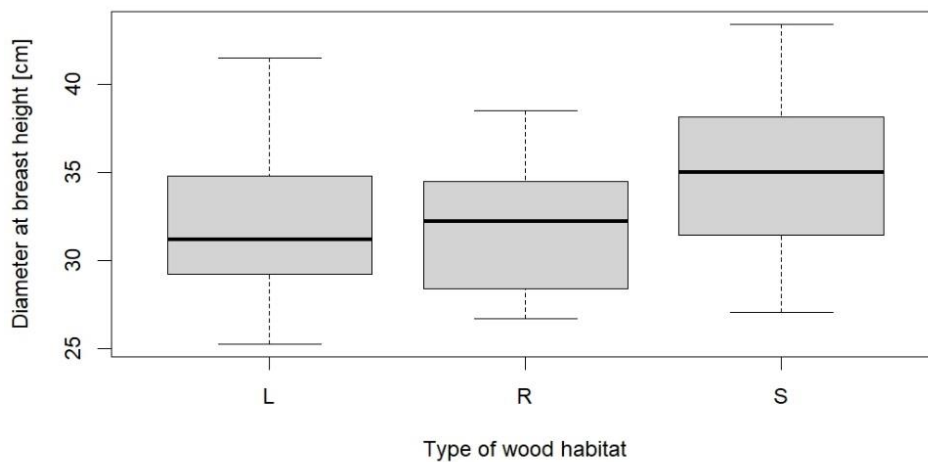


Figure 7. Distribution of diameter at breast height among the three types of wood: L = debarked logs, R = reference, logs with bark, S = standing wood with bark.

neighbouring trees (Figure 8). All debarked logs had 0% bark coverage, while the majority of wood with bark (either standing or logs) had nearly 100% bark coverage with only a few outliers (Figure 9). Due to this bias, bark coverage was excluded from further analysis.

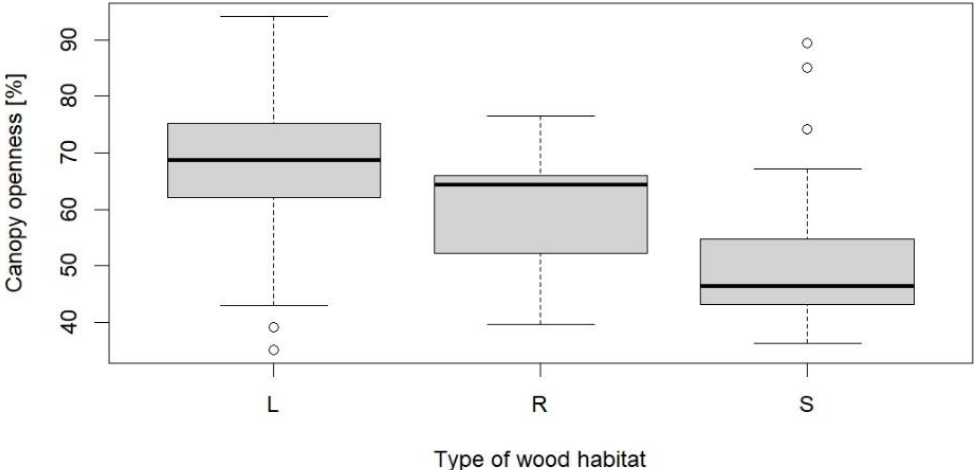


Figure 8. Distribution of canopy openness among the three types of wood: L = debarked logs, R = reference, logs with bark, S = standing wood with bark.



Figure 9. Distribution of bark coverage among the three types of wood: L = debarked logs, R = reference, logs with bark, S = standing wood with bark.

When tested together, the type of wood and diameter at breast height had a moderately positive effect on the number of species, while canopy openness showed a negative effect. However, only wood with bark (both standing and logs) and canopy openness had a significant effect on the number of species, with the type of wood having a positive effect and the canopy openness a negative one (Figure 10).

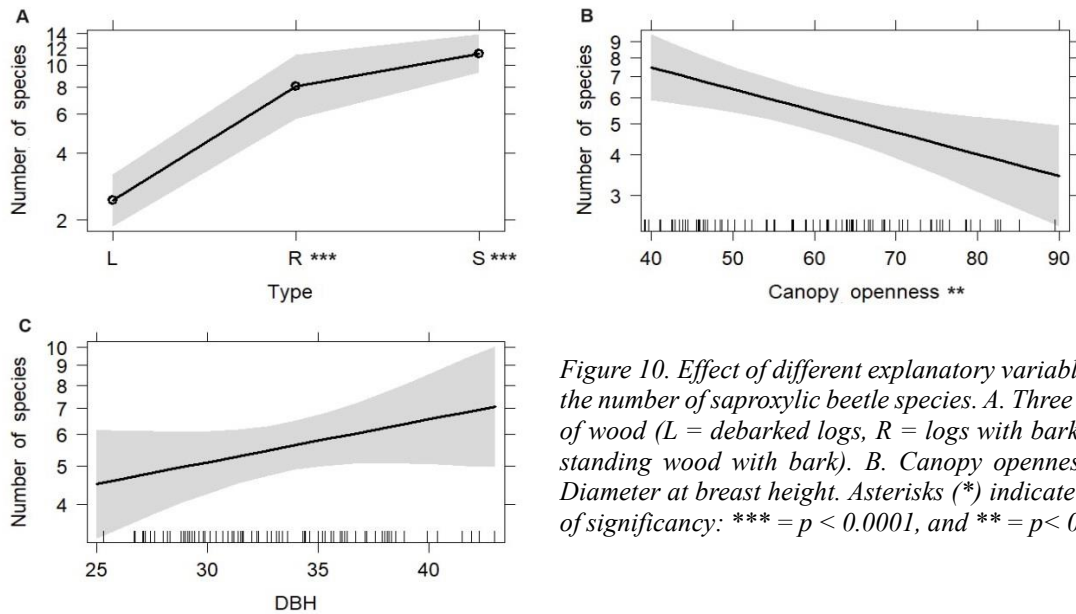


Figure 10. Effect of different explanatory variables on the number of saproxylic beetle species. A. Three types of wood (L = debarked logs, R = logs with bark, S = standing wood with bark). B. Canopy openness. C. Diameter at breast height. Asterisks (\*) indicate level of significance: \*\*\* =  $p < 0.0001$ , and \*\* =  $p < 0.001$ .

Regarding the number of individuals, all wood types had a significant positive effect, with the strongest positive one being the effect of standing wood with bark and the weakest of debarked logs. Canopy openness and diameter at breast height had a weak negative effect on the dependent variable, with only the canopy openness being significant (Figure 11).

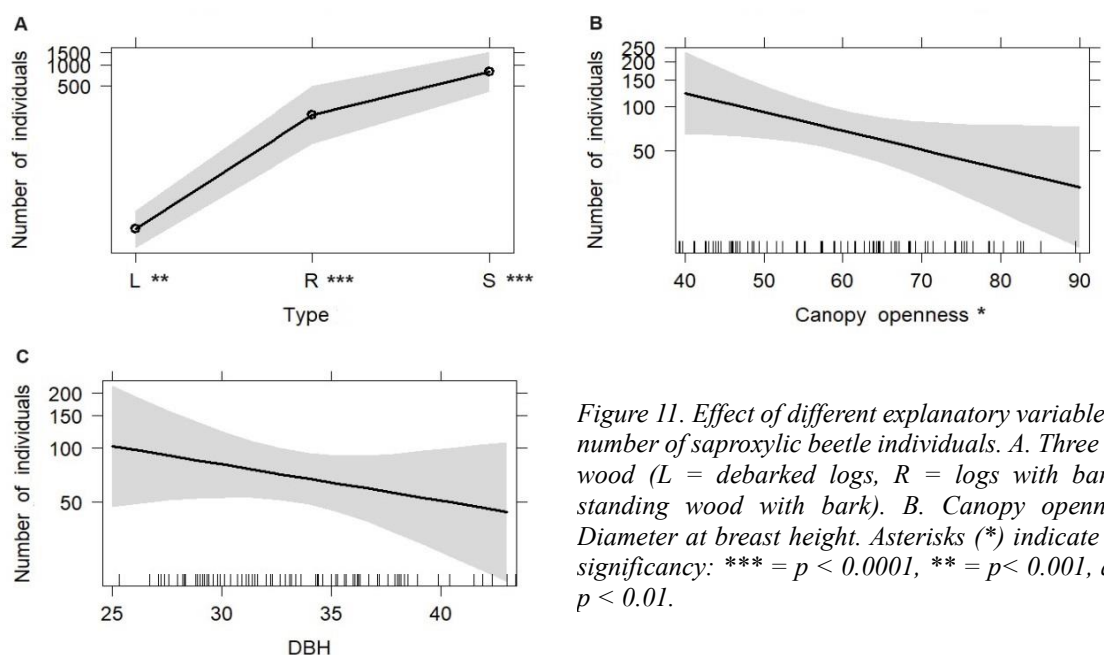


Figure 11. Effect of different explanatory variables on the number of saproxylic beetle individuals. A. Three types of wood (L = debarked logs, R = logs with bark, S = standing wood with bark). B. Canopy openness. C. Diameter at breast height. Asterisks (\*) indicate level of significance: \*\*\* =  $p < 0.0001$ , \*\* =  $p < 0.001$ , and \* =  $p < 0.01$ .



The number of species was significantly affected only by one-year-old wood (debarked or left with bark during the year 2022), canopy openness, and diameter at breast height when these factors were tested together. Age and diameter at breast height had a positive effect, while canopy openness had a negative one (Figure 12).

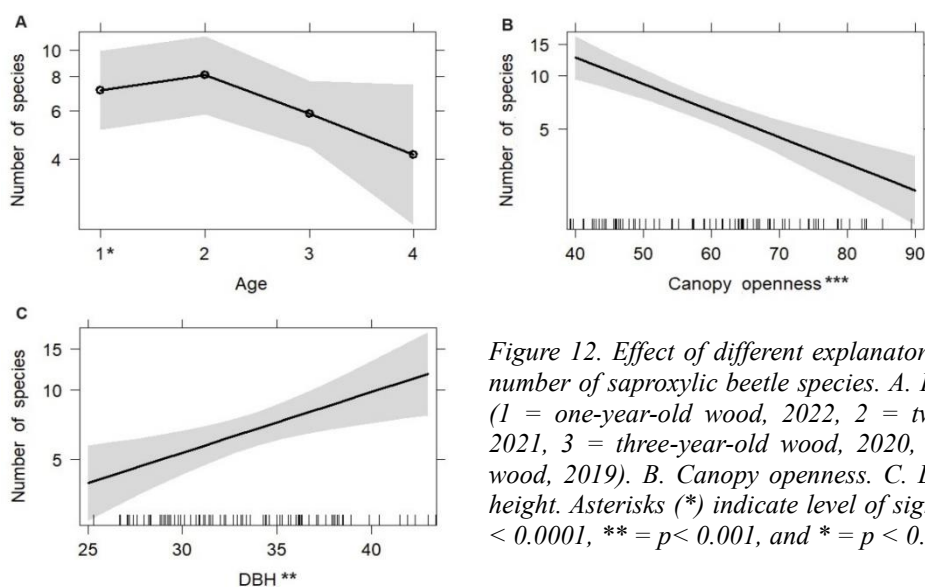


Figure 12. Effect of different explanatory variables on the number of saproxylic beetle species. A. Four ages of wood (1 = one-year-old wood, 2022, 2 = two-year-old wood, 2021, 3 = three-year-old wood, 2020, 4 = four-year-old wood, 2019). B. Canopy openness. C. Diameter at breast height. Asterisks (\*) indicate level of significancy: \*\*\* =  $p < 0.0001$ , \*\* =  $p < 0.001$ , and \* =  $p < 0.01$ .

For the number of individuals, when the effect of the age of wood, canopy openness, and diameter at breast height were considered as explanatory variables together, of all the ages only two-year-old wood did not have a significant effect on the dependent variable. One-year-old wood had a strong positive effect on the abundance of saproxylic beetles, whereas three- and four-year-old wood (debarked or left with bark during years 2020 and 2019) had a negative effect. Canopy openness had a significantly weak effect on the number of individuals. The results for the diameter at breast height were not significant (Figure 13).

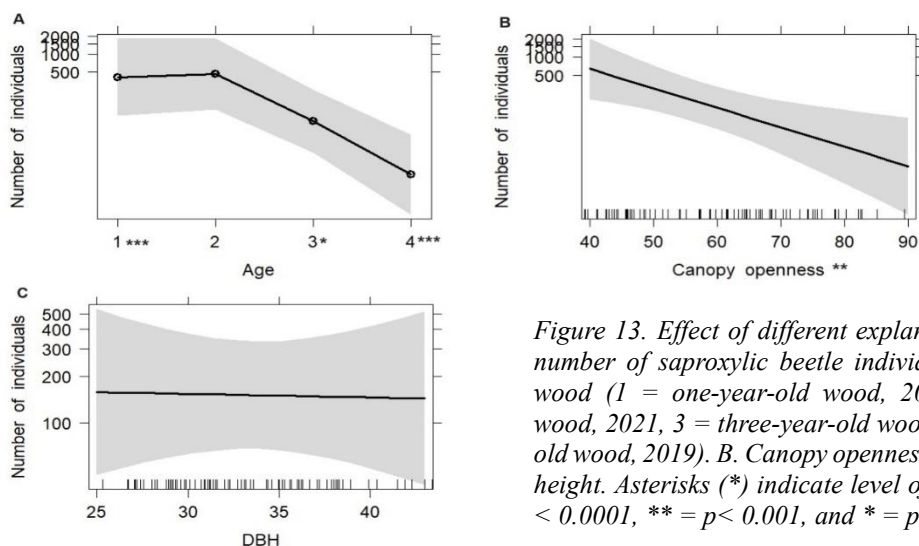


Figure 13. Effect of different explanatory variables on the number of saproxylic beetle individuals. A. Four ages of wood (1 = one-year-old wood, 2022, 2 = two-year-old wood, 2021, 3 = three-year-old wood, 2020, 4 = four-year-old wood, 2019). B. Canopy openness. C. Diameter at breast height. Asterisks (\*) indicate level of significancy: \*\*\* =  $p < 0.0001$ , \*\* =  $p < 0.001$ , and \* =  $p < 0.01$ .

### 4.3 Species composition

There was a significant difference in species composition between standing wood with bark and debarked logs across all ages (debarked or left with bark between 2019 and 2022). Approximately 10.8% of the difference could be explained by the type of wood. The species composition found in traps on standing wood with bark was relatively similar to each other, whereas species found in traps built on logs without bark varied more, both from those found in standing wood with bark and from each other (Figure 14).

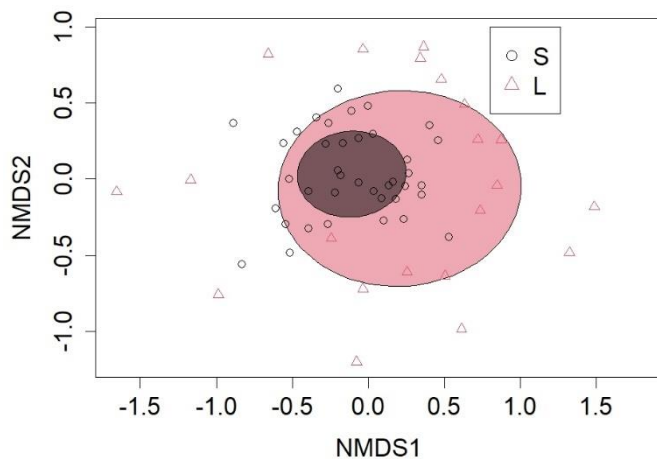


Figure 14. NMDS showing the species composition of saproxylic beetles. The plot shows two ellipses: black S (standing wood with bark), and red L (debarked logs) of all four ages (debarked or unmanaged in years 2019-2022). The overlapping areas and the spread of points indicate the degree of similarity in species composition between the two types of wood. The tighter clustering of points within the black ellipse suggests that the species composition is more consistent within the standing wood with bark, in contrast to the debarked logs.

The species composition was significantly different among the three types of wood ( $p < 0.003$ ), with around 12% of the differences explained by the type of wood. Three- and four-year-old logs (with or without bark) were not significantly different from each other ( $p = 0.083$ ). In general, species on bark-covered logs resembled those on bark-free logs, and they were more consistent than those on debarked logs. Part of the species composition on standing wood differed from both types of logs (Figure 15).

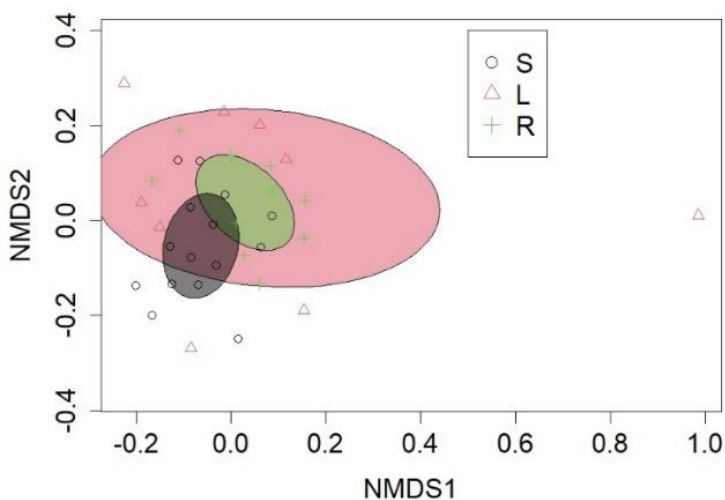


Figure 15. NMDS showing the saproxylic beetle species composition of three- and four-year-old wood (managed under years 2019 and 2020) of type S (standing wood with bark, black), L (debarked logs, red) and R (reference, log with bark, green). The plot shows that while there is some overlap between the species composition in bark-covered logs and standing wood, the debarked logs form a distinct group. The tighter clustering of black (standing wood with bark) and green ellipses (logs with bark) suggests more consistent species composition than in red ellipse (debarked logs). Part of the black ellipse does not overlap with the other two, indicating some degree of dissimilarity in species composition between the different types of wood.

Comparing standing wood with bark of different ages revealed significant distinctions in species composition between the ages. The species composition changed significantly over time and the difference was largest between one- and four-year-old wood. Approximately 19% of the variation was explained by age ( $p < 0.001$ ), with the most pronounced difference seen between one- and four-year-old wood (left with bark years 2022 and 2019, respectively) (Figure 16). There was no significant difference in species composition between debarked logs of all ages ( $p < 0.213$ ).

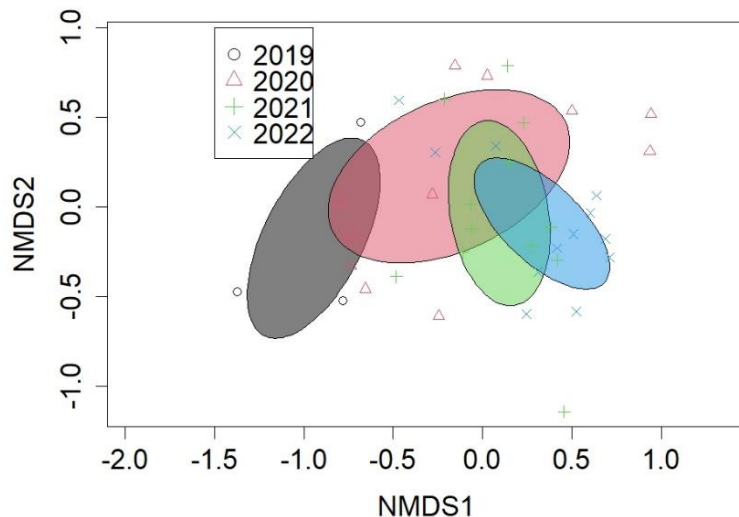


Figure 16. NMDS showing the saproxylic beetle species composition of standing wood with bark of all ages. Black 2019 = four-year-old wood, red 2020 = three-year-old wood, green 2021 = two-year-old wood, and blue 2022 = one-year-old wood. The lack of overlapping of the black and blue ellipses highlight a big dissimilarity between one- and four-year-old standing wood with bark, showing variation in species composition. Some degree of overlapping between the ellipses indicate that the species composition progressively changes as the wood ages.

## 5 Discussion

The findings of this study indicate that there is a substantial difference in the number of species, number of individuals, and species composition of saproxylic beetles between spruces that were left untreated after the colonisation of European spruce bark beetles and those that were felled and debarked. Particularly in the early years after a tree's death, standing trees with bark harboured more species and individuals of beetles than debarked logs. Furthermore, standing trees with bark could potentially serve as habitats for more threatened species in contrast to debarked logs. Nevertheless, the dissimilarity in beetle community composition between the types of wood decreased with the increasing age of the wood.

The results seem to align with prior studies. The presence or absence of bark on the wood, especially the recently deceased, is of great importance for saproxylic insects. Thorn et al. (2016) conducted a comparative study involving debarked, bark-scratched, and untreated logs with each other to investigate how they differ from one another in impacting the emergence of the European spruce bark beetles and other saproxylic beetles. The study revealed that debarking and bark-scratching were almost equally successful in restraining the emergence of the European spruce bark beetle in comparison to unmanaged logs. On the other hand, they differed in their effect on other saproxylic beetles. Unmanaged (neither debarked nor bark-

scratched) logs exhibited a similarly high abundance of saproxylic beetles compared to the low numbers of those insects emerging from debarked logs (Thorn et al., 2016). According to Graham (1925), inner bark along with cambium are the most nutrient-rich parts of the wood, followed by sapwood, heartwood, and outer bark. Debarking can lead to the depletion of available food sources not only by the disappearance of bark itself but also by the drying of other consumable parts of wood. Wood without bark, which has moisture-maintaining properties, dries out at a faster pace, and the dryer and more lignified wood, the harder it is for insects of early succession to consume and digest it (Graham, 1925; Ulyshen et al., 2016). Moreover, debarking reduces the density of wood-inhabiting fungi (Thorn et al., 2016), which also makes the wood of debarked trees harder than that of those that kept their bark. Because of that, some beetle species that usually inhabit spruces can probably not find their needed habitats (Thorn et al., 2016).

Furthermore, the age of the dead wood also appears to be an important factor influencing the presence of saproxylic beetles. It is due to the changes in the substrate occurring over time. Assemblages of insects (Coleoptera included) tend to change following the decay stages of wood. Studies have demonstrated that when it comes to dead conifer wood, the number of saproxylic beetle species is highest in the early stages of decomposition, especially xylophages and predators like beetles from the families Scolitidae, Staphylinidae, Cerambycidae, and Nitidulidae (Vanderwel et al., 2006; Saint-Germain et al., 2007). This patterns could likely be explained by alterations in the wood's chemical composition and physical attributes.

The position of dead spruce wood – whether standing or downed (log) – can also influence saproxylic beetle assemblages, although findings vary among studies. Some studies suggest a preference for logs over standing trees (Jonsell and Weslien, 2003; Gibb et al., 2006). According to Gibb et al. (2006), early successional saproxylic beetles generally favour logs over standing trees, with the exception of red-listed species that prefer standing dead wood. However, it is important to note that none of the experimental logs in Gibb's et al. study (2006) underwent mechanical debarking; instead, they were subjected either to burning, overshadowing, or were left in an unchanged, natural state, probably resembling the reference logs used in this study. The researchers highlighted that standing trees supported distinct assemblages of saproxylic beetles, likely influenced by factors such as full exposure to air and a stronger defence mechanism against fungi and insects due to their root connection (Gibbs et al., 2006). In Jonsell and Weslien's study (2003), high stumps were compared to short and long logs, none of which were debarked. They found that logs, regardless of length, hosted more individuals and species

than standing dead wood, although the preferences of individual species varied (Jonsell & Weslien, 2003). The differences between the types of wood were attributed to the substrate's moisture. However, the results from this study indicate a preference for standing dead wood with bark, contradicting previous findings. It is important to remember that the mentioned studies were conducted on clear-cuts or by the edge of forest, whereas some of the locations in this study still consisted of relatively intact forests, especially where many standing trees with bark still remained. In this study, reference logs with bark exhibited similar species and individual counts as standing dead trees with bark of the same age (three- and four-year-old). There is a possibility that standing dead trees with bark collapsed shortly before this study was conducted and, in turn, became logs suitable for being references; however, it was not possible to assess when the trees fell to the ground.

Moreover, the ecological significance of bark beetles (Fam. Curculionidae, Un.Fam. Scolytinae) cannot be left out. These organisms play an important role in creating diverse habitats for numerous species, including other beetles. By feeding and breeding on the phloem or xylem either weakened or newly dead trees, they initiate wood decay succession by altering the food material, breaking it down and making it available for other organisms of succeeding stages, e.g., fungi and bacteria (Graham, 1925; Bouget & Duelli, 2004). In addition to that, bark beetles frequently act as vectors of fungal spores, thereby further contributing to the process of future patterns of wood decay, with effects noted even a decade later (Paine et al., 1997; Persson et al., 2009; Jacobsen et al., 2015). This means that a lack of bark beetles in the early stages of the decomposition of dead trees could result in decreased biodiversity in the future. In the present study, the debarked logs hosted very little to no bark beetles alongside the already low numbers of saproxylic beetles captured in them.

The higher diversity of saproxylic beetles observed on standing wood with bark could also be a result of not only the higher moisture of the substrate but also of the presence of the European spruce bark beetle itself. From one point of view, the European spruce bark beetle consumes cambium and phloem and leads to reduced bark cover of trees, which, as mentioned above, can cause the wood to become dry faster (Graham, 1925; Hedgren & Schroeder, 2004; Fossetøl & Sverdrup-Thygeson, 2009; Ulyshen et al., 2016). From another point of view, several studies show that the bark beetle increases the biodiversity of other beetles and insects. According to Weslien (1992), approximately 140 arthropod species are associated with the European spruce bark beetle in Europe, many of them from the order Coleoptera. Both Weslien's (1992) and Hedgren and Schroeder's (2004) research showed that beetles of different trophic functions and

feeding habits are linked to *Ips typographus*. Among them were predators like *Nudobius lentus*, *Plegaderus vulneratus*, *Thanasimus spp.*, *Rhizophagus spp.*, and *Corticeus spp.*, competitors to European spruce bark beetle like *Rhagium inquisitor*, *Dryocetes autographus*, and *Pityogenes chalcographus*, as well as some genera and species of unknown feeding habits like *Leptusa fumida*, *Phloeonomus pusillus*, and *Epuraea spp.* The present study confirmed these findings; all the abovementioned species or genera were found on wood previously colonised by the European spruce bark beetle. Interestingly, none of these species were found on debarked logs. Other arthropods (28 823 individuals of 13 orders or classes, Acari excluded) were also found in this study; however, because they were not the focus of this paper, they were not identified to species or genera and thus cannot be compared to other studies.

In the long term, the European spruce bark beetle creates habitats for even more species by altering forest ecosystems (Lehnert et al., 2013). Colonisation and killing of trees lead to the creation of early successional ecosystems characterised by gaps and canopy openings, warmer soils, high volumes of dead wood, and uncovered understorey vegetation (Müller et al., 2008; Lehnert et al., 2013). Consequently, a diverse array of species of different kingdoms colonises the newly created habitats (Müller et al., 2008; Lehnert et al., 2013). In Lehnert et al. (2013), results showed that most of the significant indicator species of the study preferred open forest. Organisms representing Coleoptera, Arachnea, Bryophyta, Lichens, and Spermatophyta were present both in closed and open forests, but more species favouring the latter. Müller et al. (2008) proposed classifying the European spruce bark beetle as a keystone species due to its association with numerous other species living with it on dead wood, as well as because of its contribution to creating habitats for a broad spectrum of organisms benefiting from bark beetle created gaps in forest stands.

In conclusion, the results indicate that debarking is a suitable method for mitigating the emerging of European spruce bark beetles from colonised spruces, but at the same time, it is not suitable for preserving the biodiversity of other saproxylic beetle species. Therefore, if enhancing biodiversity is one of the goals of forest nature reserves, alternative, less deleterious methods of controlling the pest species would be considered. This study provides valuable insights into the ecological consequences of the debarking of spruces following bark beetle colonisation, thereby contributing to future research and conservation efforts aimed at preserving the biodiversity of saproxylic beetles and other organisms in forests. It would be interesting to follow the aging process of the dead wood tested in this study to understand how saproxylic beetle species are affected in the later successional stages of wood decomposition.

## **6 Societal and ethical considerations**

Forests are important because of the ecosystem services they provide. Among them are economic ones connected to wood production for building materials, fibre, and fuel, although this aspect does not apply regarding nature reserves. Forests in nature reserves are essential for keeping the air clean, binding carbon dioxide, and filtering water. They also play a great role in recreation and overall cultural enrichment. All of that is enhanced by the biodiversity that forests sustain. Understanding how species richness changes due to spruce bark beetle colonisation and forest management is an important part of protecting and keeping forests alive and available for current and future generations.

This project was performed using slightly destructive methods; it required cutting off small branches of logs and standing dead trees, scraping bark off some dead trees, and putting screws into dead trees. This caused small changes in 89 dead standing trees and logs, and was a source of noise in the forests, which could have temporarily disturbed wildlife. However, this impacted the wildlife much less than the previous debarking and falling of dead trees by forest managers. The biggest impact on wildlife was caused by the traps themselves. All invertebrates caught in the eclector traps (~77 000) ended up being killed.

## **7 Acknowledgments**

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## Appendix 1

Total number of individuals caught during the study, divided into different types of dead wood (S = standing with bark, L = debarked log, R = log with bark) and years of debarking (or leaving with bark). For every species, its Catalogous number (Lundberg, 1995), red-list status, nature value indication and saproxylic category (facultative or obligate) is specified.

Species	Catalogus number 1995	Red list 2020	Nature value indicator	Saproxylic class	S	L	R	2019	2020	2021	2022	Total
<i>Acanthocinus griseus</i>	3588	NT	1	O	11	0	0	0	0	5	6	11
<i>Agathidium laevigatum</i>	866	LC	0	F	0	0	1	0	1	0	0	1
<i>Ampedus balteatus</i>	2447	LC	0	O	8	3	0	1	2	6	2	11
<i>Ampedus nigrinus</i>	2453	LC	0	O	0	1	0	0	0	1	0	1
<i>Ampedus sanguineus</i>	2437	LC	0	O	0	0	1	0	1	0	0	1
<i>Ampedus tristis</i>	2451	LC	0	O	2	2	2	3	1	2	0	6
<i>Anaspis flava</i>	3425	LC	0	O	6	1	1	1	6	1	0	8
<i>Anaspis frontalis</i>	3417	LC	0	O	6	2	1	2	6	1	0	9
<i>Anaspis marginicollis</i>	3419	LC	0	O	2	0	0	0	0	2	0	2
<i>Anaspis rufilabris</i>	3424	LC	0	O	25	2	3	3	22	1	4	30
<i>Anaspis thoracica</i>	3420	LC	0	O	7	0	0	0	5	2	0	7
<i>Anobium punctatum</i>	2641	LC	0	O	3	0	0	0	0	1	2	3
<i>Anobium thomsoni</i>	2646	LC	1	O	2	0	0	0	0	0	2	2
<i>Anomognathus cuspidatus</i>	2120	LC	0	O	1	0	1	0	1	0	1	2
<i>Anthribus nebulosus</i>	3918	LC	0	O	20	0	0	0	0	0	20	20
<i>Arthopalus rusticus</i>	3489	LC	0	O	1	0	0	0	0	1	0	1
<i>Atheta crassicornis</i>	1994	LC	0	F	1	0	0	0	0	0	1	1
<i>Atheta sodalis</i>	1925	LC	0	F	1	1	1	0	1	0	2	3
<i>Bibloporus bicolor</i>	1330	LC	0	O	3	0	7	0	10	0	0	10
<i>Buprestis heamorrhoidelis</i>	2497	NT	1	O	0	1	0	0	0	1	0	1
<i>Cardiophorus ruficollis</i>	2469	LC	0	O	1	0	0	0	0	1	0	1
<i>Cartodere nodifer</i>	3166	LC	0	F	1	0	0	0	1	0	0	1
<i>Cerylon deplanatum</i>	3040	NT	1	O	2	0	0	0	2	0	0	2

<i>Cerylon ferrugineum</i>	3038	LC	0	O	1	0	0	0	1	0	0	1
<i>Cerylon histeroides</i>	3037	LC	0	O	2	1	0	0	2	0	1	3
<i>Cis festivus</i>	3238	LC	0	O	0	1	1	0	1	1	0	2
<i>Cis punctulatus</i>	3225	LC	0	O	0	0	5	0	5	0	0	5
<i>Corticaria lateritia</i>	3191	LC	0	O	67	1	0	3	6	25	34	68
<i>Corticaria longicornis</i>	3182	LC	0	F	79	4	0	1	1	25	56	83
<i>Corticarina similata</i>	3198	LC	0	F	1	0	0	0	1	0	0	1
<i>Corticeus fraxini</i>	3391	VU	1	O	104	0	0	0	8	74	22	104
<i>Corticeus linearis</i>	3396	LC	0	O	1	0	0	0	0	0	1	1
<i>Corticeus suturalis</i>	3393	NT	1	O	12	0	0	0	6	4	2	12
<i>Corticeus unicolor</i>	3389	LC	1	O	4	0	0	0	0	0	4	4
<i>Cortinicara gibbosa</i>	3197	LC	0	F	5	0	0	0	0	0	5	5
<i>Cryptolestes abietis</i>	2888	LC	0	O	82	0	0	0	0	2	80	82
<i>Crypturgus cinereus</i>	4505	LC	0	O	8	3	0	0	1	3	7	11
<i>Crypturgus pusillus</i>	4506	LC	0	O	5	1	0	0	0	5	1	6
<i>Crypturgus subcribrosus</i>	4504	LC	0	O	19	3	1	1	3	6	13	23
<i>Crypturgus spp.</i>	-	LC	0	O	40 304	67	2034	28	2833	4913	34 631	42 405
<i>Curtimorda maculosa</i>	3433	LC	0	O	0	1	0	0	0	1	0	1
<i>Dasytes caeruleus</i>	2709	LC	0	O	9	1	0	0	2	3	5	10
<i>Dasytes niger</i>	2710	LC	0	O	1	1	0	0	0	1	1	2
<i>Dasytes plumbeus</i>	2712	LC	0	O	1	0	0	0	0	1	0	1
<i>Diaperis boleti</i>	3343	LC	0	O	1	2	0	0	1	2	0	3
<i>Dienerella elongata</i>	3150	LC	0	F	1	0	0	0	0	0	1	1
<i>Dromius agilis</i>	344	LC	0	O	3	0	0	0	0	0	3	3
<i>Dropephylla ioptera</i>	1421	LC	0	O	1	0	0	0	0	1	0	1
<i>Dryocoetes autographus</i>	4502	LC	0	O	1	0	3	0	3	0	1	4
<i>Enicmus rugosus</i>	3146	LC	0	O	6	5	3	0	6	6	2	14
<i>Epuraea angustula</i>	2753	LC	0	O	1	0	0	0	0	0	1	1
<i>Epuraea laeviuscula</i>	2750	LC	0	O	1	0	0	0	0	0	1	1
<i>Epuraea marseuli</i>	2759	LC	0	O	7	0	0	0	0	0	7	7
<i>Epuraea thoracica</i>	2752	LC	0	O	1	0	0	0	0	0	1	1

<i>Ernobius abietinus</i>	2635	LC	0	F	0	1	0	0	0	1	0	1
<i>Ernobius mollis</i>	2633	LC	0	O	1	0	0	0	0	1	0	1
<i>Euglenes pygmaeus</i>	3313	LC	0	O	20	2	2	0	6	18	0	24
<i>Euplectus decipiens</i>	1341	LC	0	O	0	0	3	0	3	0	0	3
<i>Euplectus karsteni</i>	1349	LC	0	F	1	2	1	0	3	1	0	4
<i>Euplectus nanus</i>	1338	LC	0	F	3	1	6	0	9	1	0	10
<i>Euplectus punctatus</i>	1347	LC	0	O	15	4	15	0	26	6	2	34
<i>Gabrius splendidulus</i>	994	LC	0	F	2	2	4	0	6	1	1	8
<i>Globicornis emarginata</i>	2576	LC	1	O	0	1	0	0	0	1	0	1
<i>Grynocharis oblonga</i>	2682	LC	1	O	1	0	0	0	1	0	0	1
<i>Hadreule elongatula</i>	3239	LC	0	O	3	0	1	2	2	0	0	4
<i>Hylastes cunicularius</i>	4449	LC	0	O	1	0	0	0	0	0	1	1
<i>Hylis olexai</i>	2486	LC	1	O	0	0	2	0	2	0	0	2
<i>Hylurgops palliatus</i>	4446	LC	0	O	28	0	1	0	1	1	27	29
<i>Ipidia binotata</i>	2827	LC	1	O	51	1	8	3	36	18	3	60
<i>Ips typographus</i>	4496	LC	0	O	1803	1	9	0	9	1022	782	1813
<i>Latridius hirtus</i>	3134	LC	0	O	0	3	1	2	1	1	0	4
<i>Latridius minutus</i>	3137	LC	0	F	1	0	0	0	0	0	1	1
<i>Leiestes seminiger</i>	3848	NT	1	O	1	0	0	0	0	1	0	1
<i>Leptophloeus alternans</i>	2889	LC	0	O	20	0	2	0	2	3	17	22
<i>Leptusa fumida</i>	2111	LC	0	O	104	0	0	0	1	54	49	104
<i>Leptusa pulchella</i>	2109	LC	0	O	6	0	0	0	0	4	2	6
<i>Malthinus frontalis</i>	2373	LC	0	O	25	1	1	1	5	7	14	27
<i>Malthodes guttifer</i>	2380	LC	0	O	0	0	1	0	1	0	0	1
<i>Malthodes sp.</i>	-	LC	-	O	0	1	0	0	0	1	0	1
<i>Megatoma undata</i>	2579	LC	0	F	2	0	6	0	6	1	1	8
<i>Melanotus villosus</i>	2458	LC	0	O	4	0	0	2	1	0	1	4
<i>Microbregma emarginatum</i>	2647	LC	1	O	13	0	0	0	10	0	3	13
<i>Nemozoma elongatum</i>	2684	LC	0	O	3	0	0	0	0	0	3	3
<i>Nudobius lentus</i>	1162	LC	0	O	33	0	4	0	7	12	18	37
<i>Orthoperus atomus</i>	3126	LC	0	F	3	1	3	0	4	2	1	7

<i>Palorus depressus</i>	3364	LC	0	F	11	0	0	0	3	1	7	11
<i>Paromalus parallelepipedus</i>	680	LC	1	O	205	1	5	0	29	100	82	211
<i>Phloeonomus pusillus</i>	1445	LC	0	O	714	5	5	0	5	30	689	724
<i>Phloeopora nitidiventris</i>	1799	LC	0	O	48	0	0	0	1	16	31	48
<i>Phloeopora testacea</i>	1798	LC	0	O	48	0	0	0	15	7	26	48
<i>Phyllodrepa melanocephala</i>	1412	LC	0	F	0	0	1	0	1	0	0	1
<i>Pityogenes chalcographus</i>	4480	LC	0	O	2	0	0	0	0	0	2	2
<i>Pityophagus ferrugineus</i>	2839	LC	0	O	0	1	0	0	0	0	1	1
<i>Placusa depressa</i>	2128	LC	0	O	207	0	1	0	2	21	185	208
<i>Platysoma lineare</i>	703	NT	1	O	8	0	0	0	0	4	4	8
<i>Plegaderus caesus</i>	652	LC	1	O	1	0	0	0	0	0	1	1
<i>Plegaderus vulneratus</i>	651	LC	0	O	194	0	3	0	9	49	139	197
<i>Polygraphus poligraphus</i>	4466	LC	0	O	471	0	0	0	0	0	471	471
<i>Proteinus brachypterus</i>	1395	LC	0	F	0	0	1	0	1	0	0	1
<i>Ptinus dubius</i>	2615	LC	0	O	5	0	0	0	1	0	4	5
<i>Ptinus subpilosus</i>	2622	LC	0	O	46	1	0	1	14	12	20	47
<i>Pytho depressus</i>	3291	LC	0	O	3	0	1	0	4	0	0	4
<i>Quedius mesomelinus</i>	1105	LC	0	F	5	0	0	1	0	0	4	5
<i>Quedius xanthopus</i>	1118	LC	0	F	0	0	1	0	1	0	0	1
<i>Rhagium inquisitor</i>	3499	LC	0	O	6	0	1	0	4	2	1	7
<i>Rhizophagus depressus</i>	2846	LC	0	O	2	0	0	0	0	0	2	2
<i>Rhizophagus dispar</i>	2851	LC	0	F	2	0	0	0	0	2	0	2
<i>Rhyncolus ater</i>	4296	LC	0	O	24	1	0	3	11	4	7	25
<i>Rhyncolus elongatus</i>	4295	NT	1	O	1	0	0	0	0	1	0	1
<i>Rhyncolus sculpturatus</i>	4298	LC	0	O	1	0	0	0	0	0	1	1
<i>Scymnus limbatus</i>	3074	LC	0	F	2	0	1	0	1	1	1	3
<i>Serropalpus barbatus</i>	3474	LC	1	O	2	0	1	0	1	1	1	3
<i>Stenichnus bicolor</i>	950	LC	0	F	0	3	1	3	1	0	0	4
<i>Stenichnus godarti</i>	948	LC	0	O	0	2	2	1	2	0	1	4
<i>Strophosoma capitatum</i>	4084	LC	0	O	1	1	0	0	0	0	2	2
<i>Tetropium castaneum</i>	3493	LC	0	O	6	0	0	0	0	5	1	6



<i>Tetropium fuscum</i>	3494	LC	0	O	113	0	0	0	0	13	100	113
<i>Thanasimus formicarius</i>	2691	LC	0	O	9	0	3	0	4	5	3	12
<i>Thiasophila wockii</i>		LC	0	F	0	0	1	0	1	0	0	1
<i>Tomoxia bucephala</i>	3427	LC	0	O	1	0	0	0	1	0	0	1
<i>Trypodendron lineatum</i>	4510	LC	0	O	4	0	0	0	0	0	4	4
<i>Trypodendron lineatum/laeve</i>		LC	0	O	394	1	1	0	2	0	394	396
<i>Tyrus mucronatus</i>	1382	LC	0	F	0	0	1	0	1	0	0	1
<i>Zilora ferruginea</i>	3477	NT	1	O	1	0	0	0	1	0	0	1
Total individuals					45 512	141	2165	62	3197	6529	38 030	47 818
Total species					102	43	50	19	76	69	77	124

## Appendix 2

Detailed information about every trap, including: in which nature reserve the trap was placed, on what kind and age of dead wood it was installed (S = standing wood with bark, L = debarked log, R = log with bark), how many individuals and species of saproxylic beetles were caught in the trap, the trap's circumference and diameter at breast height, the degree of canopy openness above the trap, its bark coverage and coordinates.

Reserve	Type	Number of trap	Year of debarking	Age	Number of individuals	Number of species	CBH [cm]	DBH [cm]	Canopy openness [%]	Bark cover [%]	N-coor.	E-coor.
Loreberg	S	1	2019	4	3	3	108	34,4	74,2	85	58°44.85449'	15°47.50830'
Loreberg	S	2	2019	4	6	5	121	38,5	59,8	90	58°44.85428'	15°47.50289'
Loreberg	S	3	2019	4	14	7	98	31,2	62,7	90	58°44.85421'	15°47.49492'
Loreberg	L	1	2019	4	4	4	92,1	29,3	64,5	0	58°44.83348'	15°47.52805'
Loreberg	L	2	2019	4	0	0	107,8	34,3	64	0	58°44.83255'	15°47.53234'
Loreberg	L	3	2019	4	5	2	111	35,3	62,7	0	58°44.83929'	15°47.54129'
Loreberg	R	1	2019	4	4	1	86	27,4	66,6	0	58°44.86032'	15°47.52614'
Loreberg	R	2	2019	4	5	3	85	27,1	55,1	50	58°44.82035'	15°47.56183'

Loreberg	R	3	2019	4	21	4	84	26,7	64,7	100	58°44.81887'	15°47.54656'
Loreberg	S	1	2020	3	45	14	125,5	39,9	45,9	100	58°44.40718'	15°48.21686'
Loreberg	S	2	2020	3	26	9	85,3	27,2	44,2	100	58°44.41078'	15°48.20870'
Loreberg	S	3	2020	3	16	9	102,8	32,7	41,1	100	58°44.40034'	15°48.20125'
Loreberg	L	1	2020	3	1	1	97,6	31,1	73	0	58°44.86193'	15°47.59661'
Loreberg	L	2	2020	3	0	0	89	28,3	78,6	0	58°44.85840'	15°47.58718'
Loreberg	L	3	2020	3	2	2	79,5	25,3	39,2	0	58°44.40518'	15°48.23173'
Loreberg	R	1	2020	3	89	18	116,5	37,1	41,2	100	58°44.41849'	15°48.20910'
Loreberg	R	2	2020	3	44	8	108,1	34,4	39,7	90	58°44.42225'	15°48.20684'
Loreberg	R	3	2020	3	9	7	108,7	34,6	49,4	100	58°44.41147'	15°48.27052'
Loreberg	S	1	2021	2	736	21	119,1	37,9	45,8	100	58°44.76219'	15°47.54821'
Loreberg	S	2	2021	2	256	5	98,1	31,2	85,1	100	58°44.74880'	15°47.53403'
Loreberg	S	3	2021	2	372	22	113	36	89,4	95	58°44.78566'	15°47.57112'
Loreberg	L	1	2021	2	7	2	100,6	32	94,2	0	58°44.77210'	15°47.53003'
Loreberg	L	2	2021	2	7	3	97	30,9	63,9	0	58°44.75556'	15°47.52763'
Loreberg	L	3	2021	2	11	1	92,2	29,3	82,5	0	58°44.75563'	15°47.53652'
Loreberg	S	1	2022	1	1624	16	93,6	29,8	39,3	50	58°44.70987'	15°47.30774'
Loreberg	S	2	2022	1	7670	22	98,7	31,4	42,7	100	58°44.71175'	15°47.31665'
Loreberg	S	3	2022	1	9544	18	91,5	29,1	36,3	60	58°44.71004'	15°47.32166'
Loreberg	L	1	2022	1	1	1	93	29,6	80,3	0	58°44.63475'	15°48.33893'
Loreberg	L	2	2022	1	0	0	84	26,7	74,3	0	58°44.63641'	15°48.32962'
Loreberg	L	3	2022	1	2	2	86,7	27,6	66,1	0	58°44.63168'	15°48.32759'
Ösbyskogen	S	1	2020	3	253	5	108	34,4	46,6	100	58°43.72310'	16°13.28255'

Ösbyskogen	S	2	2020	3	8	6	104	33,1	51,5	85	58°43.72891'	16°13.27064'
Ösbyskogen	S	3	2020	3	4	2	133	42,3	55,2	95	58°43.73076'	16°13.26758'
Ösbyskogen	L	1	2020	3	1	1	91,1	29	70,4	0	58°43.73378'	16°13.25797'
Ösbyskogen	L	2	2020	3	4	4	97	30,9	82,8	0	58°43.73772'	16°13.26338'
Ösbyskogen	L	3	2020	3	1	1	110,7	35,2	82,1	0	58°43.73598'	16°13.27789'
Ösbyskogen	R	1	2020	3	27	7	101,2	32,2	76,5	100	58°43.72949'	16°13.28446'
Ösbyskogen	S	1	2021	2	192	8	108	34,4	43	95	58°43.69497'	16°13.33129'
Ösbyskogen	S	2	2021	2	23	11	120,4	38,3	42,7	100	58°43.68184'	16°13.31667'
Ösbyskogen	S	3	2021	2	11	8	105,6	33,6	43,5	95	58°43.68695'	16°13.32466'
Ösbyskogen	L	1	2021	2	17	2	99,3	31,6	74,3	0	58°43.69690'	16°13.32383'
Ösbyskogen	L	2	2021	2	7	4	91,8	29,2	68,6	0	58°43.69220'	16°13.31086'
Ösbyskogen	L	3	2021	2	0	0	114	36,3	79,1	0	58°43.69399'	16°13.29977'
Ösbyskogen	S	1	2022	1	12 696	28	127	40,4	38,7	75	58°43.75574'	16°13.44926'
Ösbyskogen	S	2	2022	1	1836	14	85	27,1	43,9	90	58°43.75661'	16°13.43357'
Ösbyskogen	S	3	2022	1	1411	20	90,5	28,8	41,1	65	58°43.76000'	16°13.41256'
Ösbyskogen	L	1	2022	1	6	4	113,3	36,1	69,2	0	58°43.71315'	16°13.44205'
Ösbyskogen	L	2	2022	1	4	1	112,3	35,7	62,7	0	58°43.72103'	16°13.42996'
Ösbyskogen	L	3	2022	1	2	1	98	31,2	78,5	0	58°43.71717'	16°13.40162'
Storskogen	S	1	2020	3	419	10	111,8	35,6	61,7	100	58°13.28773'	16°12.65948'
Storskogen	S	2	2020	3	185	18	119,3	38	67,1	95	58°13.29206'	16°12.65097'
Storskogen	S	3	2020	3	18	6	110	35	48,7	90	58°13.28625'	16°12.65302'
Storskogen	L	1	2020	3	4	3	85,2	27,1	61,5	0	58°13.28820'	16°12.65159'
Storskogen	L	2	2020	3	2	2	89	28,3	60,7	0	58°13.28748'	16°12.65640'

Storskogen	L	3	2020	3	6	2	94,5	30,1	71,4	0	58°13.28618'	16°12.65491'
Storskogen	R	1	2020	3	1925	13	92,5	29,4	65,2	100	58°13.28622'	16°12.65656'
Storskogen	R	2	2020	3	13	8	105	33,4	64,3	100	58°13.28216'	16°12.63524'
Storskogen	R	3	2020	3	9	9	121	38,5	66,8	95	58°13.28386'	16°12.62983'
Storskogen	S	1	2021	2	1274	17	120	38,2	54,2	100	58°13.44454'	16°12.60011'
Storskogen	S	2	2021	2	166	9	94	29,9	45,8	95	58°13.43930'	16°12.56298'
Storskogen	S	3	2021	2	721	13	99	31,5	42,5	75	58°13.45736'	16°12.56869'
Storskogen	L	1	2021	2	3	2	101,5	32,3	68,5	0	58°13.42805'	16°12.57793'
Storskogen	L	2	2021	2	1	1	88,6	28,2	74,2	0	58°13.42827'	16°12.57823'
Storskogen	L	3	2021	2	2	2	118	37,6	57,2	0	58°13.43960'	16°12.58147'
Storskogen	S	1	2022	1	812	27	113,8	36,2	47,9	100	58°13.35167'	16°12.66709'
Storskogen	S	2	2022	1	1360	37	135	43	46	100	58°13.34887'	16°12.66874'
Storskogen	S	3	2022	1	773	26	107,9	34,3	41,1	100	58°13.34806'	16°12.66727'
Storskogen	L	1	2022	1	6	2	99,2	31,6	75,7	0	58°13.36337'	16°12.64315'
Storskogen	L	2	2022	1	0	0	121	38,5	75,4	0	58°13.36185'	16°12.63808'
Storskogen	L	3	2022	1	1	1	117	37,2	68,3	0	58°13.36219'	16°12.64902'
Hälla	S	1	2020	3	19	8	136,4	43,4	54,1	100	58°24.11644'	16°27.85863'
Hälla	S	2	2020	3	19	9	131,6	41,9	46,9	15	58°24.11812'	16°27.85934'
Hälla	S	3	2020	3	18	9	87,9	28	46,4	100	58°24.11276'	16°27.84851'
Hälla	L	1	2020	3	0	0	104,4	33,2	64,6	0	58°24.10804'	16°27.87941'
Hälla	L	2	2020	3	6	6	96,3	30,7	43	0	58°24.13085'	16°27.85676'
Hälla	L	3	2020	3	5	4	108,1	34,4	50,3	0	58°24.13844'	16°27.84459'
Hälla	R	1	2020	3	19	10	95,5	30,4	63,4	90	58°24.10553'	16°27.87541'

Hälla	S	1	2021	2	887	21	119,7	38,1	52,3	75	58°24.04243'	16°27.98036'
Hälla	S	2	2021	2	1814	22	110	35	57,4	100	58°24.04148'	16°27.98597'
Hälla	S	3	2021	2	12	9	103,5	32,9	59	80	58°24.03226'	16°27.99023'
Hälla	L	1	2021	2	2	2	130,5	41,5	61,6	0	58°24.05001'	16°27.95755'
Hälla	L	2	2021	2	4	4	115,4	36,7	75	0	58°24.03956'	16°27.97080'
Hälla	L	3	2021	2	4	4	94	29,9	70,8	0	58°24.04231'	16°27.95795'
Hälla	S	1	2022	1	20	14	113,7	36,2	48,5	100	58°23.86867'	16°27.88018'
Hälla	S	2	2022	1	170	13	114,1	36,3	44,5	100	58°23.86948'	16°27.87293'
Hälla	S	3	2022	1	79	12	122,2	38,9	45,6	95	58°23.87078'	16°27.86926'
Hälla	L	1	2022	1	6	5	98	31,2	35,2	0	58°23.86093'	16°27.82934'
Hälla	L	2	2022	1	5	5	90,7	28,9	57,3	0	58°23.85608'	16°27.87940'
Hälla	L	3	2022	1	2	2	102,6	32,7	58,9	0	58°23.86129'	16°27.88406'