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Long-term effects of clear-cut forestry on beetle community diversity in boreal forests of southeastern Norway

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Abstract:

Forest management regimes have led to global biodiversity declines. Norwegian boreal spruce-forests have been negatively impacted by clear-cutting for the last 70 years, a practice which shifts structural conditions of a forest. Determining whether biodiversity in these forests differ from forests never subjected to clear-cutting (hereafter termed 'near-natural') is essential to advise further forestry and conservation practices as the first clear-cut and replanted forests are now reaching a mature state. In this study, I compared forest characteristics and beetle diversity of two types of mature boreal forest which differ in previous management: near-natural forest, with a history of only selective logging, and previously clear-cut forest.

We collected nearly 4000 beetles using a total of 324 window- and malaise-traps in five pairwise plots in Southeastern Norway. Along with beetle collection, we also recorded stand variables which encompassed both macro- and micro-climate conditions. From this, I calculated differences in beetle communities between former clear-cut and mature near-natural forest through richness and abundance mixed models and assemblage through diversity metrics.

The near-natural and clear-cut forest management types were structurally different according to significant stand variables pertaining to canopy density, deadwood amount and deadwood diversity. Beetle richness and abundance as well as saproxylic beetles alone increased with the near-natural forest management type and deadwood stand variables, especially later decay stages. They also responded to macroclimate conditions like temperature. The uncommon species in the dataset, however, determined the differences between the assemblage of forest communities as they were mostly unique to different forest management types. The more abundant species were shared between the former clear-cut and the near-natural forests. These results highlight that despite 70 years since felling, clear-cut forests are different from near-natural forest in both their stand characteristics and beetle communities. As such, future conservation efforts should aim to conserve near-natural forests rather than convert them to clear-cut forests.

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1. Introduction

Modern forestry practices have led to widespread declines in biodiversity globally. Although different regimes have been implemented depending on the region, Fennoscandian boreal forests have been negatively impacted by clear-cutting. Clear-cutting, the most common forestry regime in Norway (Bartlett, 2020), superseded the previously dominant selective-cutting practice during the 1950s in order to ensure growth in the raw timber supply (Kuuluvainen et al., 2012). As a result, forest management has shifted southern boreal forest from mixed stands to dense, spruce-dominated forest with less old growth trees and, importantly, less dead wood (Gauthier et al., 2015; Seibold et al., 2015).

Although deemed politically sustainable, this even-aged regime has deleterious ecological effects (Esseen, 1997; Kuuluvainen et al., 2012). Natural forests dynamics in Fennoscandia are characterized by small-scale disturbances involving only a few trees, whereas stand-replacing disturbances like forest fires, bark beetle attacks and storm felling's are more irregular (Kuuluvainen & Aakala, 2011; Machado Nunes Romeiro et al., 2022). As such, clear-cuts' frequent stand-replacing disturbances alter disturbance dynamics and when followed by tree planting, alter composition of tree species and age classes compared to natural forests (Kuuluvainen, 2009). They additionally bring drastic increases in sun-exposure and removal of key habitat structures such as the quality, size, and quantity of dead wood by up to 98% (Esseen, 1997; Fridman & Walheim, 2000; Henriksen, 2015; Jacobsen et al., 2020; Økland et al., 1996; Seibold et al., 2016). Forest structural complexity resultantly decreases, and a once extensively biodiverse forest (Grove, 2002) is ultimately reduced from a loss of niche opportunities. Indeed, less than two percent of unmanaged old growth boreal forest remains in Norway (NIBIO, 2018).

Near-natural forests, representing nearly a third of forests in Norway, have never been clear-cut, but rather, minorly selectively felled (Storaunet & Rolstad, 2020). Since selective felling mimics natural small-scale tree mortality dynamics, these managed forests generally contain high structural heterogeneity, higher volumes of deadwood, and more variation in tree age classes which promote species diversity (Jacobsen et al., 2020; Seibold et al., 2015; Storaunet et al., 2005). As such, near-natural forests may be as valuable for conservation as unmanaged old-growth forests over time. However, near-natural forests are under threat

from modern forest management practices (Felton et al., 2020) and are inadequately protected (Sverdrup-Thygeson et al., 2014b).

To understand biodiversity impacts between managed forests, researchers often use beetles as a proxy. Beetles represent an ecologically diverse order who contribute to important ecosystem services like nutrient cycling, predation, and decomposition (Ulyshen, 2018) and house a large number of rare and red-listed species (Burner et al., 2022; Henriksen, 2015). Their loss can affect important boreal processes and are hence a valuable arthropod order to examine. Moreover, their abundance, richness, and composition in boreal forests respond strongly to stand characteristics, making them a suitable group to monitor effects of clear-cut regimes (Martikainen et al., 2000; Siitonen, 2001) Further, a limited number of effective traps can achieve a relatively thorough sample of beetles (Burner et al., 2021a). Due to these reasons, beetles have been the subject of several studies examining forest management effects in Scandinavia.

Forest management is an important predictor of beetle communities, with many species occurring more readily in near-natural forests (Burner et al., 2021b). Jacobsen et al. (2020) found that management is significant in explaining beetle diversity; they discovered species richness of natural-forest indicators, saproxylic beetle species and red-listed beetles species were all greater in near-natural mature forests than in intensively managed mature forests, likely because key forest structural elements are missing. Another study demonstrated clear-cut and thinned stands contained beetle species assemblages that were significantly further from the species assemblages of old growth and uneven-aged mature forests subject to selective felling (Joelsson et al., 2018). Other studies have investigated specific stand characteristics in relation to beetle diversity; they agree that deadwood volume, size, and decay stage affect assemblages of saproxylic beetles overall as well as rare and red-listed ones (Burner et al., 2022; Dahlberg & Stokland, 2004). Other structural features such as forest openness also impact beetle diversity (Lassauce et al., 2011; Økland et al., 1996; Seibold et al., 2016; Stenbacka et al., 2010). Non-saproxylic species can also be affected despite no reliance on deadwood (Johansson et al., 2016; Sippola et al., 2002). Thus, it seems different groups of beetles as well as total assemblages are severely impacted by forest management.

Effects of boreal forest management need to be considered over greater time scales. Most studies do not investigate management's long-term effects on biodiversity, yet forestry regimes can impact stand structural elements from decades to centuries which would influence species diversity (Aakala et al., 2009). Additionally, there is often a delay between forestry-related disturbances and its influence on species populations (Hanski, 2000), i.e., extinction debt is not considered. Thus, differences between undisturbed and disturbed community assemblages could increase over time. Conversely, the gap between communities could decrease over time as forests could develop 'old-growth' characteristics (i.e. structural heterogeneity) (Paillet et al., 2010), but other factors such as species interactions and different tree species could also affect these assemblages (Burner et al., 2021b). As such, results from studies investigating long-term effects could be quite different from those with a shorter timeline.

In this masters' project, I explored the long-term effects of clear-cut and near-natural forest management practices on beetle (Coleoptera) species richness, abundance, and community structure. I also studied effects on saproxylic beetle richness and abundance separately as they are most strongly related to deadwood stand characteristics. My objectives were to (1) determine if there is a difference between mature near-natural and clear-cut sites and which stand characteristics significantly explain the difference, (2) assess forest management effects on beetle composition through species richness, abundance and community assemblage, and (3) determine stand characteristics which have the strongest effects, including a seasonal element. I predicted that (1) there will be a difference in forest management types due to deadwood predictors and canopy density, (2) there will be greater richness and abundance of beetles and saproxylic beetles in near-natural forests, and that the community assemblages will be strongly different, and (3) higher richness and abundance of beetles and saproxylic beetles will be associated with structural elements such as deadwood volume, deadwood diversity, canopy density, and temperature.

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2. Materials and Methods

2.1 Selection Criteria and Study Area

This study is a part of 'Ecoforest', a research project in collaboration with University of Oslo, The Norwegian University of Life Sciences (NMBU), the Norwegian Institute of Bioeconomy Research (NIBIO) and Norwegian Institute for Nature Research (NINA). The project is financed by The Norwegian Research Council with the goal to compare mature near-natural forest to mature forests which were clear-cut 60-70 years ago. Specifically, the overall aim of the project is to investigate the long-term effects of clear-cutting as a forestry practice on biodiversity, nutrient cycling, and in turn, carbon storage in Norway. This study will be part of the first comprehensive comparison of biodiversity in near-natural and former clear-cut forest stands in Norway.

For the purposes of this thesis, 'pair' refers to both the near-natural (NN) and clear-cut (CC) sites, 'site' refers to either the near-natural or the former clear-cut forest management type inside the pair, and the 'group' will refer to the four groups of traps within each site (Figure 2). The study pairs were located in Southeastern Norway, ranging 136 km in distance from the most northward pair, Gravberget, to the most southward pair, Østmarka (Appendix; Figure 1). As this study is a part of the EcoForest research collaboration project, the location of the sampling pairs was determined by the study design of the original project; the pairwise sites were selected by researchers from the EcoForest project in collaboration with site owners and local governments. Forest pairs were first selected according to their time of clear-cutting or lack thereof for comparison, then further screened for approximate equal vegetation type, productivity, soil profile levels, southward-facing aspects, and variation in canopy gaps. Lastly, sites within pairs could be no greater than five kilometers apart.

The five forest pairs that were chosen for this study were Østmarka (OST), Lunner (LUNN), Varaldskogen (VAR), Våler (VAL) and Gravberget (GRAV) (Figure 1). Gravberget, Varaldskogen, and Våler are used by the Ecoforest project, whereas Østmarka and Lunner are not due to a difference in soil profiles. The studied forests were dominated by Norway spruce (*Picea abies* L.) mixed with Scots pine (*Pinus sylvestris* L.) and some birch (*Betula spp*). Rowan (*Sorbus aucuparia* L.) also occurred, albeit infrequently. Elevation varied between 180m and 550m, with an average of 390m across all sites.
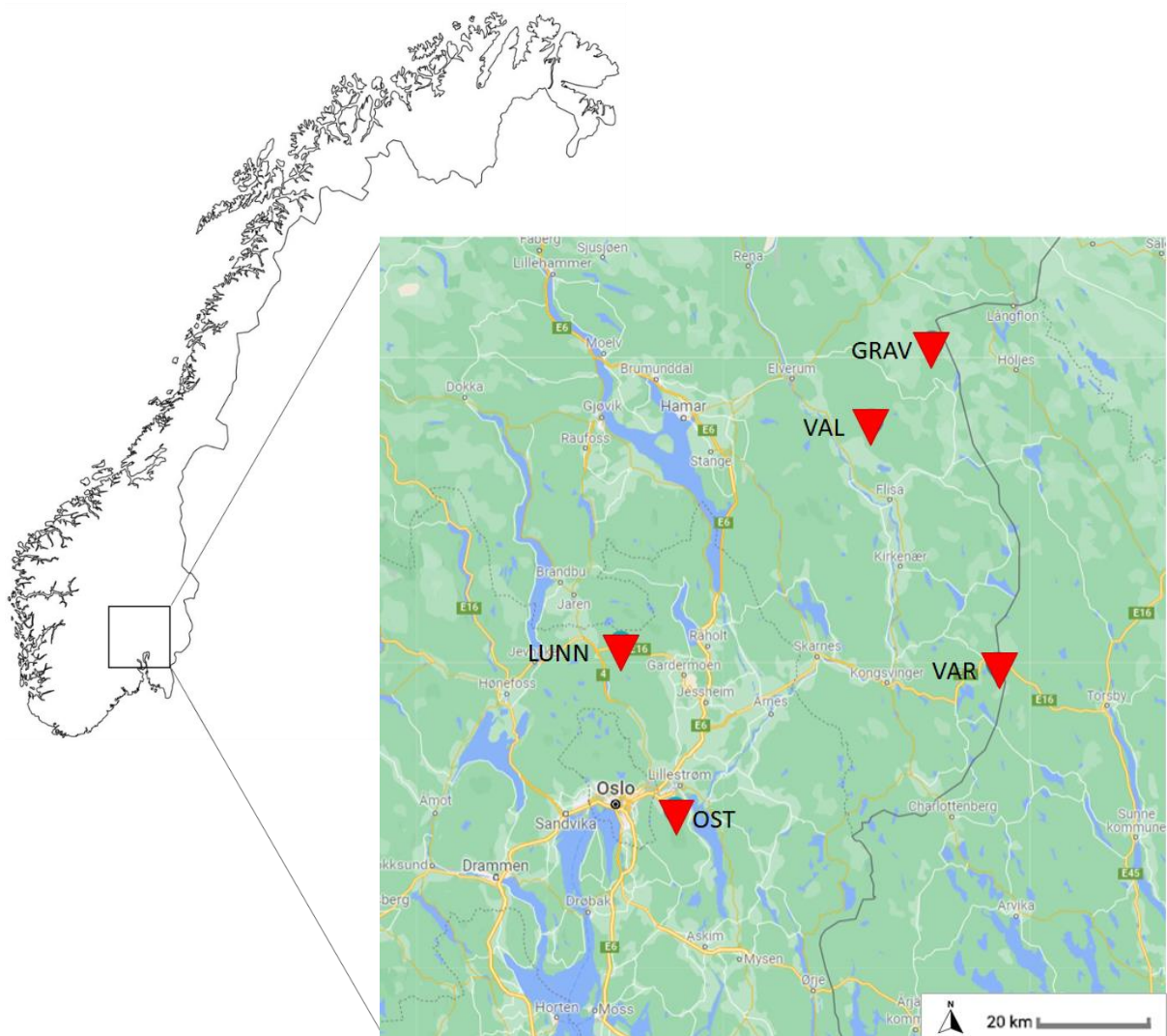
Figure 1. The five study pairs in the project; Østmarka (OST), Lunner (LUNN), Varaldskogen (VAR), Våler (VAL) and Gravberget (GRAV). Map created with Google Earth.

2.2 Study Design

We mounted four groups of insect traps within each site. Each group contained six window traps (two IBL-2 flight interception traps (CHEMIPAN, Warsaw) and four cross-pane traps), and three of the four groups contained one malaise trap (Figure 2; Figure 3). Of the four cross-pane window traps, two were fitted with a rainwater drainage module and two without. To balance the different funnels available, each cross-pane trap had one with a green funnel and one with a white funnel. In total, there were eight IBL-2 traps, 16 cross-pane traps, and three malaise tents at each site. By maximizing the number of traps, we aimed to ensure large enough catches for analysis.
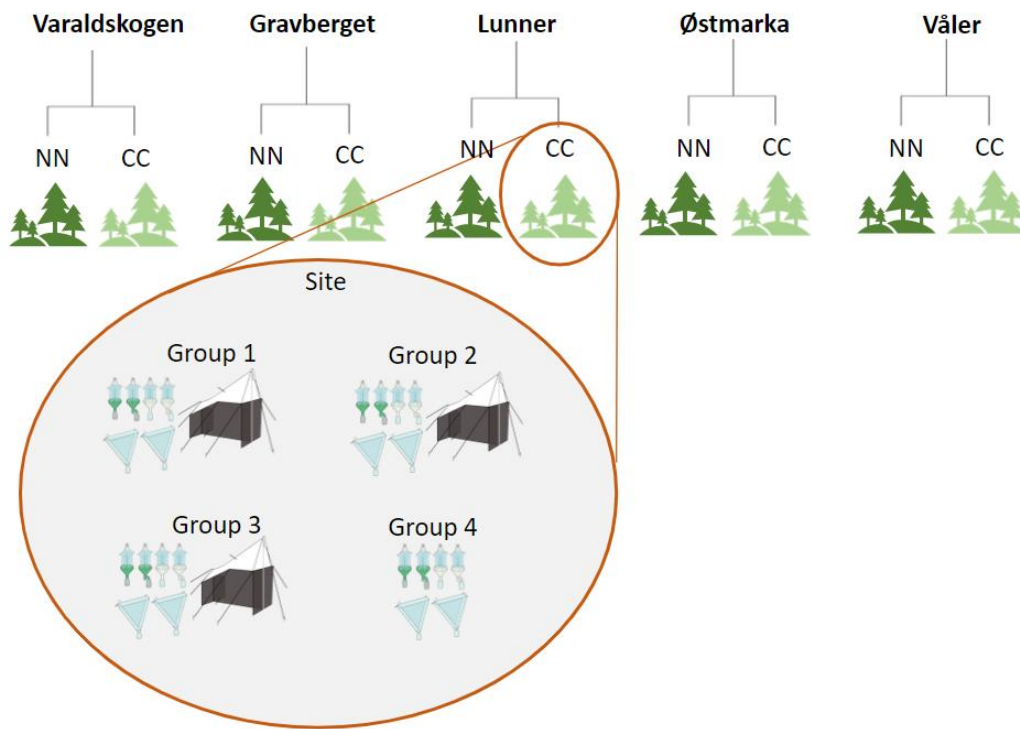
Figure 2. The study design of this project included five pairs, two sites within each pair, and four groups within each site. There were two IBL-2 traps and four cross-pane traps in each group, and one malaise tent in three of the four groups for a total of 27 traps per site.

The group of traps within sites were 20-50m apart. Additionally, the traps within the groups were randomly spaced two to five meters apart and window traps hung above the deadwood at approximately 1.5m above the ground. The insects were collected in bottles one-third filled with a mix of 70% propylene glycol + 30% ethanol (already diluted to 85%) for the window traps, and the malaise trap bottles had a mixture of 85% ethanol (96% ethanol diluted with water). Each bottle was labeled with a unique code with information about the pair, site, trap type, color, group number and month.

The traps were activated from 26-28th of July to 1-3rd of September, and the Østmarka pair was additionally activated from 29-30th of June to 28th of July. The bottles were collected in the same order of activation in order to reduce collection variation.

Figure 3. Each trap used, from left to right, was an IBL-2 trap, green cross-pane trap with water module, white cross-pane trap without water module, IBL-2 trap, malaise tent, white cross-pane trap with water module, and green cross-pane trap without water module.

2.3 Environmental Variables

We constructed 25x25m plots around the center point of each group by measuring, in a random orientation, 17.7m out in opposite directions to form an X formation and flagging the four corners. We measured number of stems, a proxy for canopy density, with a relascope at the center of the plot. Temperature was measured hourly with TinyTag loggers at 2m height within each trap group. Deadwood was measured with the following protocol; starting at one corner of the established plot, we followed parallel transects across the plot to record all standing and lying deadwood. If the tree was rooted outside of the plot, it was not recorded. Conjunctively, if the tree was rooted inside the plot but fell outside, it was measured. Qualitative data recorded for each dead tree included the species, deciduous/coniferous, quality (snag/log), and decay class (see below). Quantitative data included the diameter at breast height (DBH), diameter at base, diameter at top (if not 5cm), and length of the trunk. Only deadwood that was greater than 10cm DBH and longer than 0.5m was recorded (Jacobsen, 2013). Diameters were measured using a caliper. Length was measured using a

measuring tape and was terminated once the bole had tapered to five-centimeter diameter. Snag height was approximated to the nearest half-meter.

Dead wood were characterized into decay stages following Lilja et al. (2006), modified from Renvall (1995): (I) freshly dead, a tree that has died during the last year, needles usually still attached; (II) hard, a knife penetrates by pushing only a few millimeters into the wood; (III) soft surface wood, knife penetrates 1–2 cm; (IV) relatively soft, knife penetrates 3–5 cm; (V) soft throughout; knife penetrates easily to the handle, even almost completely decayed logs partly buried into the ground.

We calculated the deadwood volume using the Huber (1839) formula:

$$Vol = \frac{\pi L d_m^2}{4}$$

Figure 4. *Vol* = deadwood volume, *L* = length, and d_m = mid-diameter of the log (modified from Öder et al., 2021).

2.4 Laboratory Processing
I conducted all field and laboratory work together with Oda Jørgensen. Together, we sorted approximately 4,000 beetles from 45,000 other collected insects from October 5th to November 15th. Collected beetles were then identified to species by expert Sindre Ligaard.

2.3 Data Analysis
All data was analyzed using R version 4.1.2 (R Core Team, 2021) and RStudio version 1.4.1717 (RStudio Team, 2021).

2.3.1 Difference in forest management types
I used Analysis of Similarities (ANOSIM) test to determine if there was a difference in forest management type between the near-natural and former clear-cut sites. ANOSIM tests whether distances between groups are greater than within groups. It is similar to an ANOVA hypothesis test, but it uses a dissimilarity matrix instead of raw data and is non-parametric to accommodate skewed data. The R value in this test is a ratio of the between groups variation to the within group variation.

I used a mixed-effects logistic regression with logit link model using the 'lme4' R package (Bates et al., 2015) to determine which stand characteristics significantly determine

forest management type. Logistic regression was used because the response variable was binary (clear-cut or near-natural), and the model included nested 'Site' and group 'ID' random effects. Random effects can cause spatial pseudoreplication if not addressed, involving several measurements taken from the same vicinity (Crawley, 2013). The means or sums of all predictors were calculated at the group level. Two temperature loggers (VAR-N-1 and GRAV-N-2) were missing, so we took the average of the other three groups in that site to fill in the data points. The predictor variables were standardized with Z-score standardization to ensure each variable contributed equally to the analysis in order to understand the relationship between several predictor variables and a response variable. I used candidate model selection to determine the most appropriate model, focusing on the lowest Akaike Information Criterion (AIC) (Akaike, 1998) and Variance Inflation Factors (VIF) in the 'car' R package (Weisberg & Fox, 2011). Interactions were also tested. VIFs in the final model were all under 2.0 indicating low statistical multicollinearity. The final model was also parameterized and checked for diagnostics including over/underdispersion and residuals with the 'DHARMa' R package (Hartig, 2020), and homogeneity of variance across random effect groups with Levene's test with the 'car' R package. Random effects were also tested for justification by comparing the mixed model with a regular model.

Deadwood diversity was calculated using the Shannon-Weiner Index (H) as outlined by Oettel et al. (2020) (Appendix). A similar technique of using the Shannon-Weiner Index for stand structure was also used by Boucher et al. (2006). The diversity of deadwood was analyzed with (1) species, (2) diameter class, (3) degree of decomposition (decay class), and (4) quality of deadwood. The DBH measurements were cut into three classes: small (10-20cm), medium (20-30cm), and large (30+cm). The five decomposition classes and quality of deadwood (snag or log) were determined on-site.

$$Deadwood\ Diversity\ (H) = -\sum_{i=1-n}^{n} p_i * log_2 * p_i$$

Figure 5. p_i = proportion of the ith species, diameter class (small, medium, large), decay class (1-5), or quality (snag/log). Higher H-values indicate higher diversity (modified from Oettel et al. (2020)).

2.3.2 Differences in beetle diversity between the forest management types

I assessed community-level diversity with several analyses. I used individual-based rarefaction to test beetle diversity differences between the former clear-cut and near-natural forest management types (Chao et al., 2014). All sites and groups were pooled for the rarefaction. I also visualized the species assemblage patterns using an NMDS (non-metric multidimensional scaling) with Hellinger transformed Bray-Curtis similarity values (Apigian et al., 2006). Singletons were removed to reduce the stress down to an interpretable level. NMDS allows visualization of the levels of (dis)similarity for each pairwise comparison of individuals (Seibold et al., 2016).

To compare species richness and abundance for both saproxylic beetles only and total beetles, I used general linear mixed models (GLMM) with a log link and Poisson errors. Non-saproxylic species were not analyzed separately due to lack of statistical power. Although the traps were significant predictors of beetle abundance, they do not pertain to answering my research question and were thus pooled. The fourth group at every pair was omitted because the fourth group in each pair did not contain a malaise trap. The same random effects, model selection protocol and diagnostics were used for these four regressions as outlined above.

I separated the Østmarka site data to compare assemblages in July and August. I used a PERMANOVA test (Anderson, 2001) to determine the Bray-Curtis similarity in Hellinger-transformed species assemblages between the July and August collection periods in Østmarka using the 'vegan' package in R (Oksanen et al., 2007). PERMANOVA is a test of similarity in multivariate location and dispersion. P-values were based on 999 permutations. 'Month' was set as fixed factor in the model and site and ID as random factors. I used a regression model with Poisson errors using the 'lme4' R package (Bates et al., 2015) to determine if there was an interaction between forest management type and month of collection for both beetle richness and abundance. The same diagnostics were used for these models as outlined above.

3. Results

3.1 Differences between near-natural and clear-cut forest management types

Forest management types were significantly different based on stand variables (ANOISM test, p=0.006, R=0.023). Deadwood volume of decay class one and number of stems were higher in former clear-cut than near-natural forest (p<0.001), and diversity of deadwood and total volume of deadwood volume were higher in near-natural forest (p<0.001) (Table 1, Figure 6). The model's total explanatory power was substantial (conditional R2 = 0.97), and in part related to the fixed effects alone (marginal R2) was 0.72.

Table 1: Generalized linear mixed model with logit link: Forest management (CC vs NN) explained by the predictors given and location of pair as a random variable (Appendix). Clear-cut was the reference level.

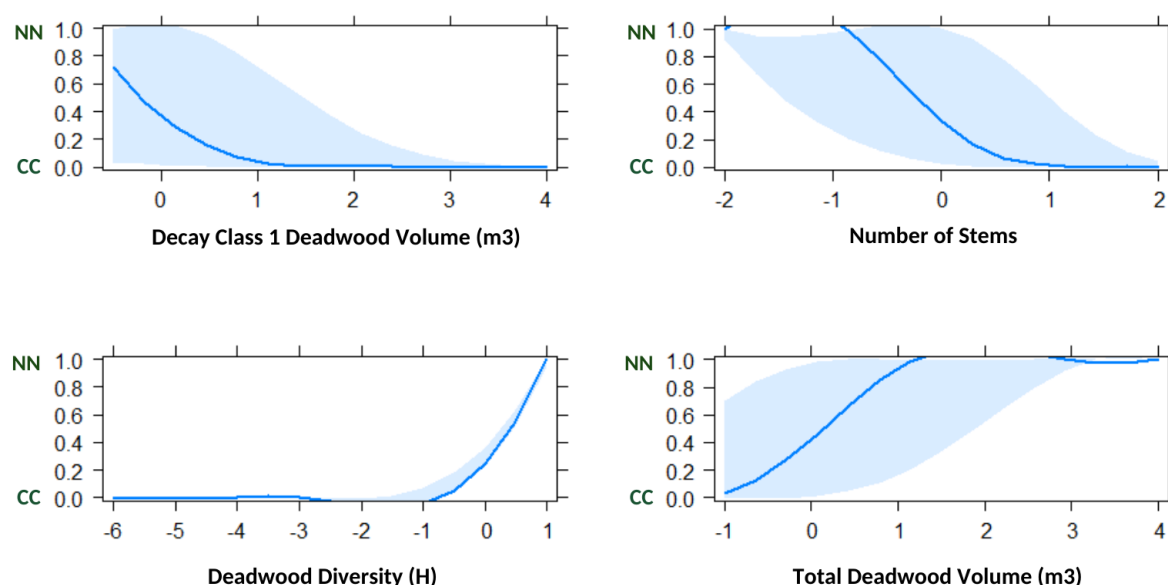| Predictors	Estimate	SE	Z	p
Intercept	-0.417	2.11	-0.198	0.84
Decay Class 1 Volume (m^3)	-2.71	0.676	-4.01	**< 0.001**
Number of Stems	-4.12	0.899	-4.58	**< 0.001**
Deadwood Diversity (H)	8.57	1.51	5.66	**< 0.001**
Total Volume Deadwood (m^3)	3.16	0.821	3.85	**< 0.001**

Figure 6. Predicted marginal means from generalized linear mixed model with logit link. These are average values of the outcome (NN or CC) at particular levels of the predictors.

Covariates have been Z-score standardized. Confidence intervals are represented by the blue shading.

3.1.1 Deadwood Diversity differences between near-natural and clear-cut forest management types

Deadwood diversity was consistently higher in the near-natural forest management type and the clear-cut forest management type had more variation between the sites. The near-natural sites had proportionally and absolutely greater amounts of later-stage decay (four and five) than the former clear-cut sites, and the former clear-cuts had absolutely and proportionally greater amounts of deadwood volume of decay class one (Appendix). The near-natural forest management type also had proportionality and absolutely greater amounts of large-size dead trees in the large DBH class (30+cm) (Appendix), as well as a greater amount in the medium DBH class (20-30cm). The near-natural sites had 1.46 times more mid-size trees and 2.65 times more large-size trees than CC. Moreover, the near-natural sites had more spruce, birch, and rowan than the former clear-cuts, and the former clear-cuts had more pine.

3.2 Species richness, abundance, and diversity differences between the near-natural and former clear-cut sites
3.2.1 Total beetle abundance and richness explained by forest management and stand characteristics

Beetle abundance in near-natural sites was 1.24 times greater than in former clear-cuts (p<0.01). Similarly, beetle richness in near-natural forest was 1.22 times greater than the beetle richness in the former clear-cut forests (p = 0.065) (Table 2). Beetle abundance and richness increased with volume of freshly dead wood (IRR>1) (Table 2). High local temperature also increased both species richness and abundance (Table 2, Figure 7). Richness additionally increased with higher numbers of tree stems and decreased with higher greater deadwood diversity (IRR<1) (Table 2, Figure 7). The final species abundance explanatory model's power was substantial (conditional R^2 = 0.71), in part related to the fixed effects alone (marginal R^2 = 0.55). The final species richness explanatory model's power was moderate (conditional R^2 = 0.47), mostly related to the fixed effects alone (marginal R^2 = 0.42).

Table 2. Generalized linear mixed models with Poisson errors: (1) richness and (2) abundance (response variables) of beetles explained by predictors given during the main collection period in August. Location of pair and group were random variables (Appendix). Standardized parameters were obtained by fitting the model on a standardized version of the dataset. Clear-cut was the reference level.

Model	IRR	Estimate	SE	Z	p
Richness (response)					
(Intercept)	40.6	3.70	0.078	47.6	**< 0.001**
Forest Management Type [N]	1.22	0.202	0.109	1.85	0.065*
Mean Day Temperature (C)	1.13	0.126	0.052	2.41	**0.016**
Decay Class 1 Volume (m^3)	1.17	0.153	0.049	3.14	**0.002**
Number of Stems	1.16	0.146	0.054	2.72	**0.007**
Deadwood Diversity (H)	0.87	-0.135	0.065	-2.07	**0.039**
Abundance (response)					
(Intercept)	81.4	4.40	0.107	40.8	**< 0.001**
Forest Management Type [N]	1.24	0.218	0.095	2.31	**0.021**
Mean Day Temperature (C)	1.34	0.293	0.081	3.63	**< 0.001**
Decay Class 1 Volume (m^3)	1.17	0.160	0.049	3.33	**< 0.001**

*Approaching significance

(a)

(b)
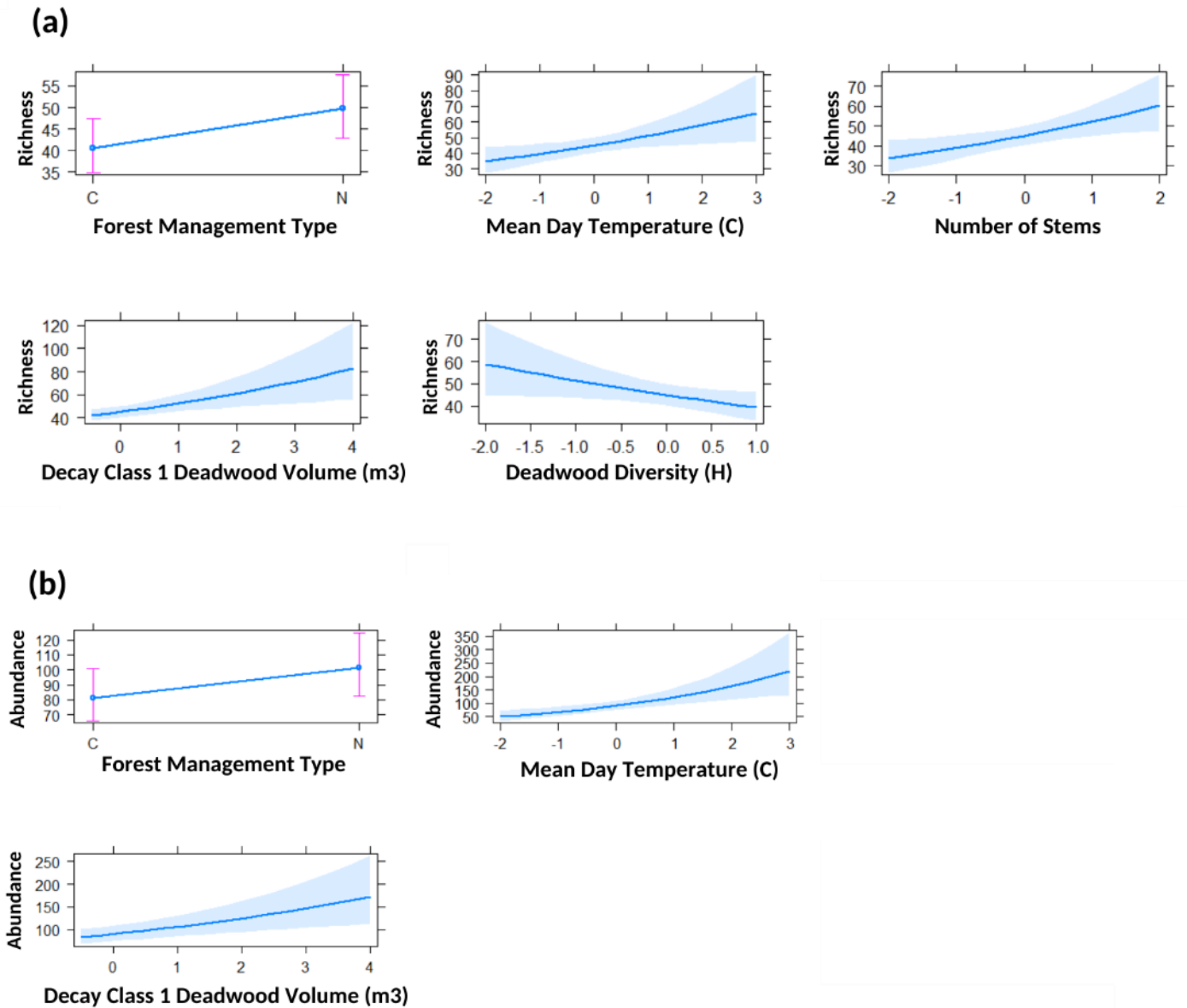
Figure 7. Predicted marginal means from generalized linear mixed model with Poisson errors of beetle (a) richness and (b) abundance. Covariates have been Z-score standardized. Confidence intervals are represented by the blue shading.

3.2.2 Saproxylic beetle abundance and richness explained by forest management and stand characteristics

The saproxylic beetles' abundance and richness in near-natural forest was 1.67 and 1.23 times greater than the beetle abundance and richness in former clear-cut forest, respectively (p < 0.05, Table 3). Moreover, beetle abundance and richness increased with mean day temperature (C), volume of decay classes one (m^3), and with an interaction between

deadwood diversity and decay class volume four (IRR>1). The volume of decay class three also significantly explained saproxylic species richness only (Table 3, Figure 8). Decay class four volume decreased with increasing saproxylic species abundance and richness but increased when interacting with deadwood diversity (Table 3, Figure 8). Deadwood diversity alone did not significantly explain patterns in saproxylic species richness or abundance. The final species abundance explanatory model's power was substantial (conditional R2 = 0.85), in part related to the fixed effects alone (marginal R2 = 0.54). The final species richness explanatory model's power was also substantial (conditional R2 = 0.76), in part related to the fixed effects alone (marginal R2 = 0.44).

Table 3. Generalized linear mixed models with Poisson errors: (1) richness and (2) abundance (response variables) of saproxylic beetles explained by predictors given during the main collection period in August. Location of pair and group were random variables (Appendix). Standardized parameters were obtained by fitting the model on a standardized version of the dataset. Reference level was clear-cut.

| Model	IRR	Estimate	SE	Z	p
Richness (response)					
(Intercept)	29.2	3.37	0.128	26.4	**< 0.001**
Forest Management Type [N]	1.23	0.207	0.101	2.05	**0.04**
Mean Day Temperature (C)	1.22	0.202	0.074	2.74	**0.006**
Deadwood Diversity (H)	0.92	-0.079	0.092	-0.851	0.39
Decay Class 1 Volume (m^3)	1.14	0.134	0.039	3.422	**< 0.001**
Decay Class 3 Volume (m^3)	1.14	0.131	0.055	2.372	**0.018**
Decay Class 4 Volume (m^3)	0.88	-0.129	0.052	-2.46	**0.014**
Decay Class 4 Volume (m^3) * Deadwood Diversity	1.07	0.068	0.103	0.660	0.51
Abundance (response)					
(Intercept)	43.1	3.76	0.182	20.69	**< 0.001**
Forest Management Type [N]	1.67	0.511	0.130	3.92	**< 0.001**
Mean Day Temperature (C)	1.53	0.427	0.098	4.37	**< 0.001**
Deadwood Diversity (H)	1.01	0.008	0.097	0.079	0.93
Decay Class 1 Volume (m^3)	1.19	0.177	0.052	3.45	**< 0.001**
Decay Class 4 Volume (m^3)	0.84	-0.174	0.064	-2.70	**0.007**
Decay Class 4 Volume (m^3) * Deadwood Diversity	1.26	0.235	0.100	2.34	**0.019**

(a)
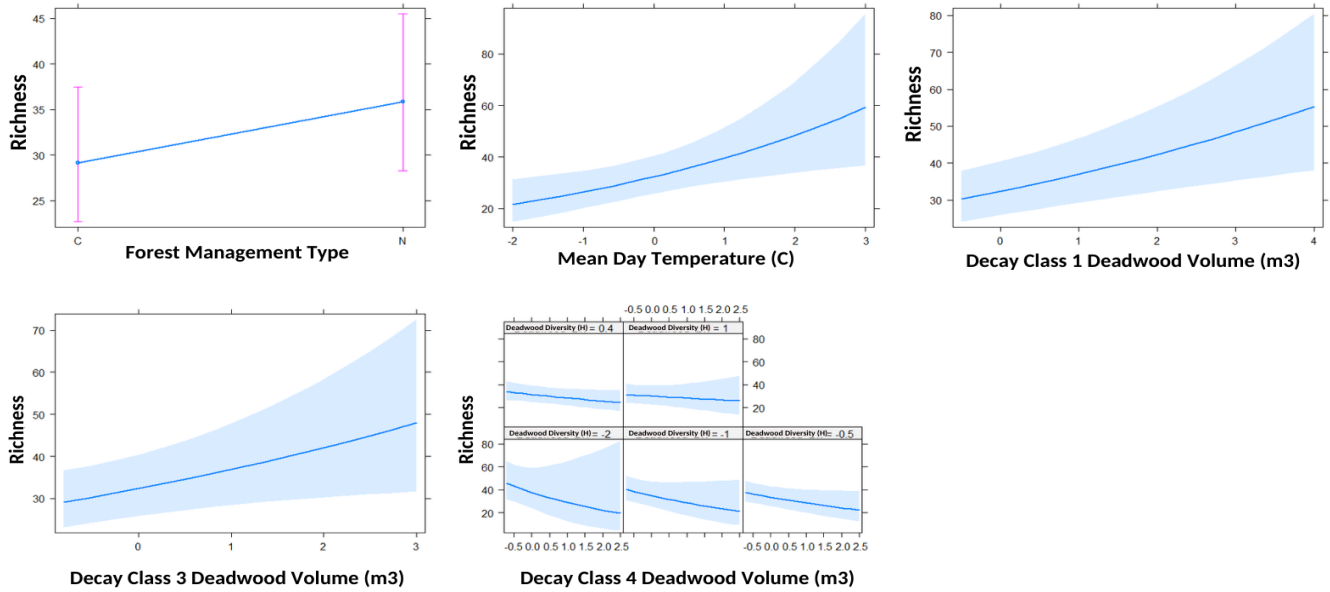
(b)
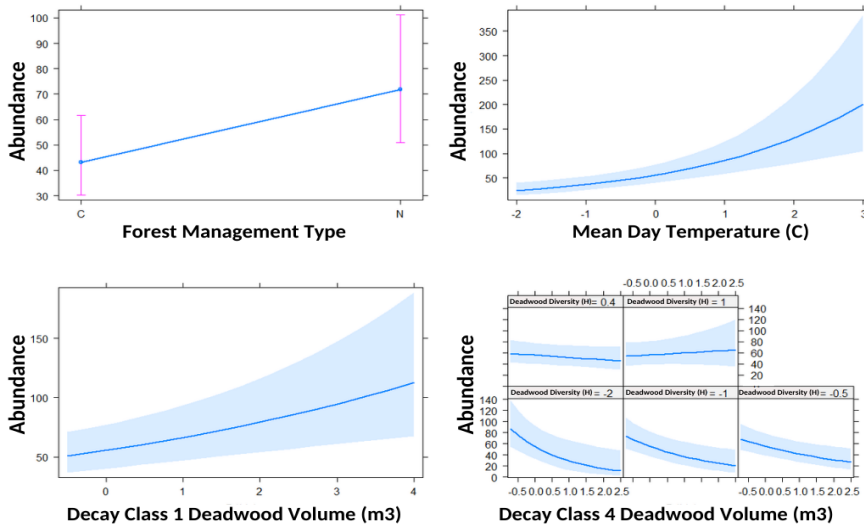
Figure 8. Predicted marginal means from generalized linear mixed model with Poisson errors of saproxylic beetle (a) richness and (b) abundance. Covariates have been Z-score standardized. Confidence intervals are represented by the blue shading.

3.2.3 Differences in beetle community diversity between the forest management types

We trapped 3613 beetle individuals and 233 species during the main collection period, of which 2523 (70%) of the individuals and 148 species (64%) were saproxylic. On former clear-cuts, a total of 176 species were trapped (of which 118, or 67%, were saproxylic), and in mature near-natural forests, 173 species were caught (111, or 64% saproxylic). Three

saproxylic species (nine individuals) were red-listed. Two Near Threatened (NT) species were found exclusively in the near-natural forest, and one Vulnerable (VU) species was found in both forest management types.

As many as 36% of all species were represented by one individual only, and over half the specimens (67%), were represented by five or less individuals. In contrast, each of the eight most abundant species were represented by 78 - 516 individuals. Half of the species were found in one forest management type only (Figure 9). The species shared by both the clear-cut and near-natural forests were also the most abundant; out of the 116 species shared between the forest management types, 64% had an abundance over six individuals. Those species that were only present in one forest management type occurred at low abundances; 72% of species unique to the near-natural forest management type only occurred once and 71% in the former clear-cut. 70% of a random subset with the unique species were also singletons.
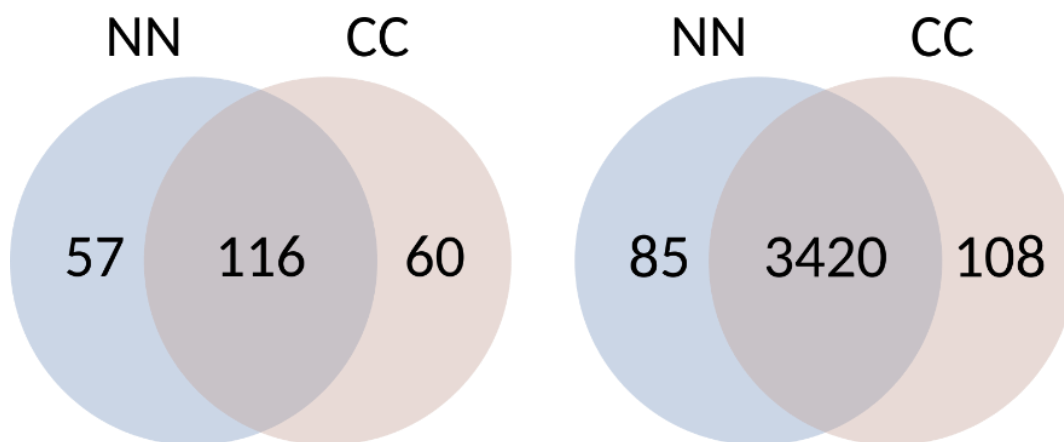
Figure 9. Venn-diagram of the number of unique and shared species (left) richness and (right) abundance between the two forest management types.
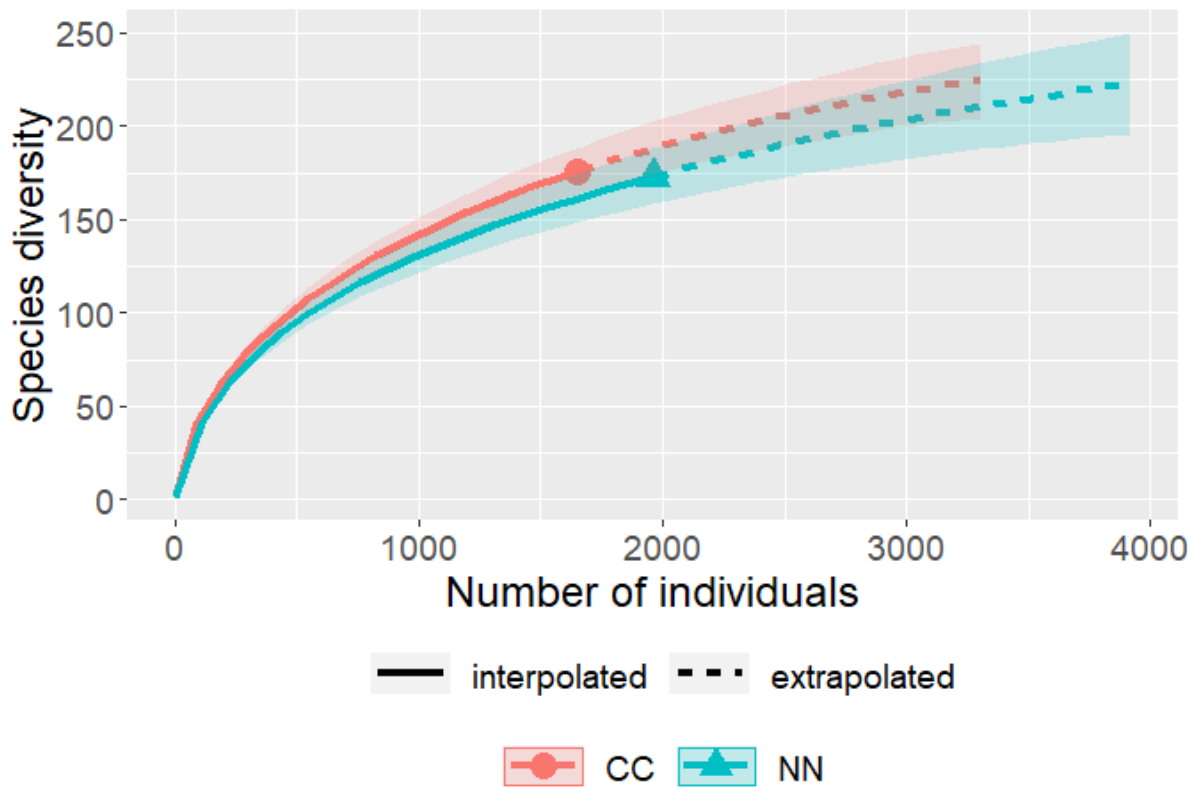
Figure 10. Individual-based rarefaction (mean and 95% CI) for beetles in each forest management type separately, all sites aggregated. Individual-based rarefaction revealed that beetle richness at former clear-cut sites was comparable to near-natural sites.

The NMDS plot (K = 2, stress = 0.2) revealed a slight difference in multivariate location (along one axis) and dispersion between the two stand types, with greater dispersal in former clear-cut stands than near-natural stands (Figure 11). The NMDS plot also indicated that the higher dispersion among the clear-cut was a result of larger differences between sites.
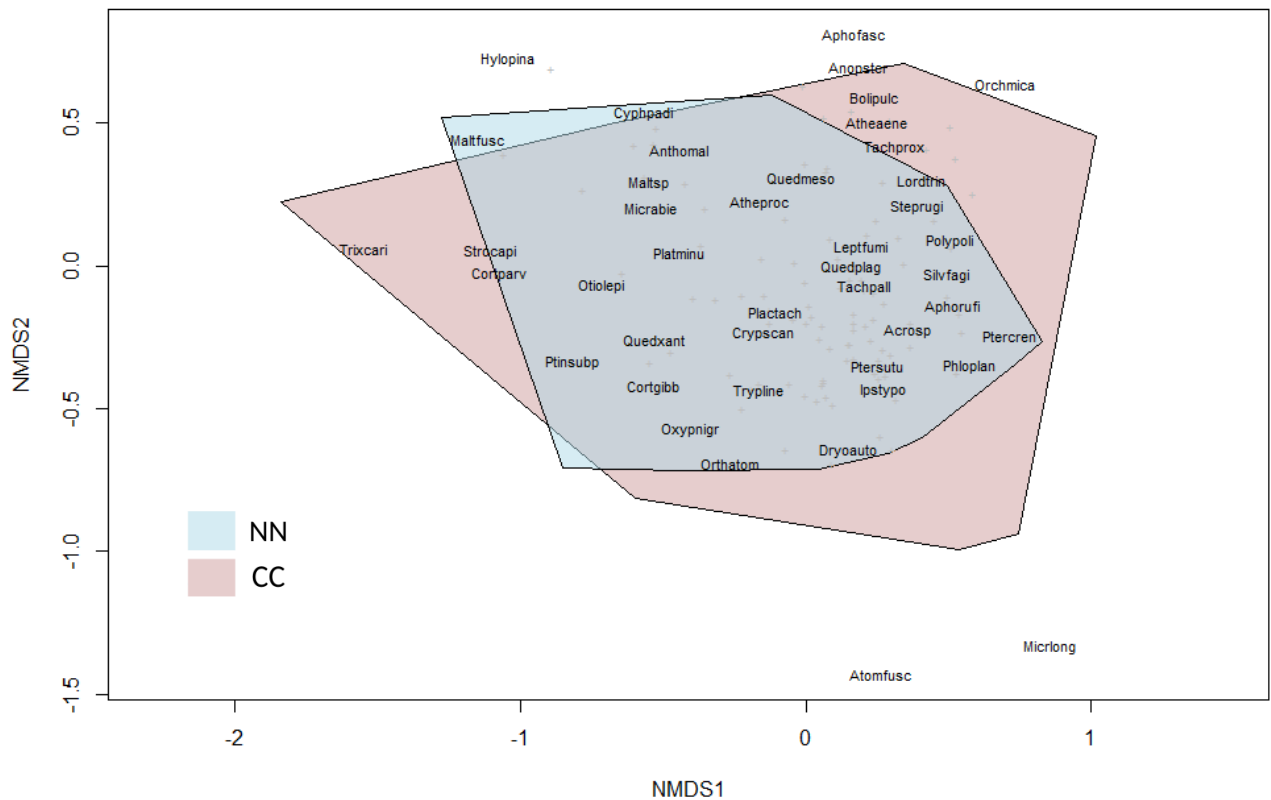
Figure 11. NMDS plot visualizing the differences in beetle community structure among forest management types. A hull has been drawn around the edges of each stand type cluster. The NMDS is based on Bray-Curtis similarity of beetle species calculated from Hellinger transformed species abundance data and excluding singletons. The axes are dimensionless and points closer together represent more similar compositions. The centroids of the forest management types are very close together. Species shown have the greatest abundance. K = 2; Stress = 0.202.

3.2.4 Beetle community differences due to seasonality

In the PERMANOVA for the Østmarka dataset, 'Month' (Sums of Squares = 0.73; F = 127.26; p =0.03; R^2 = 0.93) was significant demonstrating a difference in the dispersion and/or location between the two months' beetle communities. The abundance and richness of beetles were greater in July, but the interaction between month and forest management type was only significant for beetle abundance (Table 4, Figure 12).

Table 4. Generalized linear mixed models with Poisson errors: (1) richness and (2) abundance (response variables) of beetles explained by predictors given in Østmarka. Reference levels were clear-cut and August.

| Model	IRR	Estimate	SE	Z	p
Richness (response)					
(Intercept)	55	4.01	0.0778	51.5	**<0.001**
Month [J]	2.33	0.848	0.0930	9.11	**<0.001**
Forest Management Type [N]	0.85	-0.157	0.115	-1.37	0.171
Month[J]*Forest Management Type[N]	1.19	0.178	0.135	1.31	0.189
Abundance (response)					
(Intercept)	117	4.77	0.0534	89.2	**<0.001**
Month [J]	3.51	1.25	0.0605	20.7	**<0.001**
Forest Management Type [N]	1.13	0.126	0.0732	1.72	0.086*
Month[J]*Forest Management Type[N]	0.83	-0.191	0.0839	-2.28	**0.023**

*Approaching significance
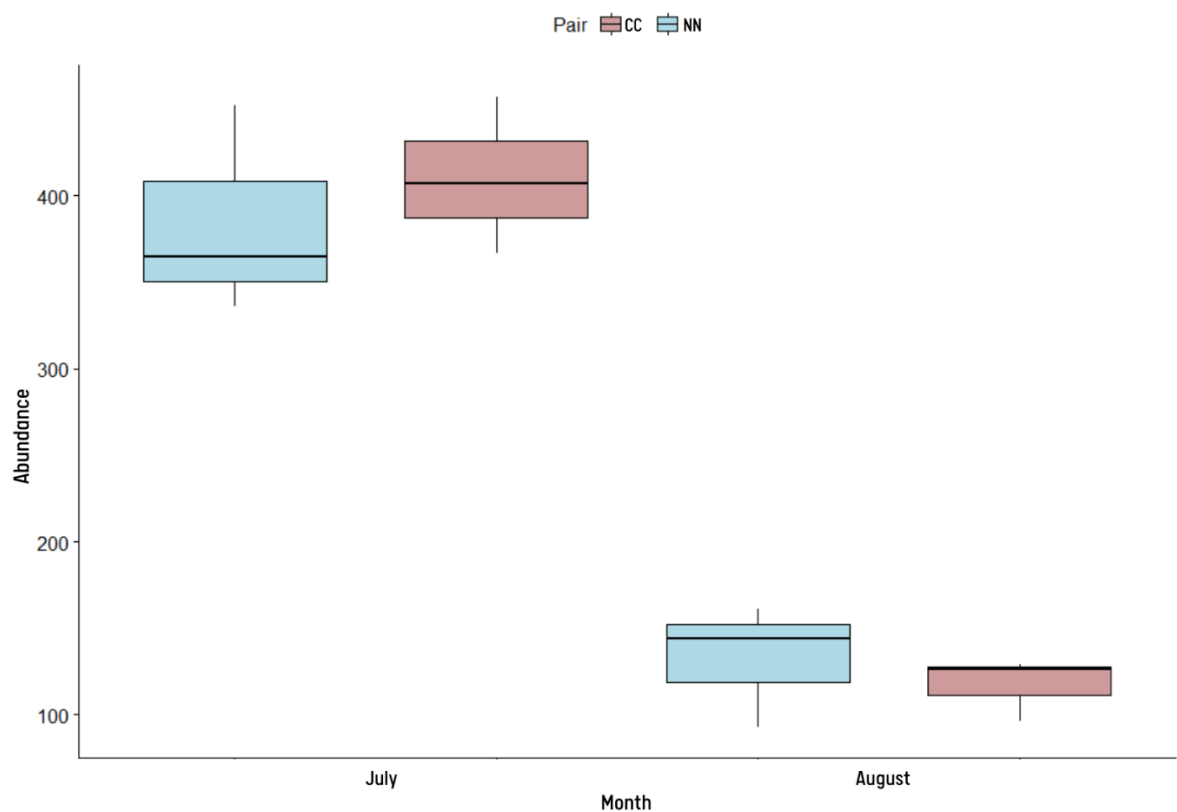
Figure 12. Abundance of beetles in July and August according to forest management type and month in Østmarka.

4. Discussion

4.1 Near-natural and clear-cut forest management types are characteristically different

The near-natural forest sites had greater volume and diversity of dead wood, and particularly more wood in later stages of decay with larger dimensions than the former clear-cut forest. Canopy density (number of stems) and deadwood in the early stage of decay, on the other hand, were highest in the former clear-cuts. Forest management intensity is known to decrease deadwood volume and diversity which corresponds well with my results (Esseen et al., 1992; Fridman & Walheim, 2000; Kohv & Liira, 2005; Storaunet et al., 2005). Deadwood diversity (H) in this study was primarily driven by greater counts of deciduous trees, trees in larger DBH classes, and deadwood at later-stages of decay. Greater deadwood diversity, especially regarding larger size classes and more advanced decomposition stages, is also found by several studies in lesser managed forest (Gibb et al., 2005; Kohv & Liira, 2005; Liira & Kohv, 2010; Rimle et al., 2017). Thus, forest management changed forest characteristics as expected given the two management regimes.

This study's finding about greater early stages of decay in former clear-cut sites was supported by Storaunet et al. (2005) who found more freshly dead wood in high-productive sites with a more intensive history of logging than at low-productive sites in National Nature Reserves in Norway. Former clear-cut sites with more freshly deadwood could be a consequence of stand density as management aims to produce the maximum volume of timber (Stokland, 2012). Denser stands, especially those of similar age, size, and species, can lead to higher tree mortality due to greater competition for resources and ultimately weaker health (Kozlowski et al., 1991; Kuuluvainen et al., 2012). Thus, higher amounts early-stage deadwood in the former clear-cut sites is expected from the management regime.

4.2 Species richness, abundance, and diversity differences between the near-natural and former clear-cut sites

4.2.1 Forest management strategy determines beetle species richness and abundance

Total and saproxylic beetle richness and abundance was greater in the near-natural sites than the former clear-cut sites. All groups increased with mean temperature and availability of

freshly dead wood, and saproxylic beetle abundance and richness additionally increased with greater amounts of late-stage decay deadwood depending on available deadwood diversity. Saproxylic species richness also increased with higher inputs of intermediate-stage decayed deadwood. This study's main results support earlier findings that the number of species and/or individuals in near-natural forest management types are higher than even-aged (i.e., former clear-cut) stands (Burner et al., 2020; Jacobsen et al., 2020; Paillet et al., 2010; Savilaakso et al., 2021). Minimal counts of large-diameter dead trees historically found in clear-cut forests would not sustain populations of species specialized in such unfavorable dead wood qualities or microclimatic conditions (Stenbacka et al., 2010). Moreover, higher counts of temporally continuous large-diameter class decaying trees and more decaying deciduous trees are known to increase beetle diversity (Esseen et al., 1992; Rimle et al., 2017; Siitonen & Saaristo, 2000; Siitonen, 2001). In fact, 15% of the species studied in Dahlberg & Stokland (2004) required deadwood with a diameter of >40cm. Other factors such as standing/lying deadwood (Similä et al., 2003), habitat continuity (Grove, 2002), and the composition of the surrounding landscape (Jacobsen et al., 2015; Økland et al., 1996; Sverdrup-Thygeson et al., 2014a) influence forest organisms, the two latter of which we failed to include in this study. Nonetheless, important structural features including more large-diameter and deciduous trees allow for greater diversity of beetles.

Richness and abundances were likely greater in the near-natural forest management type because habitat heterogeneity (i.e., deadwood diversity) is the most important predictor of species diversity (Báldi, 2008). Different deadwood types and decay stages (i.e. structural complexity) provide habitat and food resources for different assemblages (Esseen, 1997; Grove, 2002; Jonsell et al., 1998). For example, there is high saproxylic species diversity after initial tree death, followed by a quick succession of different species as the tree decomposes (Stokland, 2012; Vindstad et al., 2020). Early decay-stage deadwood was found to be the most important driver of species in one study (Joelsson et al., 2018), but others found mid-late decay stages to be the most important (Dahlberg & Stokland, 2004; Rimle et al., 2017). Hence, this study's results of the significance of different decay classes likely point to different species living on different stages of deadwood; greater diversity of deadwood in near-natural sites increase structural heterogeneity which provides a greater niche opportunity for forest-dwelling biodiversity (Báldi, 2008).

Total deadwood volume is accepted as important for diversity (Martikainen et al., 2000; Sandström et al., 2019; Seibold et al., 2015). My findings, however, do not agree likely because most of the total volume was explained by the volume of decay class two deadwood which was similar in the two forest management types, thus the total deadwood covariate was not statistically significant (Appendix). Further, Lassauce et al. (2011) suggested that total deadwood volume is generally not suited as a universal indicator of deadwood species diversity as the positive effect of high amounts of dead wood can be explained by obscured variability of dead-wood decay stages within single trees (Seibold et al., 2016). Rather, a good direct indicator of diversity could be different classes of decay, especially fresh and later-stages as both beetle richness and abundance were well explained by varying decay stages of deadwood in our study.

Warm ambient temperatures also increased beetle richness and abundance in this study. Müller et al. (2015) found that higher temperatures positively affected total species richness on both the landscape scale and microscale, indicating its importance as a major structural characteristic of boreal forests and thus forest biodiversity. High temperatures are also linked to greater trap catches as higher temperatures cause greater insect activity (Liu et al., 1995; Seibold et al., 2016). As such, greater temperatures in this study increased the beetle richness and abundance due to its effect on insect activity which increased sampling efficiency.

4.2.2. Forest management types hosted similar common species but different uncommon species.

There was a near-complete overlap of community assemblage between the forest management types once singletons, who encompassed about a third of the dataset, were removed. As such, community assemblage similarities between former clear-cut and near-natural forest were due to the abundant species in the dataset. Joelsson et al. (2017) also found mature even-aged forest and uneven-aged forest beetle assemblages to be indistinguishable; in their study, the mature uneven-aged managed stands (similar to our near-natural stands), and mature thinned stands (most similar to our former clear-cuts) did not differ in composition with the exception of cambium consumers. Contrastingly, McGeoch

et al. (2007) found that stand types in central Sweden only shared 50-67% of their species. McGeoch et al. (2007) also collected over triple the number of beetles during their collection period and only had 19% singletons in their dataset, so it is very possible our large portion of singletons was due to inadequate sampling effort. My rarefaction curve clearly demonstrates inadequate sampling as neither the former clear-cut nor the near-natural communities reached an asymptote during interpolation, thus we certainly failed to detect many species that were locally present (Burner et al., 2021a).

It is a challenge to completely sample beetle communities which are largely comprised of beetles in low abundances (Martikainen & Kouki, 2003; McGeoch et al., 2007). Aside from inadequate beetle individuals collected, the flight interception traps used in our study could have added to the randomness of singleton beetles caught; these traps can catch 'tourist species' which merely fly through the sites without necessarily reproducing there (Joelsson et al., 2017). Furthermore, some saproxylic species can disperse up to five kilometers away from their source population to find quality habitat (Komonen & Müller, 2018) thus some species caught might not have lived nearby. However, Sverdrup-Thygeson & Birkemoe (2009) found flight intercept traps clearly respond to the immediate surroundings. As such, the large percentage of singleton species are likely to be a result of too low sampling effort, randomness, and environmental conditions.

Despite a small sample size, we found two saproxylic red-listed species exclusively in the near-natural sites. These two species, *Leptophloeus alternans* and *Liodopria serricornis*, are both dependent on dead wood and red-listed due to clear-cut forestry which fragments their habitat and reduces its quality (Ødegaard et al., 2021a; Ødegaard et al., 2021b). As a result of these threats, both populations have declined by up to 90% (Ødegaard et al., 2021a; Ødegaard et al., 2021b). Since these beetles strongly require deadwood and have other strict habitat requirements, they might depend on the fragments of near-natural forests still present in Norway.

4.3 Data from August does not fully represent the patterns from main beetle flight period

There was a greater richness and abundance of beetles in July than August in Østmarka, as well as a significant difference in assemblage. Moreover, the effect of forest management

type was not equal in each month on beetle abundance, thus the patterns drawn from the main collection period of August cannot be fully applied to the main beetle flight activity period of July. Beetles are typically collected mid-May to August in southern Norway (Jacobsen et al., 2015) and new species decrease as the months pass; Burner et al. (2021a) found 83% of total species captured by late June, 60% of total species in July, and only 47% in August with less than five percent new species, meaning, August captures a mere fraction of the total beetle diversity in a complete season. We only had the opportunity to do trapping at all sites during August in this study, and it is clear there were differences in the results of July and August diversity. It is not possible to know whether this effect is site-specific, but it certainly a call to be cautious of the results. Even so, most of the results are reasonable with regards to forest qualities.

5. Conclusion: Management Implications

The five pairs of former clear-cut forests investigated in this study differ from near-natural forests in quality and beetle composition. Deadwood volume of fresh and older decay classes, and deadwood diversity explain differences in beetle diversity most consistently because the data set was dominated by saproxylic species which require variable deadwood as resources. There seemed to be an overlap of beetle diversity for common species with general habitat requirements, but the uncommon species were distinct in the forest management types, which could have implications for future management and conservation.

Deadwood has declined between 90-98% due to clear-cutting depending on the region in Fennoscandia (Siitonen, 2001), meaning a potential loss of up to 50% of saproxylic species in the long-term (Stokland, 2012). In order to successfully reduce potential loss of species, forest management should mimic the patters created by natural disturbance (Kuuluvainen, 2009). Management systems should emulate gap-phase dynamics, in which stand-replacing disturbances (i.e., clear-cutting), are rare and small-scale disturbances are more common (Stokland, 2012). In addition, management should focus on increased inputs of later-decay stage deadwood, trees with a larger diameter, and deciduous trees to increase the quality of the forests. Higher quality near-natural forests can also provide a source from which species can recolonize surrounding forest when conditions are right (Komonen & Müller, 2018), so efforts should ensure enough source (near-natural) forests are present within regions to maintain populations. The basis for forest biodiversity is the various disturbance regimes which shape the structure of forest stands. Hence, forest managers should retain, create, and maintain high-quality habitat which will ultimately aid in the conservation of beetles.

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7. Appendix

Table 1. Description of forest stand variables during the main collection period used in analyses.

| Name	Description	Mean ± SD	Unit
Mean Day Temperature	Mean temperature during daylight hours	13.8 ± 0.902	°C
Mean Day Maximum Temperature	Max temperature during daylight hours	22.6 ± 3.71	°C
Days over 15°C	The number of days with mean temperature over 15°C	11.0 ± 6.15	n/a
Number of stems	The number of trees counted with a relascope	33.6 ± 12.3	n/a
Total Deadwood Volume	Total volume of all deadwood per group	4.58 ± 4.34	m^3
Deadwood Diversity	Total diversity of deadwood per group	1.95 ± 0.314	H
Decay Class 1 Volume Deadwood	Volume of fresh deadwood per group	0.281 ± 0.562	m^3
Decay Class 2 Volume Deadwood	Volume of fresh-intermediate deadwood per group	2.71 ± 2.91	m^3
Decay Class 3 Volume Deadwood	Volume of intermediate deadwood per group	0.626 ± 0.835	m^3
Decay Class 4 Volume Deadwood	Volume of late-decay deadwood per group	0.505 ± 0.735	m^3
Decay Class 5 Volume Deadwood	Volume of latest-decay deadwood per group	0.463 ± 0.671	m^3
Decay Class 1 Volume Deadwood Relative Abundance	Proportion of fresh deadwood per group	0.129 ± 0.265	n/a
Decay Class 2 Volume Deadwood Relative Abundance	Proportion of fresh-intermediate deadwood per group	0.534 ± 0.287	n/a
Decay Class 3 Volume Deadwood Relative Abundance	Proportion of intermediate deadwood per group	0.115 ± 0.125	n/a
Decay Class 4 Volume Deadwood Relative Abundance	Proportion of late-stage deadwood per group	0.083 ± 0.124	n/a
Decay Class 5 Volume Deadwood Relative Abundance	Proportion of latest-stage deadwood per group	0.127 ± 0.210	n/a
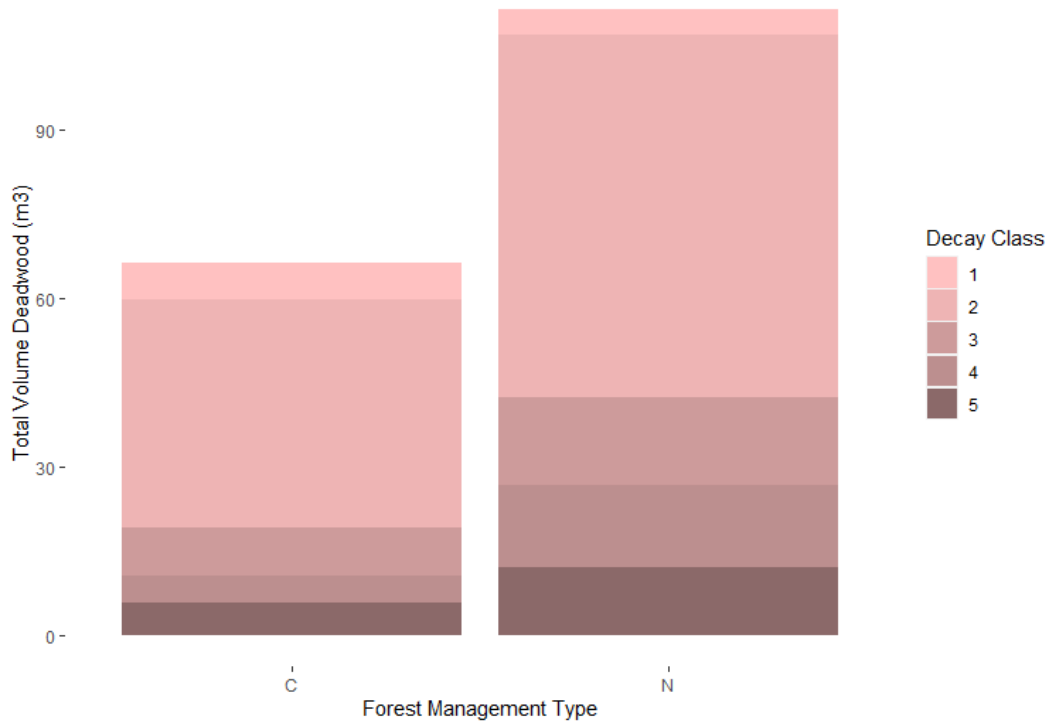
Figure 1. Deadwood volume (m^3) per decay class of deadwood and forest management type. All sites are pooled per forest management type.
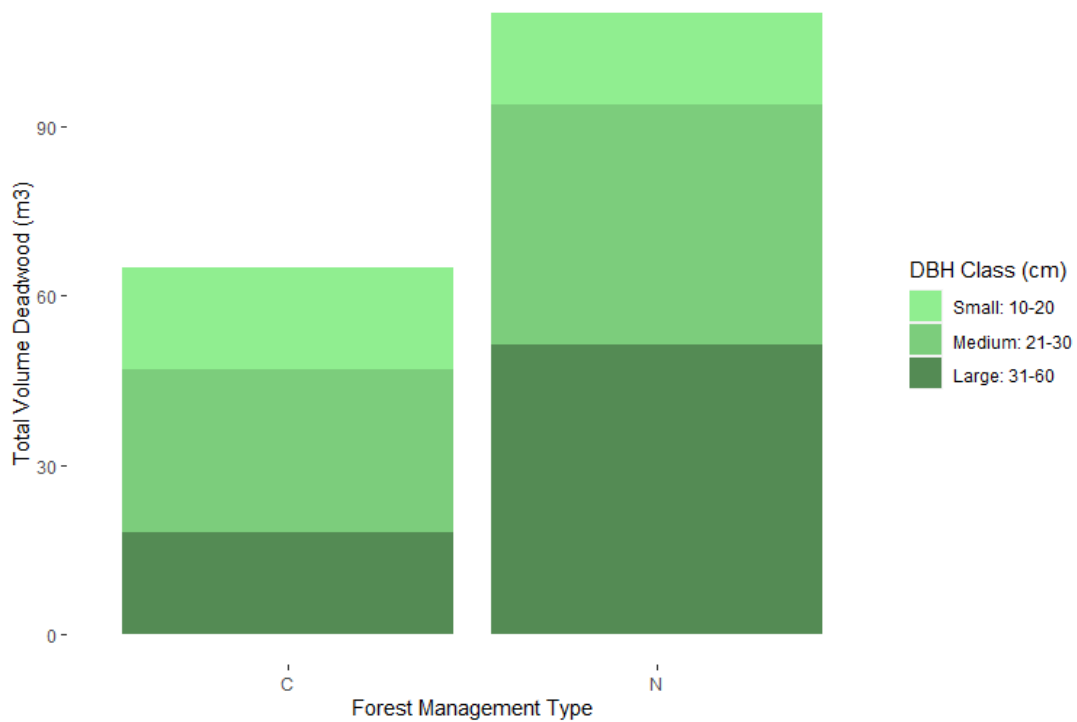

Figure 2. Deadwood volume (m^3) per DBH class (cm) of deadwood and forest management type. All sites are pooled per forest management type.

Table 2: Deadwood diversity calculations of all CC and NN sites pooled. Tree species, DBH class, decay class, and quality (snag/log) encompass the 'taxon' of which the diversity is calculated. 'P' indicates the proportion of each taxon's count in the overall counts. Deadwood diversity (H) is indicated in bold.

CC

Taxon	Count	P	P*Ln(P)	P*Ln(P)^2
Birch	9	0.00925	-0.04332	0.202865
Pine	35	0.03597	-0.11961	0.397693
Rowan	0	0	0	0
Spruce	203	0.20863	-0.32697	0.512413
SM[10-20]cm	159	0.16341	-0.29602	0.53623
MD[20-30]cm	63	0.06474	-0.17723	0.485128
LG[30+]cm	20	0.02055	-0.07985	0.310185
D1 Vol	31	0.03186	-0.1098	0.378425
D2 Vol	141	0.14491	-0.27992	0.540694
D3 Vol	26	0.02672	-0.09679	0.350612
D4 Vol	16	0.01644	-0.06755	0.277476
D5 Vol	28	0.02878	-0.10211	0.36229
Log	124	0.12744	-0.26254	0.540862
Snag	118	0.12127	-0.25585	0.539772
Total	973	1	-2.21755	5.434645
Richness	15			
SS	5.434			
SQ	4.918			
H	**2.218**			
S^2_H	0.0005			

NN

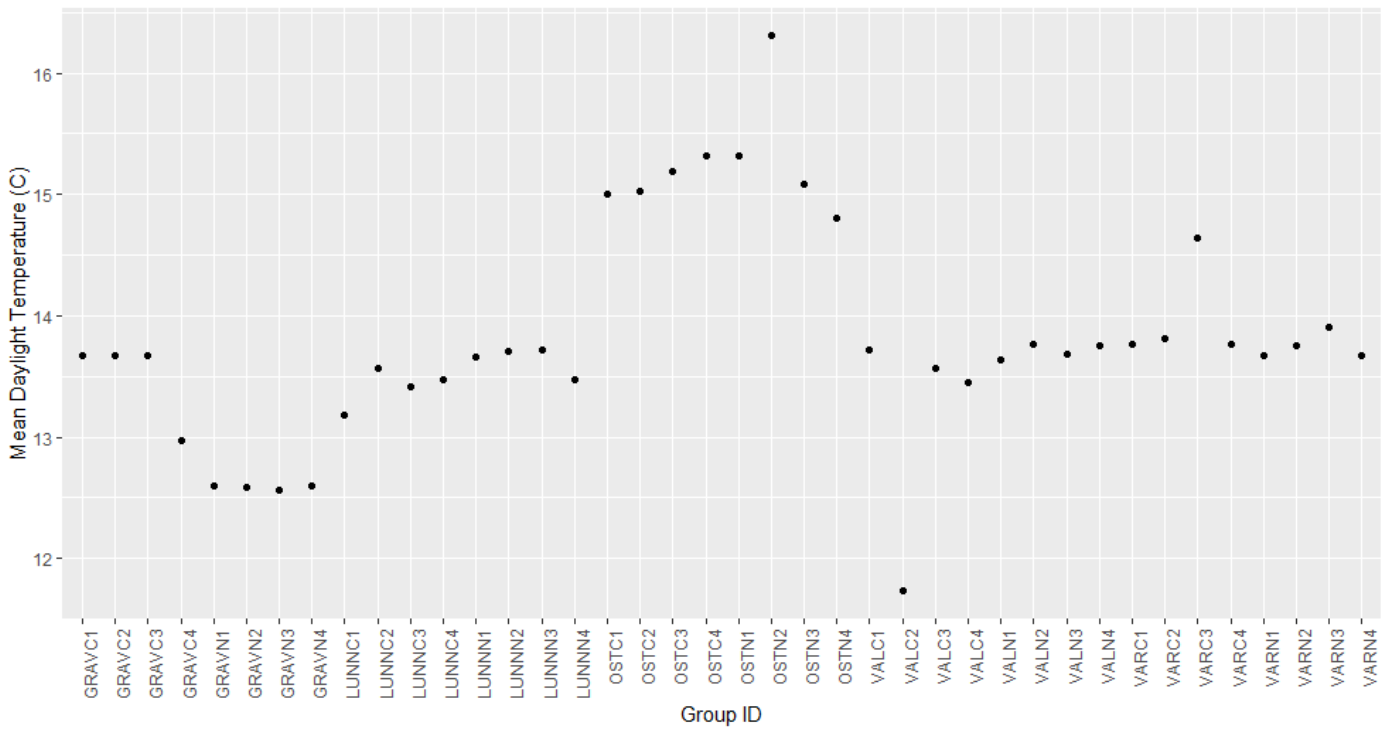| Taxon	Count	P	P*Ln(P)	P*Ln(P)^2
Birch	42	0.035533	-0.11858	0.39575
Pine	4	0.003384	-0.01925	0.109513
Rowan	3	0.002538	-0.01517	0.090652
Spruce	248	0.209814	-0.32763	0.511608
SM[10-20]cm	150	0.126904	-0.26197	0.540793
MD[20-30]cm	92	0.077834	-0.19872	0.507378
LG[30+]cm	53	0.044839	-0.13921	0.432205
D1 Vol	9	0.007614	-0.03714	0.18116
D2 Vol	178	0.150592	-0.2851	0.539742
D3 Vol	37	0.031303	-0.10843	0.375622
D4 Vol	28	0.023689	-0.08866	0.331837
D5 Vol	43	0.036379	-0.12055	0.399479
Log	158	0.133672	-0.269	0.541321
Snag	137	0.115905	-0.24977	0.538258
Total	1182	1	-2.2392	5.495316
Richness	16			
SS	5.495			
SQ	5.014			
H	**2.239**			
S^2_H	0.0004			

Figure 3. Mean temperature (°C) during daylight hours of the main collection period for each group per site. Note the y-axis does not begin with 0°C.
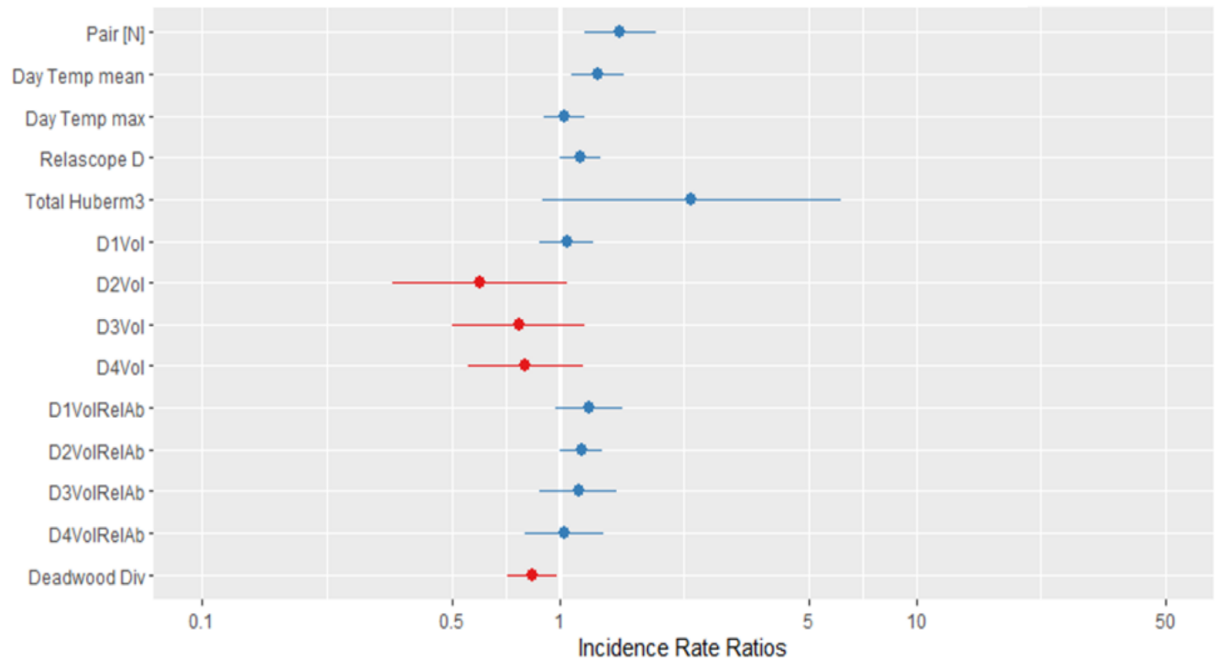

Figure 4. Forest-plot of Incidence Rate Ratio between dependent variable (beetle abundance) and all predictor variables. The bars represent the Confidence Intervals.
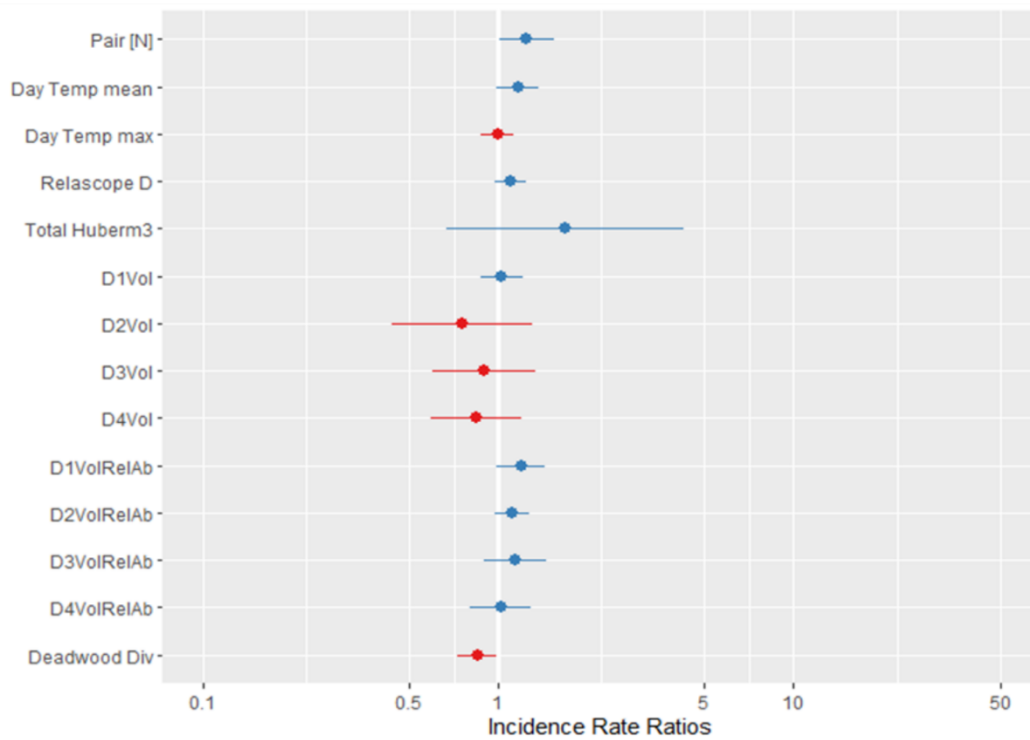
Figure 5. Forest-plot of Incidence Rate Ratio between dependent variable (beetle richness) and all predictor variables. The bars represent the Confidence Intervals.
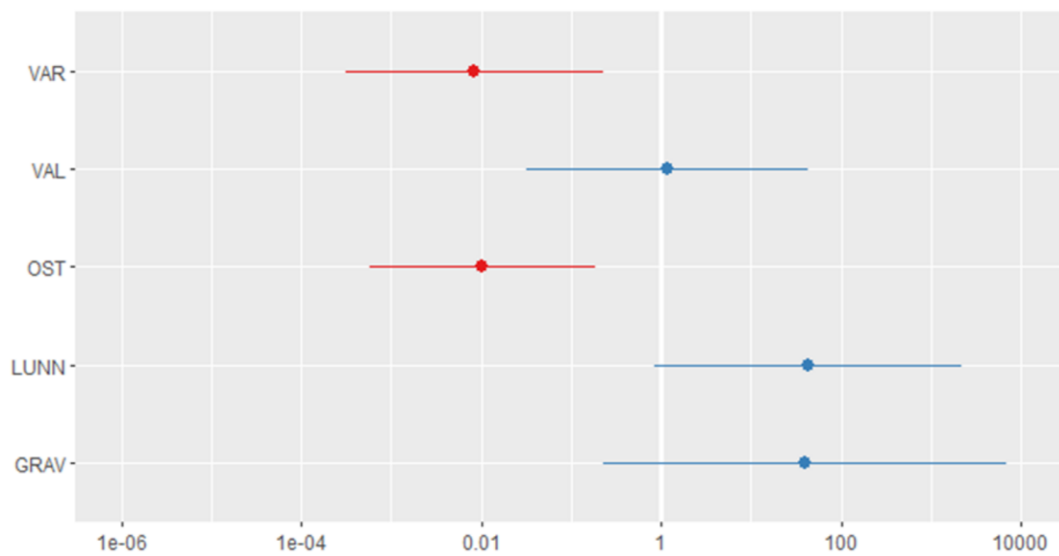

Figure 6. Forest-plot of 'Site' random effect from mixed-effects logistic regression with logit link model with forest management type as the response variable. The bars represent the Confidence Intervals.
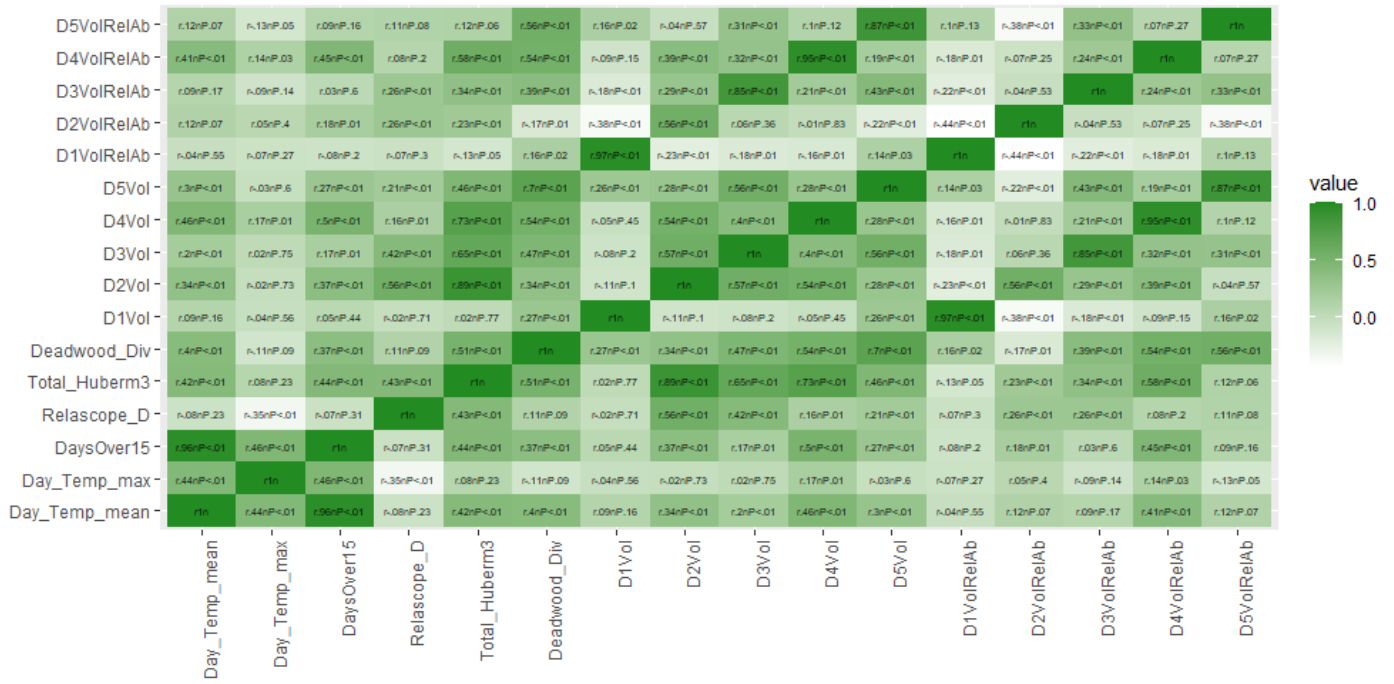
Figure 7. Spearman correlation heatmap for all fixed covariates in regressions. A darker color indicates greater correlation, and a lighter color indicates a lower correlation.

Table 3: Random effect values for all Generalized linear mixed models with response variables as (1) forest management type, (2) beetle richness, (3) beetle abundance, (4) saproxylic beetle abundance, and (5) saproxylic beetle abundance.

	Forest Management Type	Beetle Richness	Beetle Abundance	Saproxylic Beetle Richness	Saproxylic Beetle Abundance
σ^2	3.29	0.05	0.06	0.04	0.06
τ_{00} Group:Site	9.04	0.03	0.05	0.01	0.04
τ_{00} Site	19.45	0.01	0.04	0.05	0.13
ICC	0.90	0.09	0.36	0.58	0.67
N Group	4	6	6	6	6
N Site	5	5	5	5	5
Observations	242	30	30	30	30
Marginal R^2 / Conditional R^2	0.724 / 0.971	0.420 / 0.469	0.547 / 0.712	0.436 / 0.761	0.535 / 0.847

Table 4: Coordinates for all site groups in the study.

Name	Latitude	Longitude
GRAV C-G1	60.920867007225752	12.188708027824759
GRAV C-G2	60.920903971418738	12.189483018592
GRAV C-G3	60.920616975054145	12.188135040923953
GRAV C-G4	60.921161966398358	12.188148032873869
GRAV N-G1	60.915249958634377	12.2066929936409

GRAV N-G2	60.915306033566594	12.206011964008212
GRAV N-G3	60.915678022429347	12.205993020907044
GRAV N-G4	60.914829019457102	12.207146035507321
LUNN C-G1	60.23080101236701	10.762494010850787
LUNN C-G2	60.230838982388377	10.76323295943439
LUNN C-G3	60.230505969375372	10.763210998848081
LUNN C-G4	60.230718031525612	10.764095038175583
LUNN N-G1	60.235370993614197	10.775284040719271
LUNN N-G2	60.235061030834913	10.774668976664543
LUNN N-G3	60.235724039375782	10.774487005546689
LUNN N-G4	60.235779024660587	10.775211034342647
VAR C-G1	60.200301026925445	12.528118025511503
VAR C-G2	60.200304966419935	12.527022007852793
VAR C-G3	60.200412003323436	12.527601029723883
VAR C-G4	60.199955021962523	12.528050970286131
VAR N-G1	60.187967978417873	12.507943036034703
VAR N-G2	60.18802497535944	12.506982972845435
VAR N-G3	60.188141986727715	12.50725002028048
VAR N-G4	60.188109967857599	12.507613962516189
VAL C-G1	60.747482981532812	11.927160965278745
VAL C-G2	60.747294975444674	11.926627960056067
VAL C-G3	60.747825969010592	11.927640996873379
VAL C-G4	60.747105041518807	11.92768600769341
VAL N-G1	60.740155018866062	11.92626996897161
VAL N-G2	60.739802978932858	11.926655033603311
VAL N-G3	60.740060973912477	11.926952004432678
VAL N-G4	60.740458024665713	11.92678302526474
OST N-G2	59.854167988523841	11.026859991252422
OST N-G1	59.85480803065002	11.026761000975966
OST N-G3	59.854535032063723	11.027315966784954
OST N-G4	59.854887994006276	11.027470026165247
OST C-G1	59.861897025257349	10.998977003619075
OST C-G2	59.861765010282397	10.999380005523562
OST C-G3	59.861205015331507	10.998862003907561
OST C-G4	59.861673982813954	10.999068031087518