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Long-term effects of clear-cut forestry on beetle species richness and abundance in Norwegian boreal forests

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Preface

This master thesis is part of the EcoForest project, and I want to thank all sponsors for finances and all landowners for letting us use their forests as research areas. I also want to thank UNIFOR (UMBs research fund) for financial support for the fieldwork.

I want to thank my supervisors Anne Sverdrup-Thygeson and Tone Birkemoe, as well as co-supervisor Milda Norkute for all their help and guidance on the path of producing this thesis. Sindre Ligaard also needs a big thank you for identifying the beetles to species, which was a big part of making this thesis possible.

I also have to thank my fellow master students Ingvild Skjelle Fimreite and Vendel-Agathe Sundgot Hide for great teamwork in field and in lab, and all hours spent on the road. Especially to Ingvild for keeping the hopes up with me even after days of rainy weather and windthrows blocking our way, and Vendel-Agathe as a co-driver with extraordinary taste in music that led to uplifting sing-along sessions in the car.

Thanks to my classmates for all the daily lunch breaks this semester and for making long days in study hall a lot easier to get through. Lastly, I must thank all my friends as well as other fellow NMBU-students who have made my five years at Ås unforgettable.

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Abstract

For the last approximately 70 years, clear-cutting has been the common method in Scandinavian forestry. Since more than half of the Scandinavian species live in the forest, this intensive forestry method has caused concern about its effects on biodiversity. Since the early clear-cut forests now have reached the later logging class, it is possible to investigate how this forestry method impacts the ecological environment on a long-term basis. A large portion of the beetle (*Coleoptera)* species are saproxylic and thus dependent on deadwood, which is one of the ecological factors that have been altered by forestry. This study aims to investigate whether beetle biodiversity differs between older clear-cut forests and old near-natural forests.

A total of 17 970 individuals of beetles, represented by 445 species, were collected using window traps in ten site pairs of clear-cut forests and near-natural forests in Southeastern Norway. The volume and diameter of lying deadwood in each study plot were measured. From this, the variation in the number of beetle species and individuals between the two forest types was compared to see if logging history affects the beetle biodiversity. Correspondingly, the patterns of saproxylic species, different feeding guilds and red-listed species were analyzed as well. Beetle biodiversity was also examined in relation to the volumes of deadwood available.

The near-natural and clear-cut forests differed in relation to deadwood as near-natural plots always had higher volumes, even though there was a large variation between sites. In addition, there were clearly more large diameter logs of deadwood in near-natural forests. Surprisingly, forest type did not affect overall species richness or abundance to a large extent, but more saproxylic individuals were caught in near-natural plots. Deadwood, on the other hand, had more of an effect on beetle biodiversity, as higher deadwood volumes led to a higher total species richness, and large diameter deadwood was of special importance for saproxylic beetles. Detritivores also increased in both species richness and abundance with higher deadwood volumes. Even though the type of forest did not show many significant differences besides deadwood volumes, this study shows that ecological factors available in the forest stands are of importance for beetle diversity, and thus that availability of deadwood resources needs to be assessed in forest management.

Sammendrag

Gjennom de siste om lag 70 årene har flatehogst vært den vanligste hogstformen i norsk skogbruk. Over halvparten av artene i Skandinavia lever i skog, og intensivt skogbruk har derfor ført med seg bekymring for hvordan det påvirker biodiveristeten. Ettersom de første flatehogde skogarealene nå har nådd sen hogstklasse, er det mulig å undersøke hvilke effekter flatehogst har på artsmangfoldet på lengre sikt. En stor andel billearter (*Coleoptera*) lever av og i død ved, og er dermed avhengig av å ha død ved tilgjengelig. Dette er en økologisk faktor som i stor grad har blitt påvirket av skogbruk. Denne studien undersøker hvordan biodiversiteten av biller varierer mellom eldre flatehogde skogarealer og eldre naturskognære skoger.

Totalt 17 970 billeindivider, representert av 445 arter, ble samlet inn ved bruk av vindusfeller på ti studiepar bestående av tidligere flatehogde og naturnære skoger i Sørøst-Norge. Volum og diameter av liggende død ved ble målt i hvert studieplott. Dette ble brukt til å sammenligne hvordan antall arter og individer av biller varierte mellom de to skogstypene, for å undersøke om skogbrukshistorien har påvirket biodiversiteten av biller. Tilsvarende ble vedlevende arter, samt rødlistede arter og variasjon innen ulike dietter analysert. I tillegg ble sammenhengen mellom tilgjengelige mengder av død ved og biodiversiteten av biller undersøkt.

Naturnære og tidligere flatehogde skoger viste forskjeller når det gjaldt volum av død ved. Naturskognære plott hadde alltid høyere volum, selv om variasjonen var stor mellom studieområdene. I tillegg var det klart mer død ved av stor diameter i naturnære skoger. Skogtype påvirket ikke antallet arter eller individer av biller i stor grad, men det ble samlet flere vedlevende individer i naturnær skog. Mengde død ved hadde derimot en betydelig effekt, da økt volum av død ved førte til totalt flere billearter, i tillegg til at død ved av store dimensjoner viste seg å være spesielt viktig for vedlevende biller. Volum av død ved påvirket også antallet nedbryterbiller, både med tanke på antall arter og antall individer. Selv om skogtypene viste få signifikante forskjeller utover mengde død ved, illustrerer disse resultatene at tilgjengeligheten av de økologiske faktorene i skogen er vesentlig for biodiversiteten av biller, og at tilgjengeligheten av død ved er et viktig aspekt i skogbrukssammenheng.

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1. Introduction

Over the last 100 years, human activity has accelerated the rate of biodiversity loss globally, as species are going extinct and populations are declining faster than ever before (Baillie J. E. M. et al., 2004; Barnosky et al., 2011). One of the major drivers for this decline is loss and degradation of habitat (Wagner, 2020). As the Scandinavian forests are estimated to house more than half of the Scandinavian species (Miljødirektoratet, 2023; Stokland et al., 2003), to understand the effect of forestry on biodiversity is crucial.

After the 1950s, clear-cutting, often followed by tree planting, became the common forestry method in Scandinavia (Gustafsson et al., 2010; Kuuluvainen et al., 2012). This practice changed the forest structure drastically in a short time. Earlier selective logging based on tree diameter was the common method, where trees above a certain diameter were cut down, and the forest was then reestablished by natural succession (Nygaard & Øyen, 2020). During the 1800s logging was also extensive, but a forest stand of smaller dimensional trees was normally left after cutting, as today's forest management of tree planting and thinning was not yet developed (Storaunet & Rolstad, 2020).

Extensive forestry leads to removal of microhabitats that require a long time of continuity to develop, such as deadwood of large diameter and late stages of decay (Bauhus et al., 2009; Økland et al., 1996). This is crucial because deadwood is an important part of forest ecosystems, that function as habitat for many species (Grove, 2002). Old-growth spruce dominated forests in Fennoscandia can have amounts of coarse woody debris with a mean of 60-90 m^3/ha, while the clear-cut forest stands typically have about 10 m^3/ha (Ranius et al., 2003; Siitonen, 2001). Newer data, however, show that the volume has increased to a mean of 11,1 m^3/ha in Norwegian production forests (Storaunet, 2021). The diversity of the deadwood present is also of importance for biodiversity (Similä et al., 2003), which also has a tendency to be higher in old-growth forests.

Today are 84 percent of the threatened species in Norway dependent on old-growth forests (Artsdatabanken, 2021b). This indicates that intensive forestry is a threat to biodiversity. Natural, old-growth forests house a structural heterogeneity, which leads to a continuity in the supply of diverse deadwood components. They provide habitats that are important for many species, that are lacking in intensively managed forests (Berg et al., 1994; Hedwall et al., 2013; Motta et al., 2015; Siitonen & Saaristo, 2000). This is mostly related to large, old trees, dead wood, and also canopy cover, and light conditions (Berg et al., 1994). As extensive clear-cutting is quite new, these forest stands have only recently reached the later logging class. Thus, it is very interesting to investigate the potential and alterations of older clear-cut, planted forests and compare these to old-growth forests that have also been place of timber harvesting, but not to the same extent.

Species that utilize deadwood in at least one part of their life cycle are called saproxylic species. Some species are so-called opportunistic or facultative saproxylic. They are advantaged by having deadwood available, but not completely dependent on it (Stokland et al., 2012). Others are obligate saproxylics, and these depend on deadwood in some part of their life cycle. Consequently, facultative saproxylics are likely to experience a reduction in their population together with a reduction in deadwood, but obligate saproxylics might also go locally extinct (Stokland et al., 2012).

A dying tree creates microhabitats that change and develop as the decay process happens. Different species often specialize on a tree species, a specific decay class, and a tree dimension (Stokland et al., 2003). Some species specialize on deadwood of a smaller dimension, but most species prefer larger logs of deadwood (Stokland et al., 2003). Thus, a forest with a variety of deadwood in size and decay classes provides habitats for many saproxylic species. A tree can live for several hundred years before dying and the decay can last for more than a hundred years (Stokland et al., 2012). Thus, time and continuity are required to meet all species requirements of life.

Beetles (*Coleoptera*) make up one of the largest orders of insects in the world (Adamski et al., 2019), and are one of the largest saproxylic taxonomic groups (Lassauce et al., 2011). They provide several different ecosystem services, such as pollination and decomposition (Lázaro et al., 2008; Ulyshen, 2016). Beetles are hemimetabolous insects, meaning they go through a complete morphological change from larvae to adult beetle (Gimmel & Ferro, 2018). They often utilize different habitats in each life stage, and therefore one species can be dependent on several habitats and ecological factors during its lifetime. In Norway, there are about 3600 species of beetles, and 826 of these species were considered threatened on the Norwegian red list in 2021. The most common reason was a limited distribution area, in combination with an ongoing reduction of area or quality of the habitat (Ødegaard, Hansen, et al., 2021). About 25% of the beetle species in Norway are saproxylic and depend on dead wood in at least one part of their life cycle (Siitonen, 2001; Økland et al., 1996).

High biodiversity is generally thought to increase ecosystem functions (Cardinale et al., 2012). This is linked to functional diversity, often described, through differences in species traits. Mode of nutrition is an important functional trait that links to the food chain and trophic levels. Predators regulate the abundance of other species, and detritivores decompose organic litter and improve nutrient cycling. An ecosystem is functioning better with complementary functional traits, as more services are being covered (Lefcheck & Duffy, 2015). This, of course, has an increased chance of being fulfilled as biodiversity increases. With several species sharing a functional trait, the loss of a single species might not be decisive, but an ecosystem will be more resistant to disturbance, environmental change, or species loss with a higher species richness (Hooper et al., 2005).

This master thesis aims to investigate the long-term effect of clear-cut forestry on beetle diversity, abundance, and feeding guilds, which is done by comparing beetles in old clear-cut forest stands with old near-natural forests. To know the possible differences in biodiversity between the two forest types is of importance for future decisions in relation to forest management and forest preservation. In addition, I compare the occurrence of deadwood in the two forest types to see if this can explain an eventual difference in biodiversity.

The main questions of this thesis are (1) Does the number of beetle species or individuals differ between forest types? (2) Can the volume and quality of deadwood explain differences in beetle biodiversity? I predict that near-natural forests will have a higher beetle species richness compared to clear-cut forests, but that there might be more individuals in clear-cut forests. Due to a longer continuity to develop a diverse forest structure, more species should be able to find habitat in the near-natural forests. Beetle abundance can other hand be dominated by few generalist species, and therefore possibly be higher in clear-cut forests, where these species possibly will lack competition. I also predict that higher volumes of deadwood, as well as more deadwood of a larger dimension, will increase beetle diversity. I think that saproxylic and detritivorous species will be affected the most of both near-natural forests and deadwood, as they are more dependent on deadwood resources.

2. Materials and methods

2.1 Study site and criteria

This study is part of the EcoForest project with a main aim to compare biodiversity, carbon, and ecosystem functions between former clear-cut and near-natural forests in Southeastern Norway. Each of the 10 study sites include a former clear-cut (hereafter only referred to as clear-cut) and a near-natural plot. All forest stands consist of at least 70% spruce (*Picea abies*), and bilberries (*Vaccinium myrtillus*) dominates the forest floor. Clear-cut stands were cut about 70 years ago and have reached logging class 4 or 5 today. Spruce was planted after logging but the forest stand has not been thinned. No selected stands have been ditched Near-natural sites have never been clear-cut, but these stands also have traces of tree felling. The soil profile was similar within each forest pair.

Figure 1. Pictures from one near-natural plot (left) and one clear-cut plot (right). These are taken at Gullenhaugen (GUL).

All sites are in southeastern parts of Norway, in the boreal zone from 59,8 to 60,9 degrees north. The altitude varied from 205 to 667 meters above sea level. The site pairs are located with a distance of 1-5 km (Figure 2).

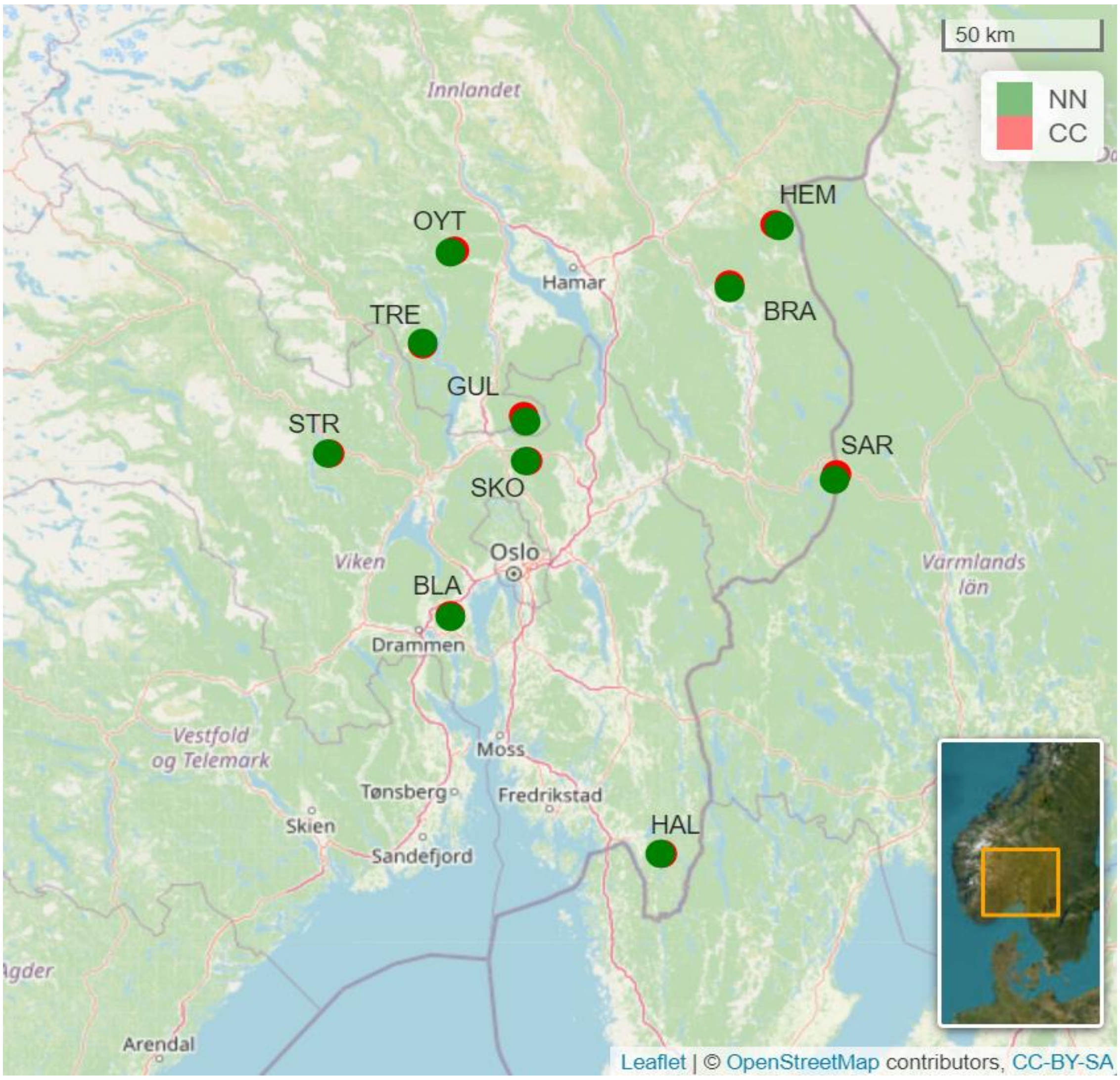

Figure 2. Location of the 10 study sites in Southeastern Norway. All consist of a near-natural plot (green) and a previously clear-cut plot (red). The plots within one site are separated by a distance of 1-5 km.

2.2 Data collection

Insects were collected using a total of 80 IBL2 window traps (CHEMIPAN, Warsaw, Poland, Figure 3). Insects collide with the trap during flight and fall through a funnel and into a liquid-filled container. In every plot four traps were placed with a 15 meters distance, forming a square around the study's main plot (Figure 3). They were hung between two trees approximately 1.5 meters above ground level, and the containers were filled with 70% propylene glycol and 30% water, as well as some dishwasher soap (Zalo) to break the water surface tension. In order to prevent rainwater from overflowing the samples, the containers got holes in each side for drainage.

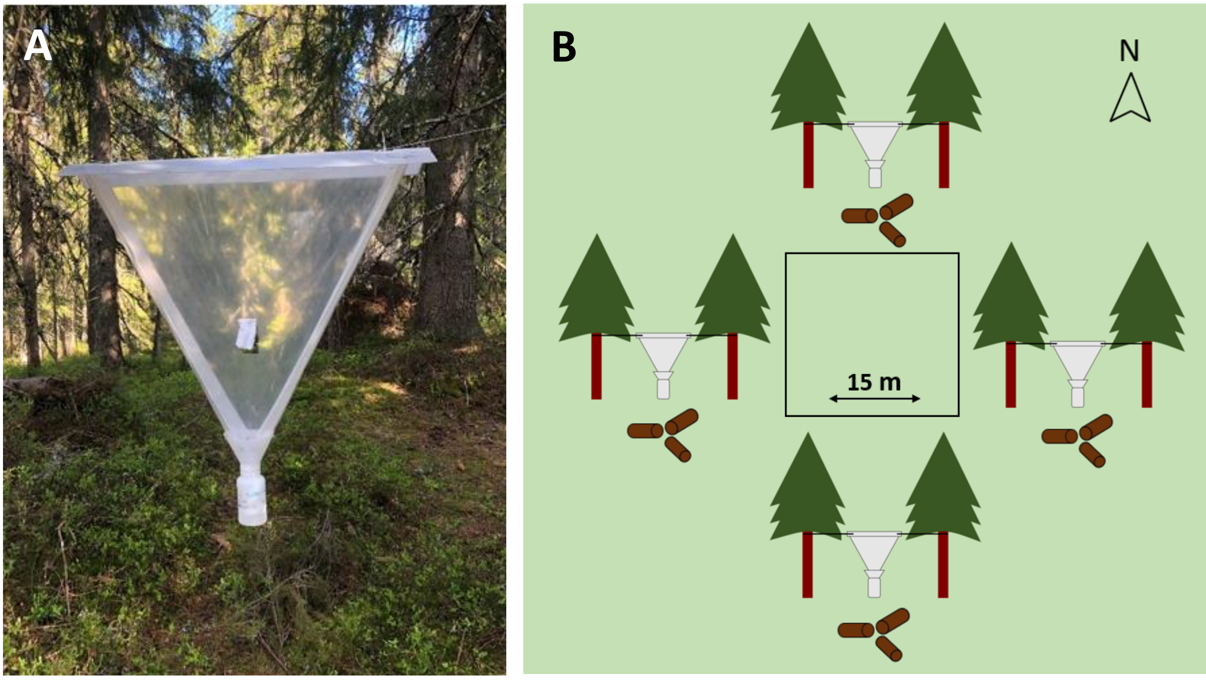

Figure 3. A. An IBL2 window trap in one of the plots. B. The placement of window traps in each plot. Four traps were placed directing north, south, east, and west around a main plot of 15x15 meters. Fresh logs were placed close to each trap for a parallel study.

A study on bark beetles (*Scolytinae*) was taking place at the same study sites, and fresh logs were put out close to the window traps for this study. Because of this, and the fact that bark beetles are attracted to the smell of alcohol (Byers, 1992), bark beetles collected in the window traps were excluded.

The study period was from late May to the end of July 2022. The containers on the window traps were collected and filled with new liquid at two-week intervals, over a total of four collecting periods. Due to time constraints was only data from the first two and the last period used in the final studies. This results in a total of 240 samples. When collected in field, the containers were poured into cups with a netting bottom, which left us with only insects and other solid substances in the cup. The waste liquid from the container was gathered in a larger container and brought back out of the forest. All samples were stored at -20 degrees for preservation, prior to handling in the lab.

2.3 Lab work and handling of data

In the lab, all beetles were transferred to 85% ethanol and identified to species by an expert in beetle taxonomy Sindre Ligaard.

The data on species that were trapped were later transformed into number of species and number of individuals per trap period per plot.

2.4 Deadwood data

Deadwood data was sampled by Siri Khalsa, Jenny Nordén, and Tom H. Hofton. It was sampled in a total transect of 133.33 x 15 meters, with the main 15x15 plot in the middle. The length (cm) and diameter of all dead wood logs above 130 cm and 5 cm in diameter within the transect were measured, and decay class was recorded, according to a five class system (Maser et al., 1979). Diameter was measured at breast height (1,3m) when possible, otherwise at the base. Only data on downed dead wood (hereafter; dead wood) were included in this study. The volume of dead wood per site was calculated with the formula for a cut of cone:

$$1/3\pi h(R^2 + Rr + r^2)$$

Deadwood logs were also grouped into four categories to estimate deadwood diversity after diameter and decay class:

1) Logs under 20 cm in diameter of decay class 1-3 (slightly decomposed).
2) Logs under 20 cm in diameter of decay class 4-5 (severely decomposed)
3) Logs over 20 in diameter of decay class 1-3.
4) Logs over 20 in diameter of decay class 4-5.

The volume of each group was calculated per plot.

2.4 Data on saproxylic species, feeding guilds and red-listed species

The beetles were grouped into categories based on the feeding guild: detrivore, predator, herbivore, or mixed feeder. Data on feeding type was collected from the Swedish database for species (Artdatabanken, n.d.), and an article by Seibold et al. (2015), and refer to the adult life stage of the species.

All deadwood-dependent (saproxylic) beetle species were identified (both obligate and facultative) and separate analyses were carried out to identify the factors that drive their diversity and abundance. The list of saproxylic species was obtained from The Saproxylic Database (Dahlberg & Stokland, 2004), and the same article by Seibold et al. (2015).

Information on red-listed species was gained from the Norwegian Red List of Species from 2021 (Artsdatabanken, 2021a).

2.5 Statistical analyses

One sample from the second trap period (location: Särlikampi – SAR, clear-cut plot) went missing. To account for this missing data, I calculated beetle abundance based on the mean abundance of the three remaining traps in the same plot in the same period. For number of species, I calculated the mean percentage of unique species from each of the three traps and multiplied by the mean number of species.

All data analyses were done using R version 4.1.2 (R Core Team, 2021) and RStudio version 2022.12.0 (R Core Team, 2021). I used the performance package (Lüdecke et al., 2021) to check for overdispersion and multicollinearity in my dataset. I checked model fit by investigating residual variance plots with the DHARMa package (Hartig, 2022). All figures in the result section were made with the package "ggplot2" (Wickham, 2016).

To analyze variation in deadwood volumes between forest types I used a linear model (LM), with volume as response variable, and forest type as predictor variable. The response variable was transformed with the square root (sqrt) function to normalize the distribution.

Total number of species or individuals, as well as only saproxylic species, were analyzed with a negative binomial general linear mixed model (GLMM), with the lme4 package (Bates et al., 2015). Here two models were used: one with forest type and total deadwood volumes as predictor variables, and one with deadwood categories as predictor variables. The total deadwood volumes and the deadwood categories were placed in separate models because of high correlation, causing multicollinearity when put in the same model. I used the negative binomial model because of overdispersion in the dataset and put site as random effect to account for repetitive sampling from the same sites. I also used the lmerTest package (Kuznetsova et al., 2017) to summarize the results of these analyses. Feeding guilds and red-listed species were analyzed with the same negative binomial GLMM with forest type and total deadwood volume as predictor variables.

3. Results

3.1 Amounts of downed deadwood

Altogether there was a significantly higher volume of deadwood in near-natural than in clear-cut sites ($p<0.001$). The near-natural plots had a mean of 6.96 m^3, while clear-cuts had a mean of 2.03m^3 (Figure 4). This means that there was 243% more deadwood in the near-natural plots than in the clear-cut plots. When calculated into hectares, to make numbers comparable with previous studies, near-natural plots have a mean volume of deadwood of 35 m^3/ha, and clear-cut plots a mean of 10 m^3/ha (Appendix 3 for calculations). There was a large variation between sites, as the difference in total volume between forest pairs varied from having 0.5 m^3 to 15.1 m^3 more in near-natural than in clear-cut plots (Figure 4).

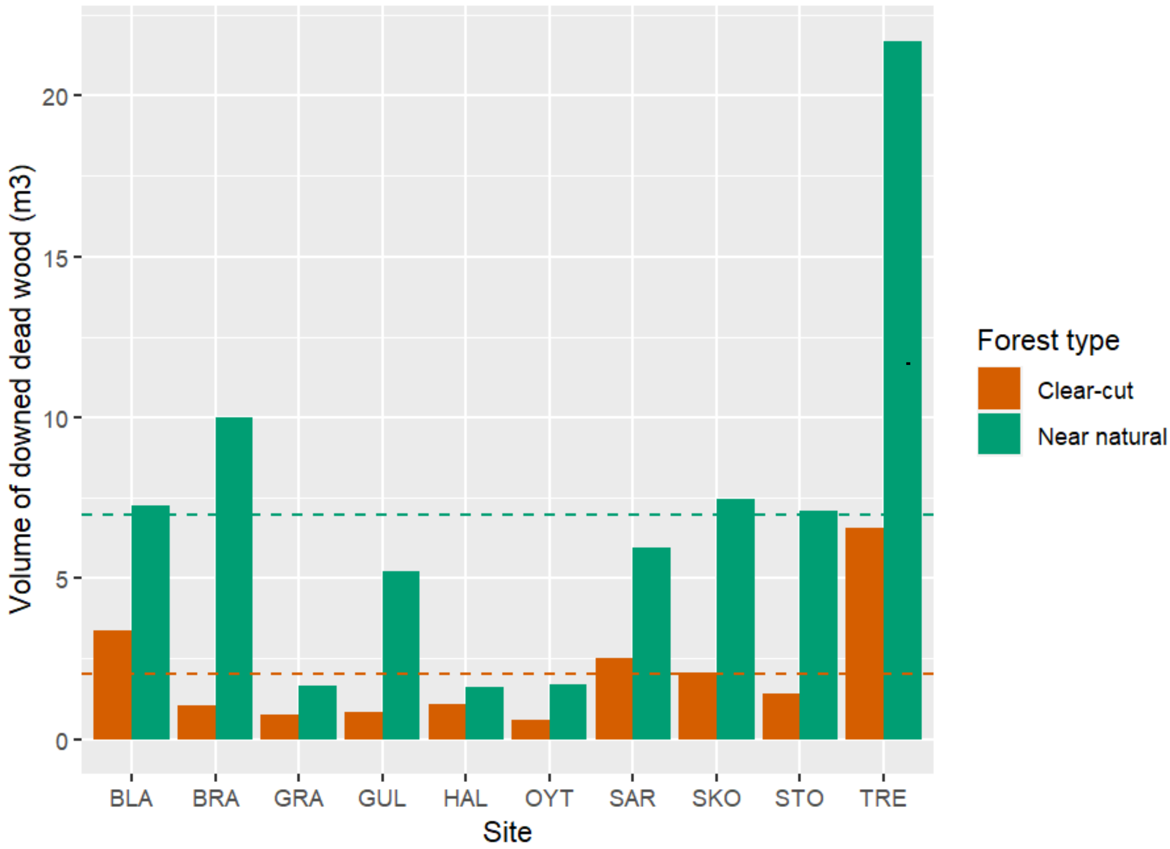

Figure 4. Total volume (m^3) of deadwood at each study site. The dashed lines represent the mean for near-natural plots (green) and clear-cut plots (red-brown).

When grouping the total volume of deadwood into categories of size and decay class, it showed that logs above 20 cm in diameter are in general more common in near-natural sites, both when slightly and severely decomposed ($p<0.001$). In contrast, the volume of logs with a diameter under 20 cm did not differ significantly between forest types, in either of the decay categories ($p=0.301$, $p=0.639$).

In all ten sites, the near-natural plot had either more or the same volume of large diameter logs as the paired clear-cut plot (Figure 5, C-D). With the smaller diameter categories this was not the case. In total, clear-cut plots did have higher volumes of small diameter logs than near-natural plots (Table 1), but within site pairs the near-natural plot had more than the clear-cut plot in several sites (Figure 5, A-B).

Table 1. Results from linear models (lm) analyzing the patterns of total deadwood volume and volume of deadwood in different categories in the two forest types. Centimeters refer to a DBH under or over 20 cm. “Slightly” refers to decay class 1-3, and “severely” refers to decay class 4-5. Clear-cut is the reference level for forest type. Significant values are given in bold font.

Predictor	*Estimate*	*SE*	*t*	*p*
Total deadwood				
(Intercept)	1.323	0.262	5.043	<0.001
Forest type	1.126	0.371	3.034	**<0.001**
	R^2: 0.261			
Deadwood groups				
<20 cm, slightly				
(Intercept)	1.062	0.118	8.963	<0.001
Forest type	-0.178	0.168	-1.064	0.301
	R^2: 0.059			
<20 cm, severely				
(Intercept)	0.433	0.046	39.335	<0.001
Forest type	-0.031	0.066	-0.472	0.639
	R^2: 0.004			
>20 cm, slightly				
(Intercept)	0.465	0.144	3.222	<0.001
Forest type	1.408	0.204	6.895	**<0.001**
	R^2: 0.450			
>20 cm, severely				
(Intercept)	0.188	0.086	2.182	0.033
Forest type	0.764	0.122	6.262	**<0.001**
	R^2: 0.403			

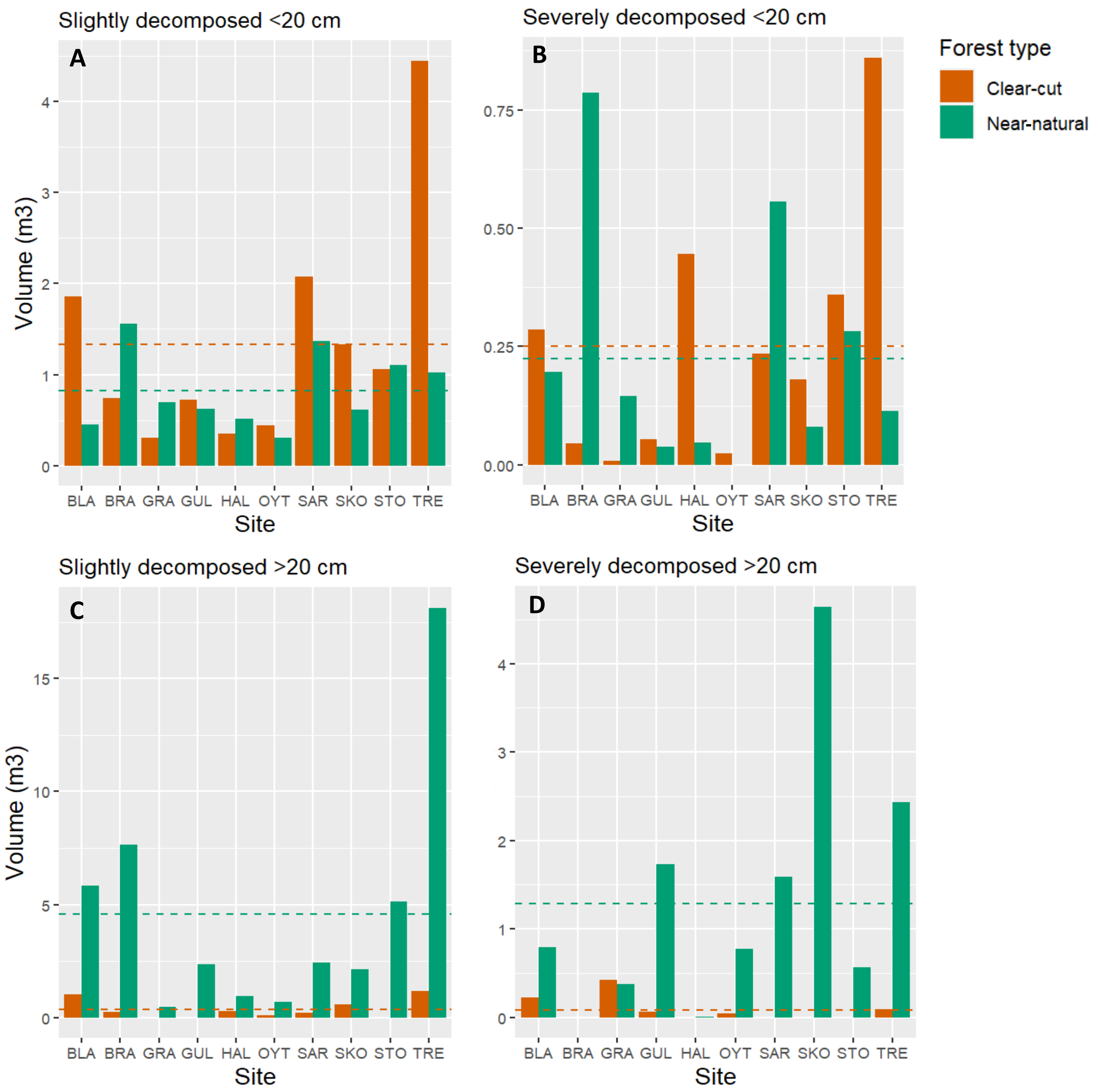

Figure 5. Volumes (m^3) of deadwood grouped by diameter and decay class for the 10 site pairs of near-natural (green) and clear-cut (red-brown) plots.

3.2 Total beetle species richness and beetle abundance

We caught a total of 17 970 individual beetles, representing 445 species. Of these, 8 958 individuals were caught in near-natural plots, representing 378 species, and 9 012 in clear-cut plots, representing 345 species. As many as 66 species were only found in clear-cut plots, and 99 species were unique for near-natural plots.

The forest type did not have a significant effect on number of species caught (Table 2, Figure 6), but the number of beetle species increased with higher total volumes of deadwood. Neither forest type nor total deadwood volume had any effect on beetle abundance.

The amount of slightly decomposed logs under 20 cm showed no effect, but the severely decomposed ones under 20 cm in diameter were on the other hand close to having an increasing effect on both species richness and abundance (Table 2). The large, slightly decomposed logs had no effect on the number of individuals either but did show a tendency to affect the number of species (p=0.097). Severely decomposed logs over 20 cm in diameter had no effect on neither number of species nor number of individuals.

Table 2. Results from the generalized linear mixed models with a negative binomial distribution estimating the effect of forest type and volume of deadwood on number of species and individuals. Clear-cut is the reference level for forest type. Significant values are given in bold font, and asterisks represent values that tend to have an effect.

	Species				**Individuals**			
Predictor	*Estimate*	*SE*	*z*	*p*	*Estimate*	*SE*	*z*	*p*
(Intercept)	4.125	0.051	80.034	<0.001	5.680	0.095	59.858	<0.001
Forest type	-0.098	0.073	-1.327	0.184	-0.062	0.116	-0.535	0.593
Deadwood	0.019	0.009	2.095	**0.036**	0.006	0.016	0.398	0.691
	Conditional R^2: 0.199				Conditional R^2: 0.324			
Deadwood categories								
(Intercept)	4.031	0.056	72.156	<0.001	5.514	0.117	47.155	<0.001
<20 cm, slightly	0.021	0.047	0.437	0.662	0.045	0.087	0.516	0.606
<20 cm, severely	0.337	0.178	1.893	0.058*	0.461	0.265	1.744	0.081*
>20 cm, slightly	0.013	0.008	1.658	0.097*	0.010	0.013	0.755	0.450
>20 cm, severely	-0.009	0.030	-0.293	0.770	-0.036	0.047	-0.766	0.444
	Conditional R^2: 0.245				Conditional R^2: 0.436			

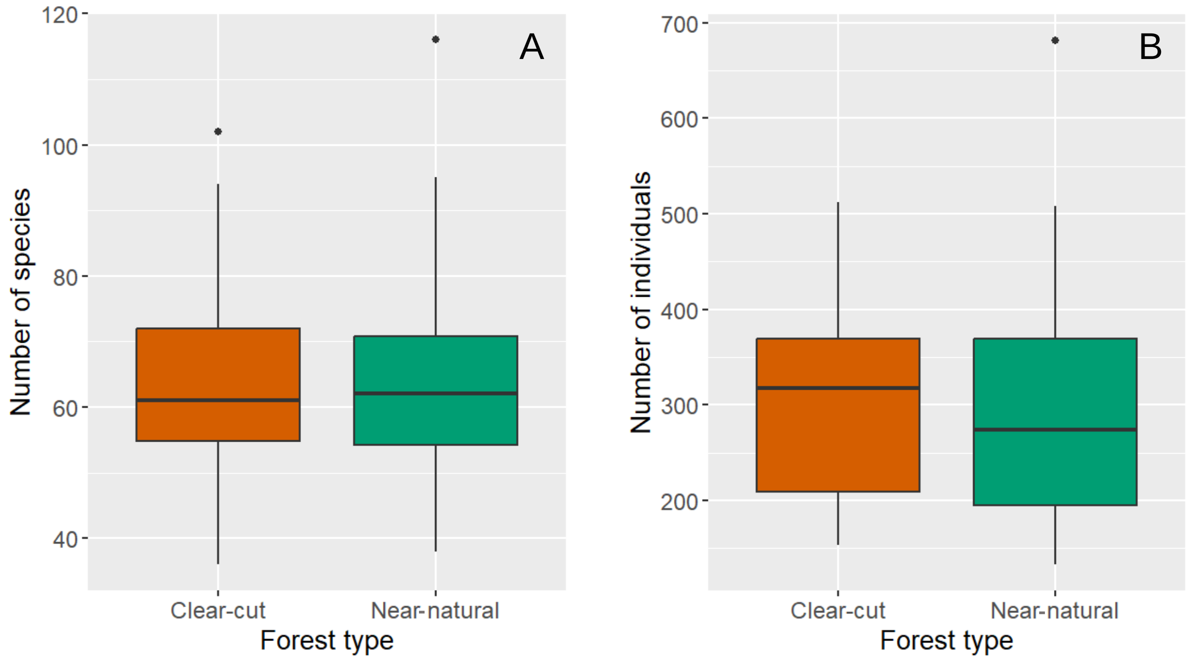

Figure 6. Species richness (A) and number of individuals (B) per plot per sampling period of beetles caught in 10 site pairs of clear-cut and near-natural plots.

3.3 Saproxylic beetles

There were 289 saproxylic species and 9 527 saproxylic individuals caught in total. This means that 65% (289 of 445) of all the beetle species and 53% (9 527 of 17 970) of the total beetle individuals caught during the sampling period were saproxylic. A total of 244 saproxylic species were found in near-natural plots, and 223 in clear-cuts, represented by respectively 5168 and 4459 individuals.

Forest type had no effect on number of saproxylic species (Table 3, Figure 7), but there were significantly more saproxylic individuals in near-natural sites (p=0.047). The total deadwood volume was close to having a positive effect on the number of saproxylic species (p=0.089), but showed no effect on number of individuals.

Logs under 20 cm in diameter, both slightly and severely decomposed, had no effect on the number of saproxylic species, but showed a tendency to affect the number of saproxylic individuals (p=0.078, p=0.067). The increase in slightly decomposed logs over 20 cm in diameter increased both the number of saproxylic species and individuals (p=0.012, p=0.019). The wide, severely decomposed logs on the other hand showed no effect.

Table 3. Results from the generalized linear mixed model with negative binomial distribution on the effect of forest type and deadwood volume on saproxylic species richness and saproxylic beetle abundance. Clear-cut is the reference level for forest type. Significant values are given in bold font, and asterisks represent values that tend to have an effect.

	Species				**Individuals**			
Predictor	*Estimate*	*SE*	*z*	*p*	*Estimate*	*SE*	*z*	*p*
(Intercept)	3.724	0.057	65.548	<0.001	4.919	0.081	60.494	<0.001
Forest type	-0.021	0.078	-0.276	0.783	0.085	0.119	0.716	**0.047**
Deadwood	0.017	0.010	1.701	0.089*	0.018	0.017	1.094	0.274
	Conditional R^2: 0.267				Conditional R^2: 0.262			
Deadwood categories								
(Intercept)	3.575	0.093	38.436	<0.001	4.636	0.131	35.355	<0.001
<20 cm, slightly	0.002	0.001	1.244	0.213	0.004	0.002	1.763	0.078*
<20 cm, severely	0.011	0.007	1.552	0.121	0.019	0.010	1.834	0.067*
>20 cm, slightly	0.010	0.004	2.519	**0.012**	0.014	0.006	2.346	**0.019**
>20 cm, severely	0.000	0.012	0.060	0.952	0.011	0.017	0.663	0.507
	Conditional R^2: 0.322				Conditional R^2: 0.370			

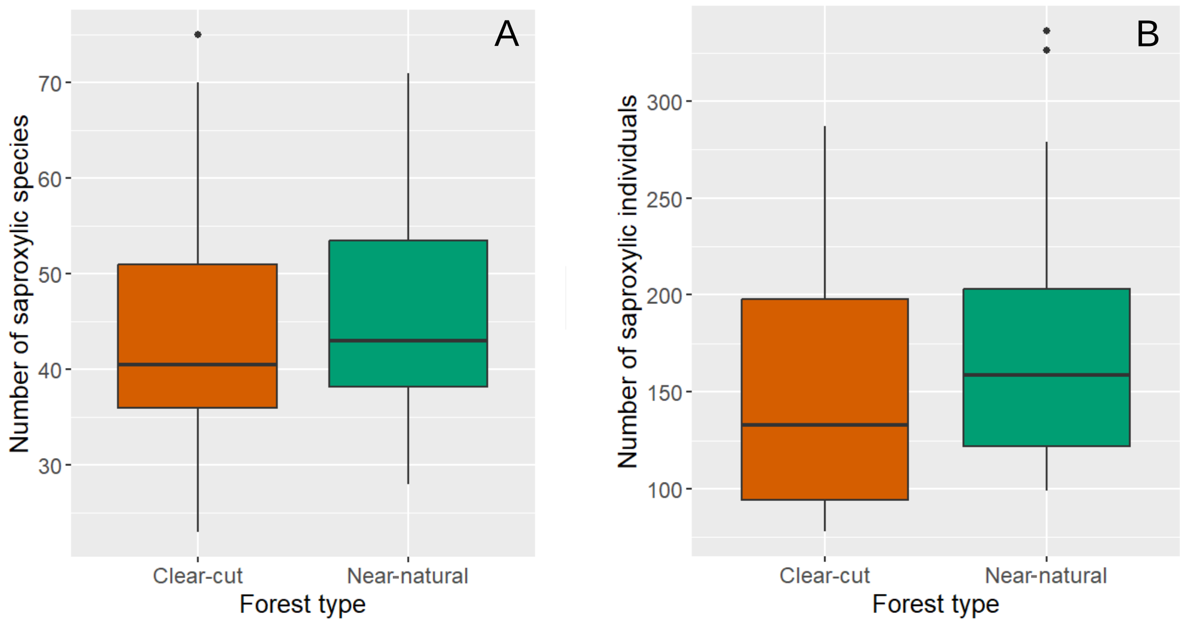

Figure 7. Species richness (A) and number of individuals (B) of saproxylic beetles per plot per sampling period caught in 10 site pairs of clear-cut and near-natural plots.

3.4 Effect of forest type and deadwood on beetle feeding guilds

The majority of beetle species caught were either predators (48%) or detrivores (42%). Only 0,06% of the species were herbivores and 0.03% had a mixed diet. Three individuals were not identified to species, and thus were not included in this particular analysis.

Beetle species richness between feeding guilds did not differ between the two forest types (Table 4). When looking at number of individuals on the other hand, more herbivore individuals were trapped in clear-cut sites (p=0.015), and the number of predatory individuals was almost significantly higher in clear-cuts as well (p=0.056).

Both species richness and abundance of detritivore species increased with total deadwood volume (p=0.002, p=0.023). For the other feeding types, deadwood volume had no effect.

Table 4. General linear mixed models with negative binomial distribution on the effect of forest type and deadwood volume on species richness and abundance according to feeding type. Clear-cut is the reference level for forest type. Significant values are given in bold font, and asterisks represent values that tend to have an effect.

	Species				**Individuals**			
Predictor	*Estimate*	*SE*	*z*	*p*	*Estimate*	*SE*	*z*	*p*
Detritivores								
(Intercept)	3.166	0.058	54.603	<0.001	4.614	0.077	59.492	<0.001
Forest type	-0.098	0.090	-1.093	0.274	-0.160	0.119	-1.343	0.179
Deadwood	0.029	0.009	3.048	**0.002**	0.035	0.015	2.268	**0.023**
	Conditional R^2: 0.159				Conditional R^2: 0.192			
Predators								
(Intercept)	3.439	0.052	65.637	<0.001	4.927	0.087	56.537	<0.001
Forest type	-0.009	0.0682	-0.129	0.897	-0.245	0.128	-1.912	0.056*
Deadwood	0.012	0.009	1.394	0.163	0.009	0.016	0.585	0.559
	Conditional R^2: 0.266				Conditional R^2: 0.161			
Herbivores								
(Intercept)	0.456	0.177	2.571	0.010	0.913	0.243	3.748	<0.001
Forest type	-0.140	0.263	-0.053	0.593	-0.879	0.360	-2.443	**0.015**
Deadwood	0.035	0.028	1.221	0.222	0.058	0.044	1.316	0.188
	Conditional R^2: 0.130				Conditional R^2: 0.292			
Mixed								
(Intercept)	0.834	0.126	6.637	<0.001	1.845	0.199	0.239	<0.001
Forest type	-0.077	1.993	-0.387	0.699	0.355	0.276	-1.286	0.198
Deadwood	0.007	0.020	0.328	0.743	0.003	0.034	0.096	0.923
	Conditional R^2: NA				Conditional R^2: 0.205			

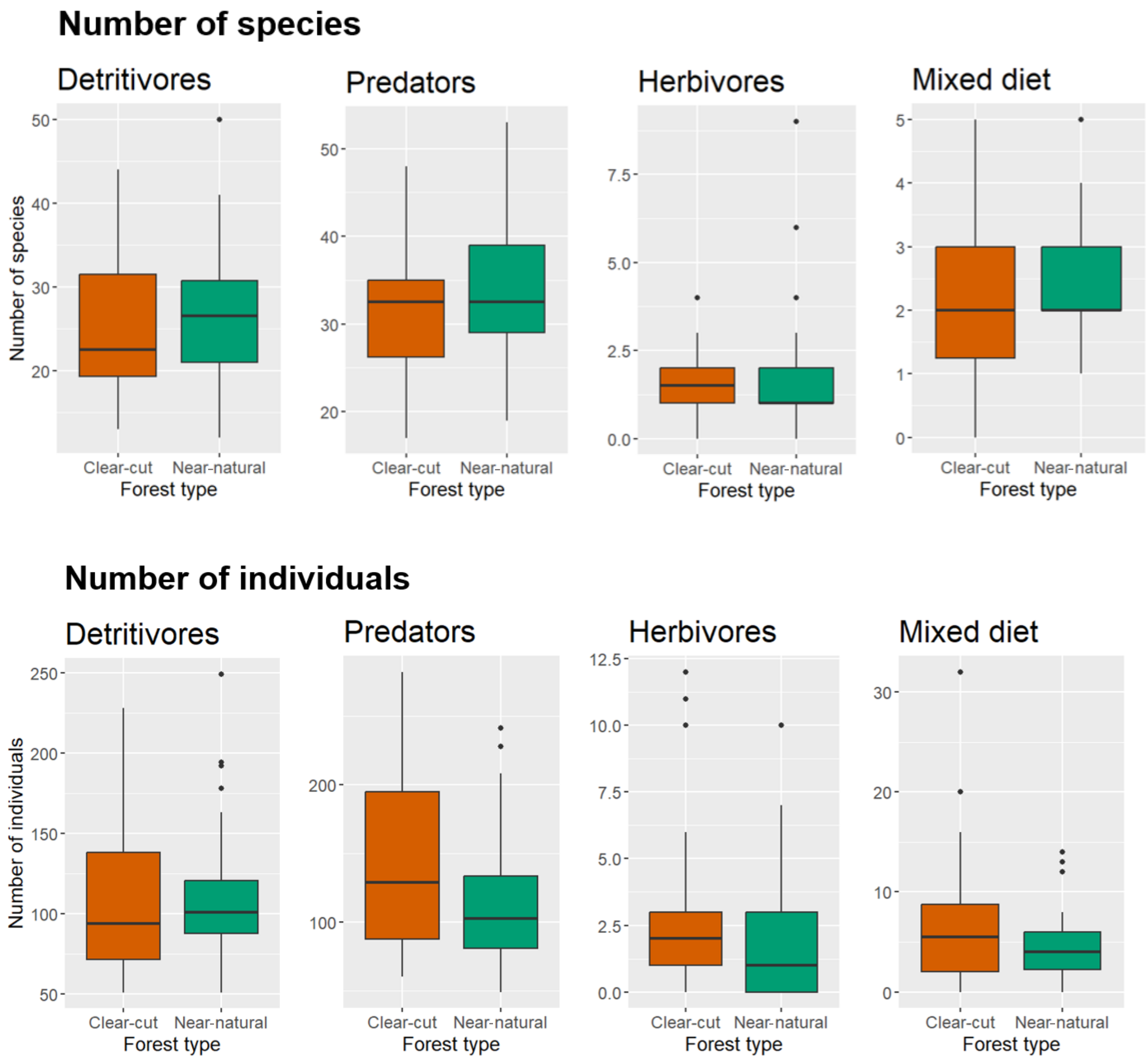

Figure 8. Beetle species richness and beetle abundance per plot per sampling period within each feeding guild. The beetles were caught in 10 site pairs of clear-cut and near-natural plots.

As shown in figure 9, most of the detritivore species caught were saproxylic (78%). In addition, over half of the predators were (55%) also associated with deadwood. Only 23% of the herbivore species, as well as 33% of the beetles with a mixed diet were saproxylic, based on the definition of a saproxylic species depending on deadwood in at least one part of their life cycle.

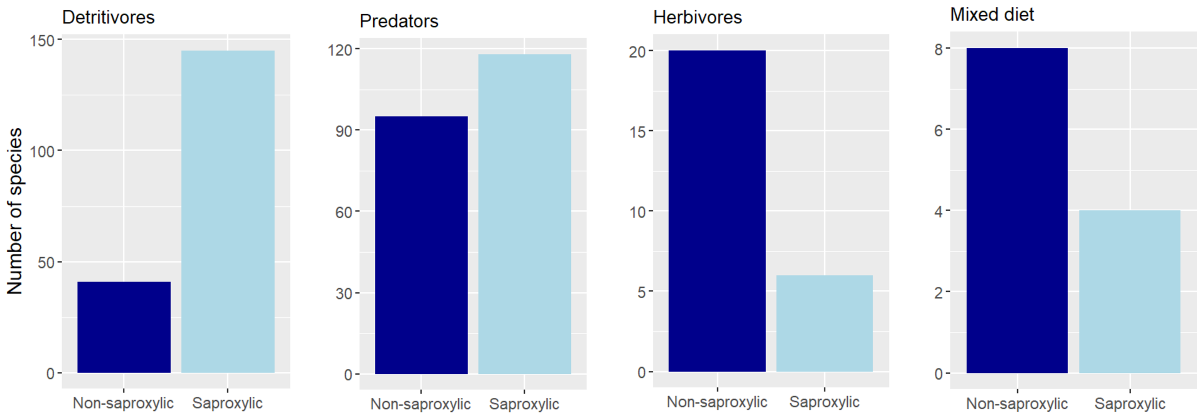

Figure 9. Number of non-saproxylic and saproxylic species caught in window traps based on feeding guild. The beetles are caught in 10 site pairs of clear-cut and near-natural plots.

3.5 Red-listed species

A total of 22 red-listed species, represented by 69 individuals, were caught in the traps. Of these, 30 individuals were caught in former clear-cuts, and 39 in near-natural forest stands. About half (13 sp.) of the species were present in clear-cuts, and 18 species were found in near-natural plots. Almost all of the red-listed species (91%, 20 sp.) and individuals (96%, 66 ind.) were saproxylic.

Neither forest type (Figure 10) nor deadwood volume showed an effect on the number of red-listed species or number of red-listed individuals caught in the traps (Table 5).

Table 5. Results from the general linear mixed model with negative binomial distribution on the effect of forest type and deadwood volume on the number of red-listed species and red-listed individuals. Clear-cut is the reference level for forest type. Significant values are given in bold font, and asterisks represent values that tend to have an effect.

	Species				**Individuals**			
Predictor	*Estimate*	*SE*	*Z*	*p*	*Estimate*	*SE*	*Z*	*p*
(Intercept)	-0.365	0.255	-1.430	0.153	-0.131	0.295	-0.446	0.655
Forest type	0.095	0.343	0.276	0.783	0.105	0.403	0.261	0.794
Deadwood	0.020	0.036	0.551	0.581	0.023	0.047	0.487	0.626
	Conditional R^2: 0.137				Conditional R^2: 0.134			

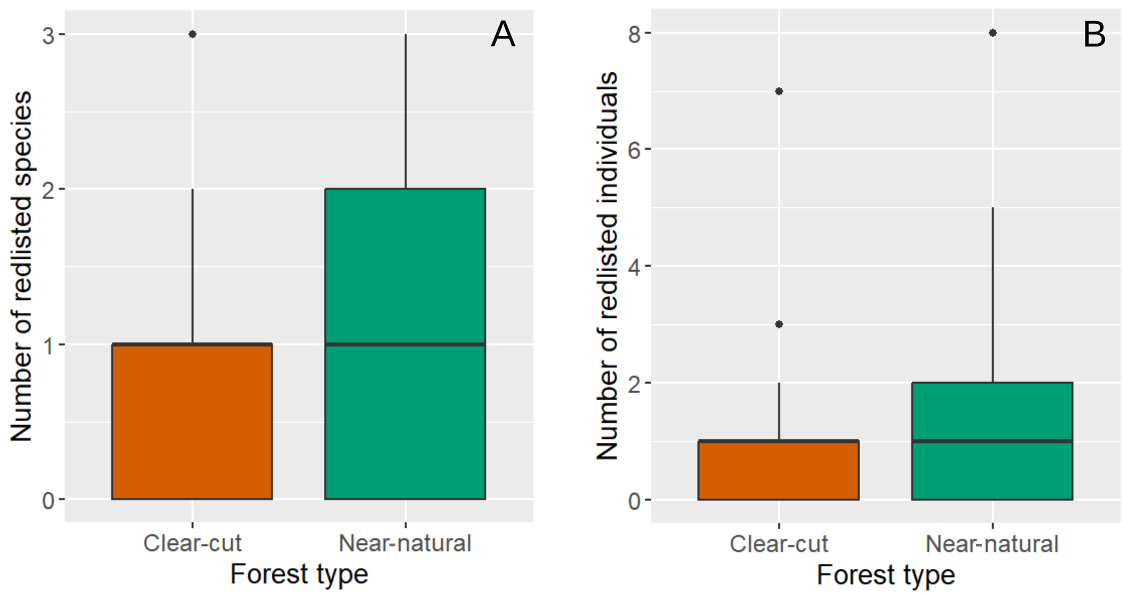

Figure 10. Number of species (A), and individuals (B) of red-listed beetle species caught per plot per sampling period in 10 site pairs of clear-cut and near-natural plots.

As many as 20 out of 23 species fall into the category of near threatened (NT), one is categorized as endangered (EN), and two are categorized as vulnerable (VU) (Table 6). *Corticaria laterita* (VU) was caught in Blåfjell (BLA); two individuals in the near-natural plot, and one individual in the clear-cut plot. One individual of *Mycetophagus decempunctatus* (VU) was caught in the clear-cut plot in Halden (HAL), and one individual of *Peltis grossa* (EN) was caught in the near-natural plot in Tretjerna (TRE).

Table 6. List of red-listed species caught in 20 locations in Southeastern Norway, with their Red List category, whether they are saproxylic, and number of individuals caught in each forest type.

Species	Red List category	Saproxylic	Number of individuals	
			Near-natural	Clear-cut
Peltis grossa	EN	yes	1	0
Corticaria laterita	VU	yes	2	1
Mycetophagus decempunctatus	VU	yes	0	1
Amphicyllis globiformis	NT	yes	1	1
Cis fagi	NT	yes	0	1
Cis quadridens	NT	yes	1	1
Corticaria polypori	NT	yes	0	1
Cryptolestes abietis	NT	yes	3	5
Cryptophagus subdepressus	NT	no	1	1
Dorcatoma robusta	NT	yes	1	0
Ennearthron laricinum	NT	yes	4	9
Enalodroma hepatica	NT	no	1	0
Euryusa castanoptera	NT	yes	9	1
Hylis carinifrons	NT	yes	2	0
Hylis procerulus	NT	yes	1	0

Leiestes seminigra	NT	yes	2	0
Leptophloeus alternans	NT	yes	1	2
Mycetophagus fulvicollis	NT	yes	3	3
Mycetophagus piceus	NT	yes	1	0
Mycetophagus populi	NT	yes	1	0
Oxypoda recondita	NT	yes	3	2
Prionocyphon serricornis	NT	yes	1	0
Scydmaenus hellwigii	NT	yes	0	1

4. Discussion

4.1 Difference in deadwood between clear-cut and near-natural forests

Previous studies have demonstrated that natural spruce forests have higher amounts of deadwood than what we find in managed forests (Siitonen, 2001). In agreement with this, I found that all sites had more deadwood in the near-natural plots. In addition, more logs below 20 cm in diameter were found in clear-cut plots, and more logs above 20 cm in diameter were found in near-natural plots, although only the larger logs differed significantly between forest types.

In compliance with my hypothesis, older forest stands provided higher total volumes of deadwood. In general, undisturbed forests provide a higher continuity in deadwood supply, as the trees are of an uneven age. This can also explain the finding that only the larger logs differed significantly between forest types. There is a higher amount of large trees in undisturbed forests, but there are still smaller trees and branches that supply smaller deadwood and therefore both categories are found. Indeed, the volume of small diameter deadwood was highest in clear-cuts. This might be due to the forest stand consisting of more tall, but smaller diameter trees because they were all planted at the same time.

Based on previous calculations, many of my near-natural plots have a lower amount of downed deadwood than the mean for Fennoscandian preserved forests, which is about 60-90 m^3/ha (Siitonen, 2001). The mean volume for the near-natural plots in my study was 35 m^3/ha, which is about half of the reference amount. Our clear-cut plots had a mean volume of 10 m^3/ha, which corresponds to the upper Fennoscandian mean for managed forests presented to be 2-10 m^3/ha in the Siitonen (2001) study, while it is slightly less than today's Norwegian mean (Storaunet, 2021). This means that most of my near-natural plots have lower volumes of downed deadwood than a typical old-growth forest, while the clear-cut plots are meeting the characteristics of a managed forest stand when it comes to deadwood volumes. On the other hand, the near-natural forest stands might have been areas of selective cutting earlier and they are located quite close to managed forest stands, so them having deadwood volumes that are lower than the mean of preserved forests is not that surprising. It is also unclear what the definition of an old-growth forest is in Siitonens study, and it therefore might refer to even more preserved forests than what is included in this study. Nevertheless, both results show that the near-natural forests have higher resources of deadwood than the clear-cut forests.

4.2 Beetle species richness and abundance

The main hypothesis that near-natural plots would have a higher beetle species richness and clear-cuts a higher beetle abundance was not confirmed. Forest type did on the other hand affect the abundance of saproxylic beetles. This indicates that saproxylic species have an advantage in near-natural forests, most likely given the large difference in deadwood volumes between the two forest types.

Higher total volumes of deadwood led to a higher total species richness, and almost to more saproxylic species as well. More than half (65%) of the species caught were saproxylic, and it was thus natural that more deadwood led to more species, as the majority were dependent on and attracted by it. The reason why only the total beetle fauna was significantly affected by total deadwood volumes may be because of trophic effects. For example, the non-saproxylic predators would be attracted by saproxylic prey species and thus deadwood resources. Even so, the non-saproxylic species do likely consist of a diverse group of species, and their mechanisms are therefore difficult to determine.

The smaller deadwood did not significantly affect beetle biodiversity, but the increase in severely decomposed logs almost significantly increased total beetle species richness as well as both total and saproxylic beetle abundance. Some species are specialized to utilize smaller logs of deadwood, but most are connected to larger diameter logs (Stokland et al., 2003). No sites had more, usually a lot less, than 1 m^3 of severely decomposed small diameter logs per transect, and thus it is surprising if this would be enough to be of importance. Even so, studies have found that deadwood diversity is more important than volume (Similä et al., 2003), indicating that both small diameter deadwood and severely decomposed wood are needed for biodiversity conservation. The difference in volumes of severely decomposed logs under 20 cm in diameter was almost non existing between the two forest types (Figure 5), while the difference was clear for the large logs, since many clear-cut sites had none. Therefore, there might be that these smaller logs become even more important in clear-cut sites, as compensation for there being no large, severely decomposed logs present.

Large logs of decay class 1-3 had an increasing effect on number of species. This effect was only almost significant for the overall beetle diversity, but it significantly increased both species richness and abundance of saproxylic beetles. A large proportion of the obligate saproxylic beetle species in the Nordics have a preference for deadwood of an early decay class (Stokland et al., 2012). These logs of a larger diameter most likely consist of several microhabitats, as bark is still present to hide under, and there is still more heartwood to decompose, and are thus a good resource for several saproxylic species. This is an interesting find in a forest management perspective, as the larger logs were the ones that were significantly more abundant in the near-natural plots.

4.3 Effect of forest type and deadwood on feeding guilds

As predicted was deadwood of importance for detritivore species, as a higher total volume of deadwood increased both species richness and abundance of detritivore species trapped. Some detritivore beetle species are decomposers of deadwood through direct consumption and would therefore find more nutrition with increasing volumes of deadwood. Thus, it is not surprising that total deadwood volumes increased both detritivore species richness and abundance. Two thirds of the detritivore species were saproxylic, and thus directly dependent on or advantaged by the presence of deadwood.

The only time forest type had a significant effect during this study was for number of herbivore individuals, which was higher in clear-cuts. It is possible that the former clear-cuts more often are close to an area of newly cut forest, where there is typically a lot of deciduous trees and plants for herbivores to eat. Milberg et al. (2021) proved that fresh, open clear-cuts held more herbivore insect species than closed-canopy forests, as they also typically provide more flowering species. It should be noted that a boreal coniferous forest is not the most typical hotspot for adult herbivore beetles, and as shown in figure 8, the mean for herbivores in clea-cuts was 1.7 species and 2.4 individuals per plot per period. Therefore, one can argue that the sample size of herbivore beetles is too small to truly draw a conclusion. The results of clear-cuts having more herbivore individuals is still a bit surprising, as one would expect either wood or plants for larval nesting sites or plants for nutrition to be drivers for herbivore abundance, ecological factors that are not typically more abundant and diverse in managed forests (Hedwall et al., 2013). Other abiotic factors not accounted for in this study might be of importance since deadwood did not have any effect in this case, such as canopy cover and light conditions.

Previous studies have found that predators are more exposed to being affected negatively by habitat degradation because they are of a higher trophic level and thus are affected by the loss of prey in addition to degradation of the habitat (Dupont & Nielsen, 2006). This does not seem to be the case in the present study, as number of predator individuals was close to being higher in clear-cut plots. Number of predatory species did not differ between forest types, and therefore it is a possibility that there are some predatory generalists that feed on species not dependent on deadwood thriving in this environment and becoming more abundant in a habitat with less competition. Johansson et al. (2007) looked at common predatory beetles and found that they differed in abundance between newly clear-cut sites and old or mature forests, but they could not detect a difference between the old-growth and mature managed forests. Together with my results, this indicates that old managed forests house qualities that provide for some predatory beetles, at least the most common generalists.

The pattern of effect of forest type and deadwood on the beetle feeding guilds is similar to that of the proportion of saproxylic species for each feeding guild (Figure 9). Most of the detritivore species were saproxylic, and thereafter have an advantage in the near-natural plots due to higher volumes of deadwood. The herbivore species, on the other hand, were mainly non-saproxylic and thus mostly dependent on other ecological variables, such as flowering plants and light conditions for survival. These are factors not included in this study. When it comes to the predators, they were showing a tendency for being more abundant in clear-cuts as well, but not significantly. About half of the predatory species were associated with deadwood, while the other half is not. Thus, there is likely that there are some factors not accounted for in this study that are important for half of the predatory beetles, but at the same time the other half is dependent on deadwood, and thus being more advantaged in the near-natural plots.

An aspect that needs to be considered is that beetles are holometabolous, meaning that their habitat often differs quite extensively between the larval and adult life stage (Gimmel & Ferro, 2018). Many lay their eggs in deadwood, meaning that the larval stage is saproxylic, even though they might not be dependent on deadwood during their adult stage other than for reproduction. In this study we have only trapped adult, flying beetles. It is likely that many of the saproxylic species were caught independently of the presence of deadwood during this particular life stage and, thus, the number of trapped beetles might not reflect the association with the amount of deadwood present in the study plots where they were trapped. This is particularly important for herbivore and predatory species, as many herbivore species live off flowers and plants, and many predators eat prey not in relation to deadwood. Nevertheless, some of these species started their life as a larva in deadwood and will depend on it again for reproduction.

4.4 Red-listed species

Neither forest type nor deadwood volume had any effect on the abundance and number of red-listed species. As the hypothesis suggested, there were more threatened species in near-natural forests, but the numbers did not differ significantly. Even so, it is interesting that almost all the threatened species caught, as well as as many as 96% of the individuals were saproxylic. Therefore, it is surprising that deadwood volumes did not have an impact, as it would seem to be an essential factor for the survival of these species.

The model with forest type and total deadwood volume only explained 13-14% of the variation of the red-listed species. When looking further into each red-listed species' main habitat, I found that many of the species are connected to polypores and deciduous trees (Appendix 5), in addition to old spruce forests. Typically, there are more deciduous trees in un-planted forest stands (Siitonen et al., 2000), but for further studies, it could be interesting to gather data on tree species composition to see if this is of importance for the red-listed species that were caught.

The majority of the red-listed species caught are categorized as near threatened (NT). Only three species and five individuals were threatened (VU and EN). Threatened species are often highly specialized, and it is therefore possible that these would show a stronger correlation to forest type than nearly threatened species (Stenbacka et al., 2010). As argued by Stenbacka et al. (2010), it is possible that a stronger pattern could be detected with a larger sample size. Nonetheless, the two vulnerable species in this study were caught in both near-natural and clear-cut plots, so drawn from this there is no pattern.

Peltis grossa, the only endangered species caught, lives in natural spruce forests. It was caught in the near-natural plot with a lot more slightly decayed, large diameter deadwood than the other plots (TRE, near-natural). Since there was only one individual caught, one cannot draw any conclusion on whether this had an influence on the species being present in this plot, but it is interesting that the habitat match with previous observations. According to the Norwegian Red List of 2021, this species has a limited geographic distribution (Ødegaard, Hanssen, et al., 2021). For the last two decades it has only been registered in Vestfold and Telemark County in Southeastern parts of Norway. In addition, more than a 100 years old registrations show that *Peltis grossa* had also been found in Innlandet county, and by the findings of this thesis we show that it likely still has a population in Innlandet.

According to the Norwegian Red List of Species of 2021, a majority of the beetles are red-listed due to a limited distribution area, and an ongoing reduction of habitat (Ødegaard, Hansen, et al., 2021). It is possible that the actual distribution area of some species is unknown, and thus these species are more common than assumed. More likely is there an ongoing extinction debt, as forest species are experiencing a reduction in habitat. Many of the species caught are not actually threatened by now (NT), but they are at risk of becoming threatened as their suited habitat continues to be degraded, in addition to an absence of other available and suitable areas. As old-growth forests are replaced with planted forest stands, the distance between suitable habitats increases, and will eventually reach a length that is too great for the beetles to migrate across.

4.5 Further studies

In resemblance to my results, Similä et al. (2003) also caught a similar amount of saproxylic species in managed and seminatural forests but found a very different assembly of species between the two forest types. For further research, it would be interesting to investigate the species composition of the species caught in the present study as well. There might be a difference in the degree of specialization for the species in the two forest types, which is not detectable through only the number of species. If this were to be true for the present study as well, and the species composition would be different between near-natural and clear-cut forests, it would support that near-natural forests are of value to maintain certain species that are likely to not exist in clear-cut forests.

Previous studies have demonstrated that canopy gaps promote beetle biodiversity (Jokela et al., 2019; Rothacher et al., 2023), as it alters the microclimate conditions considering sun exposure, temperature, and humidity. Data on canopy cover was not included in my study, but as the model including forest type and deadwood volume only explained from 13% to 32% at most, it is likely that this would be of importance in these forests as well. For further studies, it would therefore be interesting to include data on canopy cover in the model, to look at the differences and possible patterns between our forest plots, the alternative effects on beetle biodiversity, and also how it would affect the results and the R-squared of the model.

5 Conclusion – Implications for nature management

The main hypothesis that near-natural forest stands would provide for a higher beetle biodiversity than clear-cuts was not confirmed in this study, but the results do not necessarily contradict with previous studies saying that uneven-aged, near-natural forests are important for the conservation of biodiversity. The results suggest that forest history cannot predict beetle biodiversity alone, as the amount of deadwood present was of higher importance for beetle species richness, and thus that the availability of resources is the more important factor. Nonetheless, near-natural forests had more deadwood than clear-cut forests, which indicates that preservation of near-natural forests should be beneficial for the conservation of beetle biodiversity.

This study could not explain all the variation in beetle biodiversity, and the forest as a whole ecosystem should be considered when looking for old-growth indicators in forest stands. Nevertheless, deadwood components are good, long-lasting indicators that are also crucial for a large share of the forest beetles. Considering that near-natural forests have a greater amount of deadwood, especially large diameter deadwood, they should be closely evaluated before any logging is being considered. One should also strive to increase the amounts of deadwood that remain after logging in general, especially to increase the supply and continuity in large diameter deadwood, in order to safeguard the rich and unique diversity of forest-living beetles.

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Appendix

Appendix 1. Coordinates and meters above sea level for all sites

Table 1. Coordinates and meters above sea level for all 20 study plots.

Name of site	Longitude	Latitude	m.a.s
Aremark (CC)	11.559466	59.079804	205
Aremark (NN)	11.546528	59.079768	213
Blåfjell (CC)	10.386469	59.788040	322
Blåfjell (NN)	10.381227	59.783132	289
Serlikampi (CC)	12.529622	60.200016	372
Serlikampi (NN)	12.507994	60.187717	359
Skotjernfjell (CC)	10.808351	60.241347	577
Skotjernfjell (NN)	10.795978	60.242237	602
Storås (CC)	9.709073	60.261512	423
Storås (NN)	9.700640	60.259159	488
Gullenhaugen (CC)	10.787153	60.369956	590
Gullenhaugen (NN)	10.796585	60.352627	667
Tretjerna (CC)	10.228497	60.577288	516
Tretjerna (NN)	10.226511	60.583642	418
Braskreidfoss (CC)	11.926343	60.747583	367
Braskreidfoss (NN)	11.928444	60.739768	425
Øytjern (CC)	10.408953	60.843192	662
Øytjern (NN)	10.381205	60.838909	644
Hemberget (CC)	12.188810	60.921073	580
Hemberget (NN)	12.206408	60.915094	579

Appendix 2. Calculations of deadwood volume per hectare

Table 2. Total deadwood volumes calculated from volumes measured in 0.2 haa transects in field into corresponding volumes in 1 haa.

Volume per haa	CC	NN
SKO	2.08 x 5 = 10.4	7.47 x 5 = 37,35
GUL	0.84 x 5 = 4.2	5.2 x 5 = 26
GRA	0.75 x 5 = 3.75	1.7 x 5 = 8.75
BRA	1.04 x 5 = 5.2	10 x 5 = 50
SAR	2.52 x 5 = 12.6	5.9 x 5 = 29,5
OYT	0.6 x 5 = 3	1.68 x 5 = 8.4
HAL	1.08 x 5 = 5.4	1.62 x 5 = 8.1
TRE	6.57 x 5 = 32.85	21.7 x 5 = 108.5
BLA	3.38 x 5 = 16.9	7.3 x 5 = 36,5
STO	1.4 x 5 = 7	7.08 x 5 = 35,4
Mean	101,3 / 10 = **10,13**	348,5 / 10 = **34,85**

Appendix 3. Comparison of all beetles and saproxylic beetles

Table 3. A systematic comparison of effect of each predictor variable on all beetles and only saproxylic beetles caught in window traps in 10 site pairs in Southeastern Norway.

	All beetles	**Saproxylic beetles**	
Forest type	No effect	More individuals in near-natural plots	Not the same
Deadwood volume	Increased number of species	Almost increased number of species	Similar
<20 cm, slightly	No effect	Almost effect on individuals	Not the same
<20 cm, severely	Almost effect on species Almost effect on individuals	Almost effect on individuals	Similar
>20 cm, slightly	Almost efffect on species	Effect on species and individuals	Similar
>20 cm, severely	No effect	No effect	Same

Appendix 4. Further information about the red-listed species

Table 4. Information about each red-listed species (Norwegian Red List of Species 2021) caught in 10 site pairs in Southeastern Norway. All information is conducted from species information in the Norwegian Red List of Species of 2021 (Artsdatabanken, 2021a).

Species	**Red List category**	**Saproxylic**	**Main habitat**
Peltis grossa	EN	yes	Natural forests with large spruce trees (also found on beech). Moderately decayed wood.
Corticaria laterita	VU	yes	Fungi on trees, and under bark in natural spruce forests
Mycetophagus decempunctatus	VU	yes	Polypores on birch and grey alder (Alnus incana)
Amphicyllis globiformis	NT	yes	Fungi in old-growth forests
Cis fagi	NT	yes	Polypores on deciduous trees
Cis quadridens	NT	yes	The polypore Fomitopsis pinicula on spruce
Corticaria polypori	NT	yes	Fungi under bark on spruce
Cryptolestes abietis	NT	yes	In tunnels made by bark beetles in coniferous trees
Cryptophagus subdepressus	NT	no	Old-growth coniferous forests
Dorcatoma robusta	NT	yes	Tinder fungus (Fomes fomentarius) on birch
Ennearthron laricinum	NT	yes	Polypores on spruce and birch
Enalodroma hepatica	NT	no	Mostly in coniferous forests, but also found under bark and with ants

Euryusa castanoptera	NT	yes	Under bark and in tunnels in old coniferous trees
Hylis carinifrons	NT	yes	Beech (Fagus sylvatica) and spruce most common
Hylis procerulus	NT	yes	Severely decayed trunks of spruce
Leiestes seminigra	NT	yes	Stumps and snags of coniferous trees with white rot
Leptophloeus alternans	NT	yes	In tunnels made by bark beetles in spruce
Mycetophagus fulvicollis	NT	yes	White rot in spruce, birch and aspen (Populus tremula)
Mycetophagus piceus	NT	yes	Wood with a lot of fungi, mostly oak (Quercus), but also birch and aspen
Mycetophagus populi	NT	yes	Wood decayed by white rot of deciduous trees, mostly elm (Ulmus glabara) and aspen
Oxypoda recondita	NT	yes	Decisous trees with rot fungi, especially oak
Prionocyphon serricornis	NT	yes	Rainwater in hollow deciduous trees
Scydmaenus hellwigii	NT	yes	With ants, mostly in hollow trees

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