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Does species richness and abundance of saproxylic beetles differ between old near-natural and old managed forest in south-eastern Norway?

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Abstract

Humans have altered almost all forests on earth through the need for forest resources. Several scientific papers show that forestry is a threat to the biodiversity and that many forest species will go extinct unless drastic measures are taken. One of the largest groups that have suffered from forestry is the saproxylic beetles. Findings in this thesis complement what other researchers have found.

The goal was to investigate how forestry has affected species richness and abundance of saproxylic beetles. An old natural forest stand was compared with an old managed forest stand in south-eastern Norway. Both window traps and pitfall traps were placed out in 29 sites. Beetles were sampled for approximately 9 weeks. Different environmental variables were used to explain the potential differences. Other response variables investigated were red-listed species, beetle size, and specialist and generalist beetles in regards to tree types.

There were no significant differences in neither species richness nor abundance between the two forest types. However, the forest development class, amount of dead wood and basal area of standing dead and living trees affected both species richness and abundance, while species richness was also affected by elevation, which together with variance in age of trees was the only environmental variables that differed between the two forest types. Both response variables seemed to respond positively to a younger mature forest, denser tree stands, and larger amounts of dead wood. Abundance increased with decreasing elevation. Beetle size did not differ between the two forest types, but the species richness of generalists increased with the amount of dead wood. Basal area, elevation and forest development class affected species for which I had no information about regarding tree preference.

The lack of differences in the response variables between the two forests may be due to the small differences in forest characters observed in this study between the old natural forest and the old managed forest. However, by looking into the variables expected to differ between the forests (amount of dead wood, elevation and basal area), effects of these are found on species richness and abundance. The study may have had too few sites to give accurate and indicating results. In addition, the forest types were situated in a mosaic. The conclusion is that further research over larger areas and over a longer time period is needed. This can help future management regarding conservation of the remaining old natural and old near-natural forests.

Sammendrag

Mennesker har forandret omtrent alle skogområder på jorden gjennom behovet for ulike skogressurser. Flere forskere har kommet frem til at skogbruk er en stor trussel overfor biodiversiteten, og at mange skogsarter står i fare for utryddelse om ikke drastiske tiltak blir satt i gang. En av de største gruppene som lider som følge av skogbruk er ved-levende biller. Funn i denne oppgaven komplementerer hva mange andre forskere har funnet.

Målet med oppgaven var å undersøke hvordan hogst har påvirket artsrikdom og abundans av ved-levende biller. En gammel naturlig skogbestand ble sammenlignet med en gammel drevet skogbestand sørøst i Norge. Både vindusfeller og fallfeller ble plassert ut i 29 områder. Biller ble samlet inn i omtrent 9 uker. Flere ulike miljøvariabler ble brukt til å forklare potensielle forskjeller. Andre responsvariabler undersøkt var rødliste-arter, billestørrelse og generalister og spesialister på ulike treslag.

Det var ingen signifikante forskjeller i verken artsrikdom eller abundans av ved-levende biller mellom de to skogtypene. Derimot ble både artsrikdom og abundans påvirket av skogens hogstklasser (ung moden skog vs. gammel moden skog), mengde død ved og tettheten av stående døde og levende trær. Artsrikdom ble i tillegg påvirket av høyde over havet, som sammen med variansen i alder på trærne var de eneste miljøvariablene som skilte de to skogtypene fra hverandre med hensyn til skogstruktur. Både artsrikdom og abundans responderte positivt på ung moden skog (hogstklasse 4), tettere skog og større mengder død ved. Abundans økte med synkende høyde over havet. Det var ingen forskjeller i billestørrelse mellom de to skogene, men artsrikdommen av generalister var positivt knyttet til død ved. Skogtetthet, høyde over havet og hogstklasse påvirket arter jeg ikke hadde informasjon om når det gjelder tre-preferanse.

Mangelen på forskjeller i responsvariabler mellom de to skogtypene kan skylles de få observerte forskjellene i miljøvariabler. Ved å se nærmere på de vi forventet å finne forskjeller på miljøvariablene (død ved, høyde over havet, skogtetthet) mellom skogtypene, ser man at disse påvirker både artsrikdom og abundans. Siden de to skogtypene lå i en mosaikk, er det mulig at forskjeller er vanskelig å finne. Men det er også mulig at studien hadde for få undersøkte områder til at man kan komme med nøyaktige og indikerende resultater. Konklusjonen er at man bør foreta studier over større områder og over lengre tid slik at fremtidig skogbruk kan ivareta de gjenværende områdene med naturlige og nært naturlige skoger.

Contents

1 Introduction

1.1 Forest use and the impact on biodiversity

Humans have in some way altered almost all forests, and the extent of "untouched" forests is minimal (Rosenvald *et al*. 2011, Siipilehto & Siitonen 2004). According to several researchers (e.g. Richardson *et al*. 2007 and Esseen *et al*. 1997), the natural old forests and their associated ecosystems are disappearing globally due to forestry and other human activities. In Norway approximately 25 % of the forest has some natural forest characteristics (Sverdrup-Thygeson 2016), while as little as 2.4 % of the total forested area is old-growth forest (Stokland *et al*. 2014). Forests have been removed to clear land for agriculture, roads and settling, while timber has been produced for buildings, construction, fuelwood, paper (Östlund *et al*. 1997, Kouki *et al.* 2012) and more recently for biofuel (Nabuurs *et al*. 2007, Siitonen 2012). This extensive forest use is threatening the biodiversity due to deforestation and fragmentation of forest areas (Harris 1984, Wilcox & Murphy 1985) which leads to a loss of important habitats. A goal is to reduce the species loss to forest use (Primack 2012), in spite of our need for forest resources. Grove (2002) states that if not drastic measures are taken, several more of the world's forest species will face extinction.

1.2 Dead wood

A large part of the forest biodiversity is related to dead wood (Stokland *et al*. 2012, Hjältén *et al*. 2012, Harmon *et al*. 1986). Dead wood is a resource used by several animal-, plant-, and fungi species for many purposes, such as food, nesting, shelter and hibernation (Stokland *et al*. 2012, Berg *et al*. 1994, Jonsell *et al*. 1998), and is therefore a limiting factor determining survival, growth, reproduction and population size for many forest species (Stokland *et al.* 2012), especially the saproxylic species. Saproxylic means that they are in some part of their life cycle, associated or dependent on dead and dying wood, either standing or fallen (Speight 1989). The term also includes species that are dependent on wood-inhabiting fungi or the presence of other saproxylic species (Speight 1989, Stokland *et al.* 2012). Both the different decay stages in dead wood and the different tree species, provide several microhabitats for different species assemblies (Hammond *et al*. 2001, Hjältén *et al*. 2012).

In Norway, as many as 780 red-listed species are dependent on dead wood (Storaunet *et al.* 2011), and management would thus lead to a loss in biodiversity (Häliövaara & Väisänen 1984, Grove 2002) as many of the standing living trees that otherwise would die and decay are cut. Therefore, the modern forest management leads to large differences between a managed forest and a natural forest. For example, Fridman & Walheim (2000) found that managed forests only have between 2 and 30 %

of the dead wood-volume that unmanaged forests have. Furthermore, Siitonen (2001) who studied coarse woody debris and saproxylic organisms in a boreal forest found that if an old-growth forest were turned into a managed forest, the volume of dead wood would decrease by approximately 90 %. In a natural forest, the availability and amount of dead wood remains more or less the same over time as the trees are allowed to die and decay (Stokland *et al.* 2012), thus creating an opportunity for colonization of new and old dead wood. Therefore, both the amount and diversity of dead wood is higher in an old natural forest, creating a heterogeneous (Kolström & Lumatjärvi 2000) and complex environment with more niches (Penttilä *et al.* 2004). This leads to a higher species richness and abundance of saproxylic species. In a managed forest, this is not the case even if some trees are left during retention forestry. Consequently, a managed forest will not provide the same habitats and food sources many saproxylic species require (Niemelä 1997, Nilsson & Baranowski 1997, Ranius & Hedin 2001, Nordén *et al.* 2014).

To secure that the saproxylic species have a survivable habitat, several researchers have found that it is necessary to increase the amount of dead wood in managed forests (e.g. Martikainen *et al*. 2000, Kaila *et al*. 1997, Økland *et al.* 1996, Gibb *et al*. 2005, Gossner *et al*. 2013a). Placing out both small and large pieces of dead wood might therefore be positive for saproxylic species, as both large logs (Gossner *et al*. 2013a, Abrahsmsson *et al*. 2009, Fridman & Walheim 2000) and small twigs (Jonsell *et al*. 1998) are important for different saproxylic beetle assemblages.

1.3 Saproxylic beetles

The forest group contributing the most to biodiversity, and which is also the most endangered group, is the saproxylic beetles (Siitonen 1994, Irmler *et al*. 2010). Saproxylic beetles feed on either outer bark, inner bark, decaying wood, fungi-decaying wood or the fungi itself (Stokland *et al*. 2012). It is estimated that there are 965 obligate and 292 facultative saproxylic beetle species in Sweden, (Dahlberg & Stokland 2004), and in Norway the saproxylic beetles constitute 17% of all red-listed species (Kålås *et al.* 2015). This is of concern since the saproxylic beetles are important for the decomposition of dead wood, and is part of a complex food web (Stokland *et al*. 2012). The removal of dead wood may therefore have negative cascading effects on forest ecosystems. Saproxylic beetles specialized specifically on either conifer or broadleaf trees will be particularly susceptible to forestry as they are adapted to long-lasting conditions and does not tolerate change as much as generalist species do. Another group adapted to long-lasting conditions are those beetles with a large body size (Seibold *et al.* 2014). If their habitat were to change, these may face an uncertain future, as they may be poor dispersers. As the forests have changed due to the modern management, many of these adapted saproxylic beetle species now have a status as threatened (Sverdrup-Thygeson 2016). Forestry should therefore be handled in such a way that these endangered species survive.

1.4 Norwegian forestry issues

Since the 15th century, the practiced logging regime began to alter the forest structure. The forest was homogenized in regards to stand age, tree dimensions and tree species (Siitonen 2001). The division of forest areas into managed forests and "untouched forests" lead to the need for definitions of both types. In this thesis, the definition of Rolstad *et al*. (2002) and Linder *et al.* (1997) of a natural forest is used: a natural forest is a forest that is managed in such a way that the natural structure, composition and ecological processes are not changed significantly (Rolstad *et al*. 2002). In addition, the natural forest is characterized by having large amounts of dead wood in different decaying stages (Linder *et al*. 1997), and of different tree species. Coniferous trees dominate both old managed and old natural forest, but both have elements of broadleaved trees. However, the old natural have more broadleaved trees as these forest areas are not planted with any particular tree species, as many managed forests are (Stokland *et al*. 2012). The definition of a managed forest is here a forest that is planted, logged and/or fertilized (Direktoratet for naturforvaltning 1988). The managed forest is often cleared of broadleaved trees to favour the growth of coniferous trees. In this study, the old natural forest was selectively cut in the 20th century, and denoted as old near-natural, while the old managed forest was clear-cut.

During the 19th century, selective dimension felling was the common practice (Esseen *et al.* 1997), followed by clear-cutting and planting in the twentieth century (Storaunet & Rolstad 2015). The stands that were clear-cut after the Second World War are now soon mature for cutting (development class 5) (Kuuluvainen 2009). The proportion of this mature forest is 40 % of the total amount of production forest (Granhus *et al*. 2012), and there will be even more over the next 30 years (Granhus *et al*. 2014).

The old near-natural forests may obtain characteristics typical for natural forests and eventually old-growth forests after 100 years (Storaunet *et al*. 2000, 2005, Jönsson *et al*. 2009). Harvesting of the remaining old natural forests and old near-natural forests would therefore be a disaster for many species, as natural forests harbour many rare and threatened species (Sverdrup-Thygeson 2016) and the old-near natural forests can "function as substitutes for the true old-growth forests" (Sverdrup-Thygeson *et al*. 2016). The conservation of the remaining natural and near-natural forests is therefore crucial.

1.5 Research objective

The objective of this study will be to investigate potential long-term effects from forestry on saproxylic beetle diversity. It may provide some guidance to how management should be done, give insights to questions concerning restrictions on forestry in some areas, on how to maintain biodiversity, and provide knowledge about different species' ability to adapt to - and restore from -

changing forest characteristics. In this way, it will be a guidance on forest management and conservation. I will look for variations in species richness (number of species) and abundance (number of individuals) of saproxylic beetles, by comparing two forest stands with different ecological histories, compiled in a mosaic throughout the forest area. One of the forest stands is old managed (hereafter called 'old managed forest'); the other one is old near-natural (hereafter called 'old natural forest'). Previous studies have found that there are structural differences between the two forest types, but they have not assessed how this affects the insects in this area (Sverdrup-Thygeson 2000 and Sverdrup-Thygeson *et al.* 2016).

Therefore, I specifically ask these questions: 1) Are there any differences in species richness and abundance of saproxylic beetles between the old managed forest and the old natural forest? 2) Are there different environmental variables that affect the abundance and species richness? 3) Does the old natural forest contain larger beetle species? 4) Are there any differences in the species richness and abundance of specialist and generalist species? 5) Can small twigs attract more saproxylic beetles? 6) Are there any differences in the number of red-listed species between the two forest types?

I predict that the old natural forest will contain more saproxylic beetle species and individuals than the old managed forest. The old natural forest ought to have more long-lasting conditions because it has only been selectively felled. It should contain larger amounts of dead wood, which creates more microhabitats for saproxylic beetles, and makes the structure of the forest more complex. I also expect the old natural forest to contain larger beetle species and more specialists. Species dependent on conifer trees and broadleaved trees are expected to be found in larger quantities in the old natural forest as they would have had more time to specialize there. Larger beetles are not required to disperse as much since they too are adapted to long-lasting conditions. I expect there to be some differences in the number of red-listed species as these often are species adapted to natural forest-characteristics, which an old near-natural forest may have obtained.

2 Materials and methods

This study is part of the larger project "Sustainable utilization of forest resources in Norway" (KPN BIONÆR) assessing the environmental challenges of increased extraction of forest resources. One of the three sub projects focused on mapping biological old forest using airborne laser scanning (ALS). Based on old maps from the 1950's, they categorized forest stands already old in 1954 as 'old near-natural forest', and stands cut during the 1950's as 'old managed forest'. They found that ALS reflected structural differences between old natural forest and old managed forest (Sverdrup-Thygeson *et al.* 2016). This thesis is part of this sub project.

2.1 Study area and sample plots

All study plots were situated in Hurdal and Nannestad municipality (Akershus County) and Gran municipality (Oppland County) in south-eastern Norway within a 17000 ha forested area owned by Mathiesen Eidsvold Værk (Sverdrup-Thygeson *et al*. 2016). The area is in the boreal zone, with an elevation ranging from 392 – 775 m.a.s.l. The dominant tree species is Norway spruce (*Picea abies*), and the less dominant species are Scots pine (*Pinus sylvestris*), birch (*Betual pubescens*) and aspen (*Populus tremula*) (Sverdrup-Thygeson 2000). The forest floor vegetation mainly consist of *Myrtillus* spruce forest, with small elements of low-fern spruce forests, swamp spruce forest and heath forest. The forested areas contains both old natural and old managed forest stands (both older than 60 years), which are intertwined in a mosaic. The two forest types are in the forestry cutting class 4-5. The cutting classes range from 1-5, where 1 means that the forest is newly cut, and 5 means that it is old mature (Frivold 2003). The managed forest was clear-cut during the 1950's. The natural forest was already old in the 1950's and was only selectively cut. However, the exact history of the two forest stands are unknown. The ALS study found that the old managed forest is recognized by being more dense and taller than the old natural forest, but with less shrubs covering the ground. The canopy is also more layered (Sverdrup-Thygeson *et al.* 2016).

The sampling of saproxylic beetles was conducted over approximately 9 weeks, from the 2nd of June 2015 to the 8th of August 2015. Sampling took place in 29 sites. These were a subset of the 60 sites chosen in the ALS-study using maps from the 1950's. The maps showed cutting surfaces and areas with selective felling (Sverdrup-Thygeson *et al.* 2016). Fourteen sites were in old managed forest, and 15 were in old natural forest, each with a 15.45-meter radius (750 m^2) (Fig. 2.1).

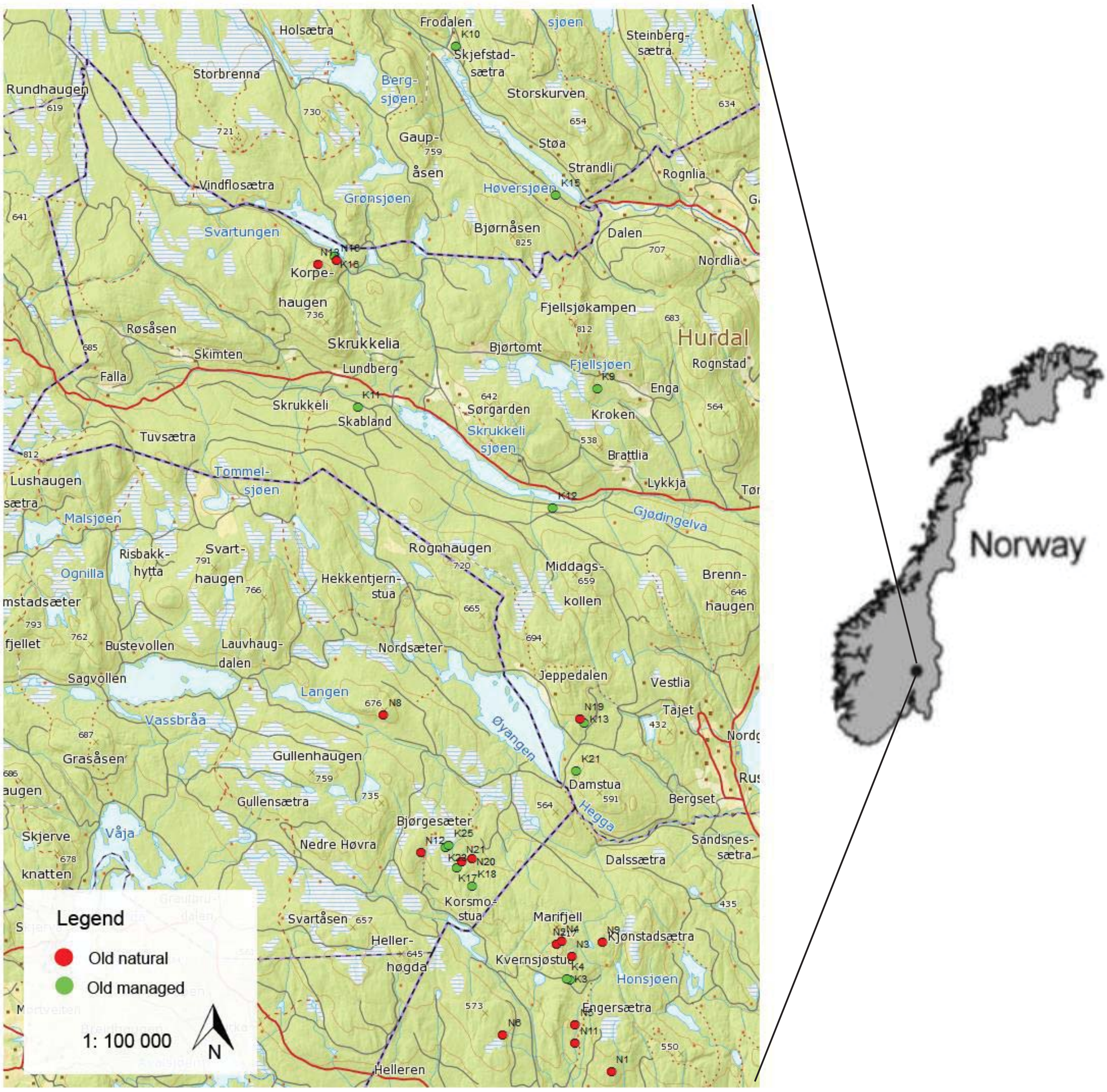


Figure 2.1: Map showing the 29 study sites. Red dots are sites in old natural forest (15 in total); green dots are sites in old managed forest (14 in total). All study sites are situated in Hurdal and Nannestad municipality (Akershus County) and Gran municipality (Oppland County) in Southeastern Norway within a 17000 ha forested area owned by Mathiesen Eidsvold Værk.

2.2 Sampling of saproxylic beetles

To ensure collection of a large quantity of beetles, two sampling methods were used. Each site had both window traps and pitfall traps (Fig. 2.2).

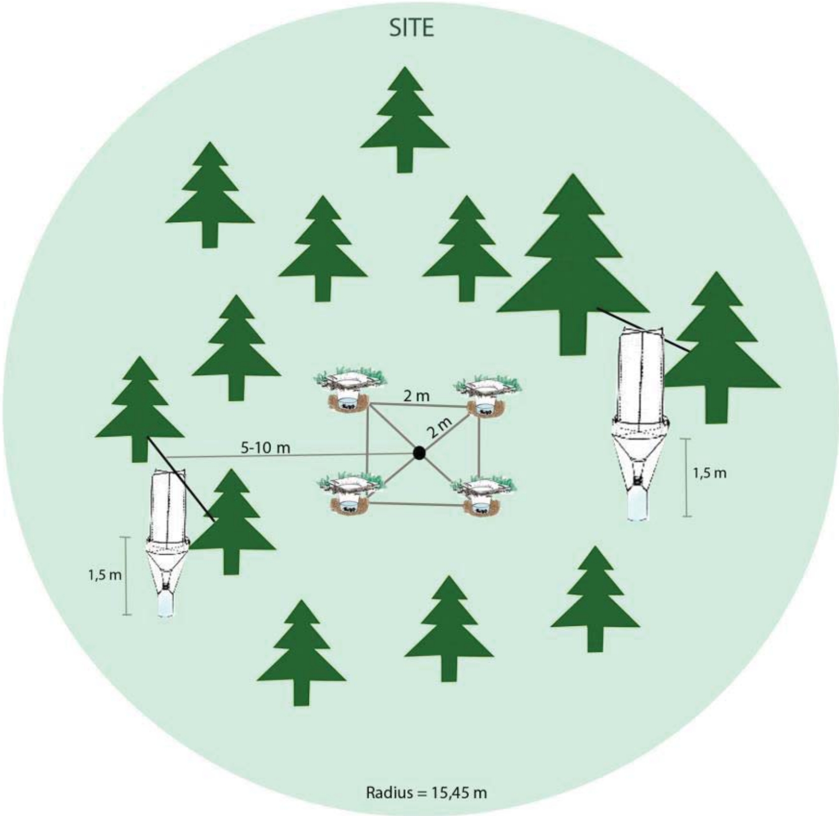


Figure 2.2 Trap setup. The pitfall traps were placed approximately 2 m from the centre of the site and 2 m from each other. The window traps were placed 5-10 m from the centre of the site, hanging between two trees. The distance from the trap to the side of the trees was approximately 0.5-1 m, and to the ground, the distance was approximately 1.5 m. Illustration made by: Helene Lind Jensen

Both pitfall traps and window traps were filled with approximately 2 dl of propyleneglycol with water and a dash of dishwasher soap (Zalo) to preserve the collected insects. The traps were emptied every three weeks (24.-27. June, 13.-17. July and 4.-8. August), and the insects were put in 70 % rectified alcohol and put in a freezer. All collected beetles were extracted from the samples. The expert taxonomist Sindre Ligaard identified the beetles to species level.

2.2.1 Window traps

Two window traps were used in each site for sampling. The window traps consisted of two crosswise transparent acrylic panes (40 x 22 cm), leading down to a funnel with a 0.5 litre bottle attached to it. The bottle had drainage holes (diameter ca. 2 mm) to avoid excess water. The traps were placed hanging between two trees, with a distance of 0.5-2 m between the two tree trunks, and approximately 1.5 m above ground (Fig. 2.3). The distance from the centre of the site was about 5-10 m.

Figure 2.3: Window traps. Four window traps were used in each site. The traps were hung between two tree trunks, with a distance of 0.5 m to each tree and 1.5 m to the ground. The traps consisted of two crosswise acrylic panes (40 x 22 cm) leading down to a funnel with a 0.5 litre bottle attached to it. The bottle was filled with 2 dl of propyleneglycol with water and a dash of dishwasher soap.

2.2.2 Pitfall traps

Four pitfall traps were used in each site for sampling. The pitfall traps consisted of a plastic cup (9.5 x 6 cm) sunk into the ground, and a plexi glass plate (15 cm x 15 cm) above, held up by a 40 cm piece of iron wire (1.5 mm in diameter) (Fig. 2.4a). The traps were placed around the centre of the site in a square, approximately 1-2 meter from the centre of the site and 2 meters apart from each other. On two of the four pitfall traps, small twigs found on the ground (ca. 10 cm long and 0.5-1 cm diameter) were placed as an extra attractant to saproxylic beetles (Fig. 2.4b). This was to see if small twigs could attract beetles searching of a hiding place.

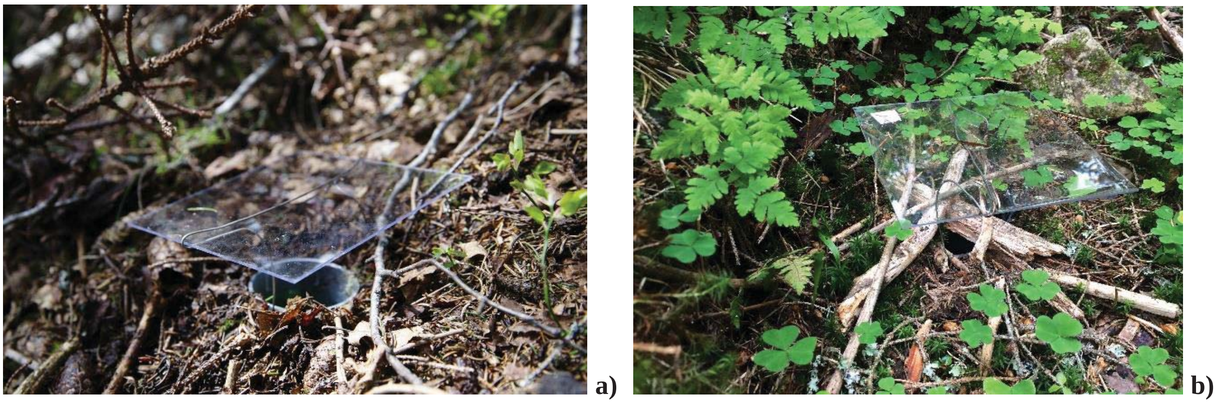


Figure 2.4: **a)** Pitfall trap **b)** Pitfall trap with twigs. Both types (four traps in total) were placed approximately 2 m apart and 2 m from the centre of the site. The traps consisted of a plastic cup (9.5 x 6 cm) and a plexi glass plate (15 cm x 15 cm) held up by iron wire (1.5 mm in diameter). Twigs (ca. 10 cm long and 0.5-1 cm diameter) found on the ground were placed on half of the traps. The traps were filled with 2 dl of propyleneglycol with water and a dash of dishwasher soap.

2.3 Study organisms and grouping

The saproxylic beetles were sorted into these categories:

- Beetle size based on Seibold *et al*. (2015) and Gossner *et al.* (2013b), plus the web sites Die Käfer Europas; www.coleo-net.de and www.zeno.org
- Functional groups based on Hansen *et al.* (1965), Palm (1959), a database compiled by (Dahlberg & Stokland (2004), and the Norwegian Red List Database (Norwegian Biodiversity Information Centre) The functional groups were divided in three:
    - Generalist species: beetles that use both conifer and broadleaf trees, and is not restricted to one tree type
    - Conifer-specialists: beetles that specialize on conifer trees
    - Broadleaf-specialists: beetles that specialize on broadleaf trees
    - 'Other': Species which tree preference is not known
- Red-listed species based on the Norwegian Red List for species 2015 (Norwegian Biodiversity Information Centre)

See the Appendix, Table 3 for more information on the species.

2.4 Environmental variables

To consider the differences between the forest types in relation to forest characteristics, I used basal area (forest density), total dead wood-volume, forest development class, variance in age of trees, elevation and number of cut stumps. This data was measured and registered within each of the sites (within the 15.45 m radius) in a field study in 2014 (unpublished data) (Table 2.1 and Appendix, Table 1).

Table 2.1: Description of environmental variables

Abbrevation	*Desciption*	*Unit*
Basal area	Density of the forest	m^2/ha
Dead wood	Total volume of dead wood	cm^3
Forest development class	Cutting class 4 – young mature forest Cutting class 5 – old mature forest	4 – 5
Age of trees (var)	Variance in age of trees (three sample trees per site)	Years
M.a.s.l	Elevation	Meter above sea level
No. of cut stumps	Number of logging traces	1 – 40

2.5 Statistical analysis

All statistical analysis was conducted in JMP pro 12.Ink. If not otherwise stated, level of significance used was $\alpha = 0.05$.

To check for normality a shapiro-wilk test was performed. Some of the response variables were log-transformed to achieve a normal distribution (W-values above 0.9 were considered within threshold for normality).

A t-test assuming unequal variances was used to

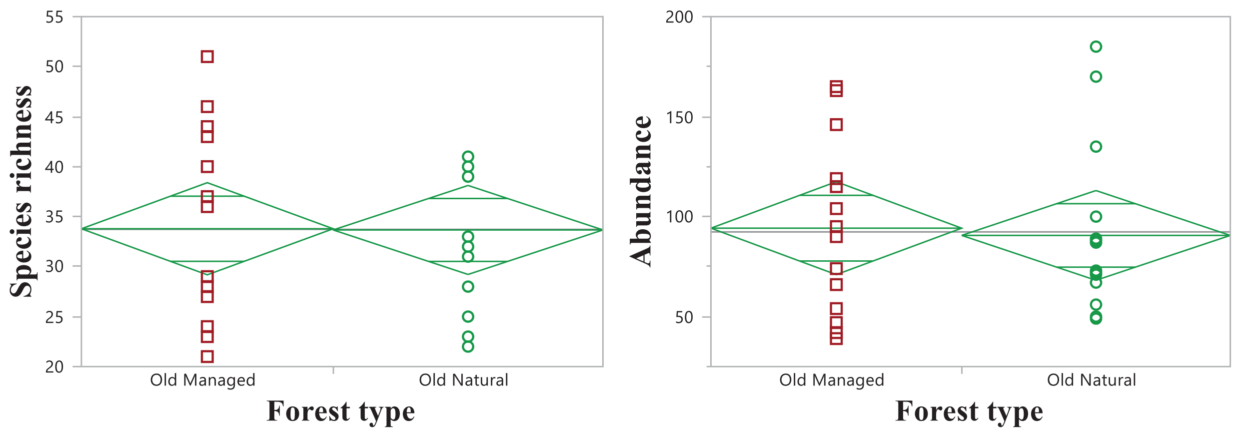
- check for differences between the old managed forest and the old natural forest in:
  - species richness
  - abundance
  - size of beetles
  - specialists and generalists
- test importance of twigs on pitfall traps for number of saproxylic beetles caught,
- differences between trap types (window vs. pitfall)

All explanatory variables were checked for multicollinearity by using a Pearson correlation test. To see if any of the environmental variables had an impact on the response variables linear models were used. Afterwards a model was selected using the backward elimination method with corrected Akaike information criterion (AICc) as the threshold level.

3 Results

3.1 Abundance and species richness

In total, 168 species (2678 individuals) of saproxylic beetles were sampled with a distribution of 131 species (77.9 % of the total) in old natural forest, and 135 (80.4 % of the total) in old managed forest. 1359 (50.8 % of the total) individuals were found in old natural forest and 1319 (49.3 % of the total) in old managed forest (Fig. 3.1). There were no significant differences in neither species richness nor abundance between the two forest types (P = 0.9703, t-test and 0.9339, t-test respectively).



a) **b)**

Figure 3.1: Mean species richness **a)** and mean abundance **b)** per site in old managed and old natural forest. The mean diamonds show the group mean and a 95 % confidence interval.

Figure 3.2 shows that there were several species unique for both the old managed forest and the old natural forest (see Appendix, Table 1 for more information).

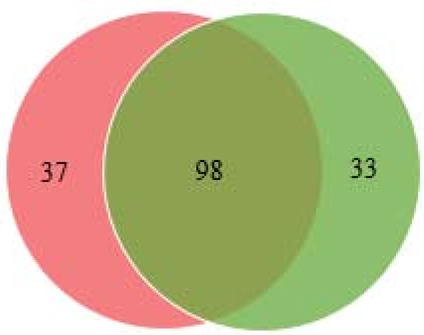


Figure 3.2 Venn-diagram showing the distribution of unique species between old natural forest (green), the old managed forest (light red) and the overlap (dark green).

3.1.1 Differences in habitat characteristics in old managed vs. old natural forest

None of the explanatory variables were correlated (Appendix, Table 2), but elevation and the variance in age of trees varied systematically between the two forest types (Table 3.1). Sites in the old natural forest had in general a higher elevation and a larger variance in age of trees than the old managed forest.

Table 3.1: Comparison of environmental variables (t-test) between old natural and old managed forest. Dead wood and age of trees (var) were log-transformed to achieve normality. Significant values (*p* <0.05) are shown with * and are bold. N = 14 in old managed, N = 15 in old natural

Environmental variable	*Mean, old managed forest*	*Mean, old natural forest*	*p-value*
M.a.s.l	564.5 m	648.6 m	**0.0429***
Basal area	23.64	21.47	0.4486
No. of cut stumps	19.21	13.87	0.1913
Dead wood (log)	2.8665	3.1545	0.0575
Age of trees (var)(log)	1.7101	2.7843	**0.0001***
*Forest dev. class**	8 (4), 6 (5)	9 (4), 6 (5)	0.8810

* Total number of the two development classes in each forest type

3.1.2 Can environmental variables explain species richness and abundance?

Results from simple linear regression show that species richness decreases with older mature forest (from development class 4 to 5) and high elevation. Abundance decreases with older mature forest, and a high elevation, while it increases with a denser forest (higher basal area) (Table 3.2).

Table 3.2: Explanatory variables and their regression coefficients and p-value from linear regression. The explanatory variables are tested one by one on species richness and abundance. Significant values (*p* <0.05) are shown with * and are bold. Abundance was log-transformed to achieve normality.

Explanatory variable	*Species richness*		*Abundance (log)*	
	Estimated β	*p-value*	Estimated β	*p-value*
Forest dev. class	-7.3480	**0.0152***	-0.1593	**0.0244***
Dead wood	0.0013	0.1997	<0.0001	0.6404
Basal area	0.3233	0.1210	0.0145	**0.0013***
Age of trees (var)	-0.002	0.1602	<0.0001	0.3071
M.a.s.l	-0.0378	**0.0046***	0.001	**0.0147***
No. of cut stumps	-0.1495	0.3068	-0.001	0.7052

After a stepwise model selection process done with all the variables, and AIC as threshold level, forest development class and dead wood were the most important in explaining species richness (Table 3.3), while forest development class, dead wood and basal area were the most important variables for abundance (Table 3.4).

Species richness

Species richness increases with amount of dead wood and decreases with forest development class (Table 3.3, Fig. 3.3). Also included in the model was elevation and forest density (basal area), which were close to significant. The species richness increases where the elevation is lower, and when the forest is denser.

Table 3.3: The best model explaining species richness (backward elimination with AICc as threshold level). N = 29. Degrees of freedom = 28. R^2 adj. = 0.4749. Significant values *(p <0.05)* are shown with * and are bold.

Explanatory variables	*Estimated β*	*p-value*
Forest dev. class[5-4]	-7.6545	**0.0076***
M.a.s.l	-0.0216	0.0741
Basal area	0.3100	0.0612
Dead wood	0.0024	**0.0052***

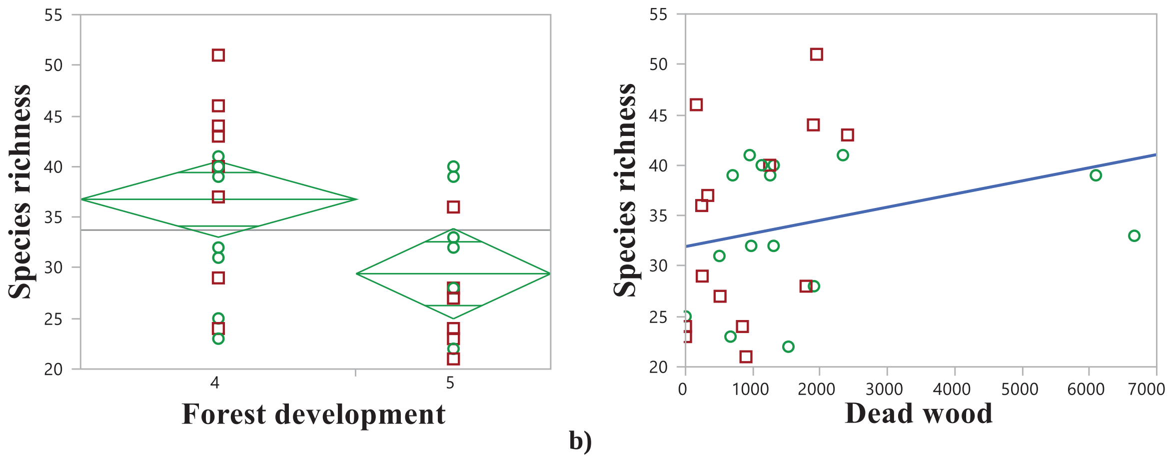


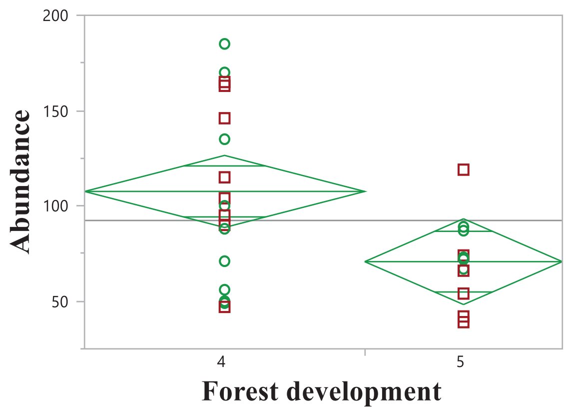
Figure 3.3: The relationship between species richness and **a)** forest development class (class 4 and 5) and **b)** dead wood (cm^3). Red squares are old managed forest and green circles are old natural. Mean diamonds in **a)** show the group mean and a 95 % confidence interval. The blue line in **b)** shows the line of best fit. When excluding the two rightmost points in figure **b)**, the result does not change notably.

Abundance

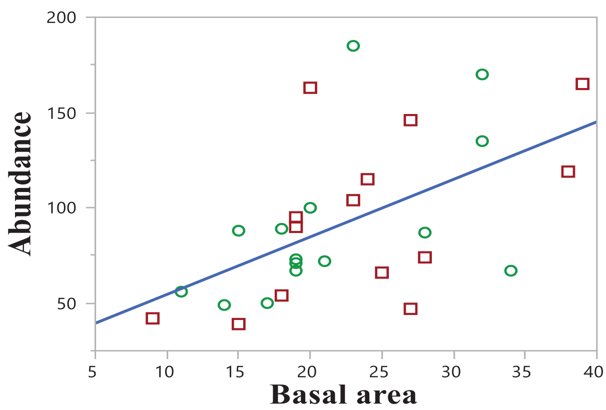
After using the same variables in the model for abundance, the abundance increased with forest development class, a denser forest and dead wood (Table 3.4, Fig. 3.4).

Table 3.4: The best model explaining (log) abundance (backward elimination with AICc as threshold level). N = 29. Degrees of freedom = 28. R^2adj. = 0.5491. Significant values (p <0.05) are shown with * and are bold.

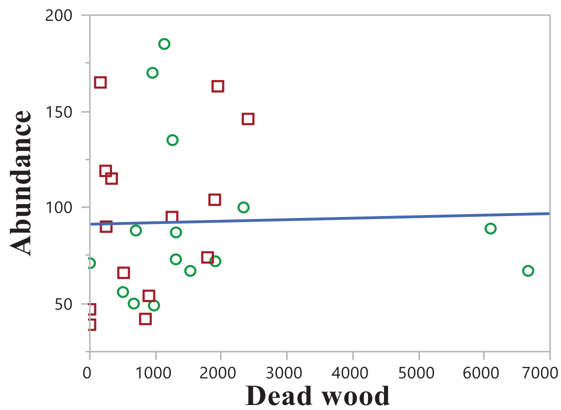
Explanatory variables	*Estimated β*	*p-value*
Forest dev. class[5-4]	-0.2003	**0.006***
Basal area	0.0157	**<0.001***
Dead wood	3.9357e-5	**0.0253***



a)



b)



c)

Figure 3.4: The relationship between abundance and **a)** forest development class (class 4 and 5), **b)** basal area (m^2/ha) and **c)** dead wood (cm^3). Red squares are old managed forest and green circles are old natural. Mean diamonds in **a)** show the group mean and a 95 % confidence interval. The blue lines in **b)** and **c)** shows the line of best fit. When excluding the two rightmost points in figure **c)**, the result does not change notably.

3.2 Pitfall traps vs. window traps

The results show that 17.9 % of the 168 species were exclusively caught in pitfall traps and 51.8 % were exclusively caught in window traps. 30.5 % of the species were caught in both trap types (Fig.3.5 and Appendix, Table 3).

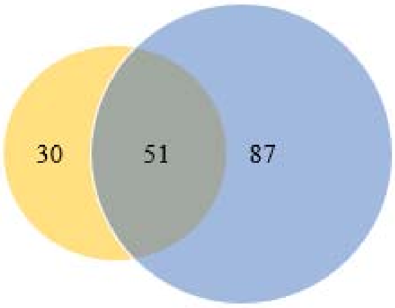


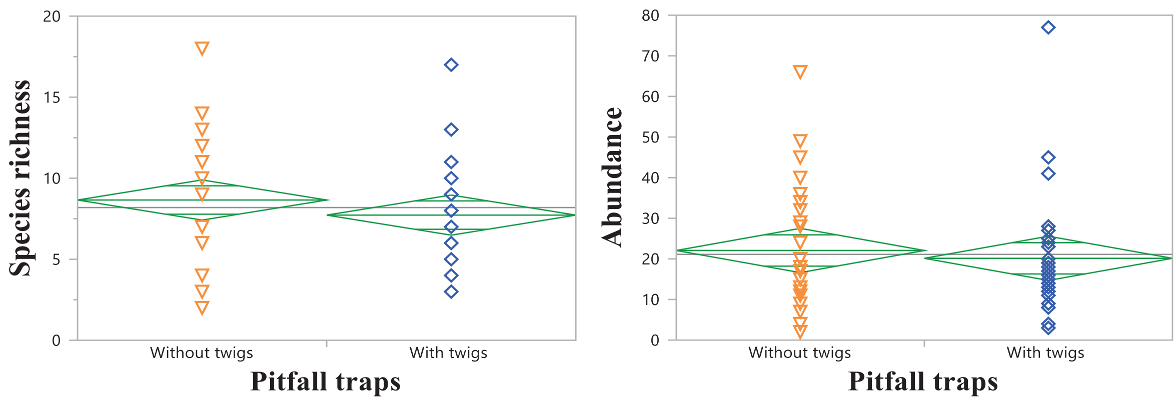
Figure 3.5: Venn-diagram showing the number of saproxylic beetle species caught in pitfall traps (yellow), window traps (blue) and both (blue-yellow).

3.3 Red-listed species

Of the 168 species found, four individuals of four species (2.38 % of the total) were categorized as threatened (Kålås *et al*. 2015) (Ptinidae: *Cacotemnus thomsoni* (NT), Staphylinidae: *Euryusa castanoptera* (NT), Mycetophagidae: *Mycetophagus populi* (VU), Curculionidae: *Pissodes harcyniae*). All red-listed species were found in old natural forest except *Pissodes harcyniae* (NT). They were all caught in window traps.

3.4 Twigs

The twigs on the pitfall traps did not increase the number of saproxylic species (P = 0.2914, t-test) or individuals (P = 0.6177, t-test) caught relative to pitfall traps without twigs (Fig. 3.5).



a) **b)**

Figure 3.6: Mean species richness **a)** and mean abundance **b)** per pitfall traps with twigs and pitfall traps without twigs. Mean diamonds show the group mean and a 95 % confidence interval.

3.5 Functional groups

3.5.1 Beetle size

Beetles in old natural forest had a mean body size of 4.72 mm, while those in old managed were 4.79 mm on average. A t-test confirmed that there were no significant differences between the forest types (P = 0.7660) (Table 3.5).

Table 3.5: Comparison of average beetle size between the two forest types (t-test). Size was log-transformed to achieve normality. Species without size information were excluded from the analysis.

Forest type	*N*	*Mean (log)size*	*p-value*
Old managed	33	0.55 ± 0.35	
Old natural	30	0.57 ± 0.28	0.7660

None of the environmental variables (those that had an effect on overall species richness and abundance) had any significant relationship with the size of beetles (Table 3.6).

Table 3.6: Results from linear regression. Environmental variables tested on size one by one.

Explanatory variables	*Estimated β*	*p-value*
Dead wood	$-7.157e^{-5}$	0.2110
M.a.s.l	-0.0004	0.6027
Forest dev. class	-0.0878	0.6251
Basal area	-0.0155	0.1896

3.5.2 Tree preference

When dividing the beetles into groups based on their tree preference, there were still no significant differences between the old natural and the old managed forest (Table 3.7).

Table 3.7: Result from t-test showing the differences in mean species richness per site connected to different tree preferences.

Tree pref.	*Forest type*	*Mean*	*p-value*
Broadleaf	Old managed	3.36 ± 0.34	
	Old natural	3.53 ± 0.46	0.7597
Generalist	Old managed	12.21 ± 5.09	
	Old natural	13.80 ± 4.23	0.3717
Conifer	Old managed	9.14 ± 4.93	
	Old natural	9.13 ± 2.97	0.9951
Other	Old managed	7.93 ± 2.97	
	Old natural	7.20 ± 2.98	0.5188

By dividing the beetles connected to different tree types, it was only the generalists that increased in relation to dead wood. The species that I did not have any information on (‘other’) were affected by elevation, forest age and basal area (Table 3.8).

Table 3.8: Environmental variables tested on tree preference one by one (linear regression). Significant values (p <0.05) are shown with * and are bold. N = 29

Expl. var.	*Broadleaf*		*Conifer*		*Generalist*		*Other*	
	Est. β	*p-val.*	Est. β	*p-val.*	Est. β	*p-val.*	Est. β	*p-val.*
Dead wood	<0.001	0.3451	<0.001	0.6173	0.001	**0.008***	$7.9965e^{-6}$	0.9827
M.a.s.l	-0.004	0.1359	-0.001	0.8447	-0.009	0.2712	-0.0150	**0.0012***
Forest dev.	-0.1961	0.7399	-1.0882	0.4763	-2.4755	0.1616	-2.6471	**0.0143***
Basal area	0.0324	0.4079	0.1549	0.1218	-0.0433	0.7180	0.1699	**0.0189***

4 Discussion

The starting point for this thesis was twofold: 1) I expected that the old natural forest would contain more saproxylic beetle species and individuals due to its older age, more niches, the different tree species and the amount of dead wood. Here the species will have had an opportunity for long-lasting colonization, and the continuity of older trees will have provided more species occupying different niches. 2) With the previous expectations, I also predicted that the old natural forest would contain a higher abundance of larger beetles because these would not have needed to disperse. I also expected the old natural forest to contain more specialized beetles, because they have had more time to adapt to their preferred tree species. Lastly, I expected the old natural forest to have more red-listed species due to their adaption to characters typical of a natural forest.

In contrast to my first prediction, there were no significant differences in neither species richness nor abundance between the old natural forest and the old managed forest. While Martikainen *et al*. (2000) and Paillet *et al.* (2009) found differences, other researcher have come to the same result as I did. Similä *et al*. (2003) who compared a managed Scots pine forest and a semi-natural Scots pine forest found that the species richness of 'other' saproxylic species was similar between the two forests. They concluded that the reason for the small differences was the selective felling practiced in the semi-natural forest, which has "broken" the continuity of dead wood. Sverdrup-Thygeson *et al.* (2014) compared nature reserve, retention patch and woodland key habitat (biodiversity hotspots) regarding newly dead aspen. They found small differences in species richness, and concluded that all three landscape types are important for different beetle assemblages, and that they all contain both rare and threatened species. Timonen *et al.,* in a meta-analysis from 2011, gathered and compared results from numerous countries. They found that in general there is no significant difference in species richness of beetles between woodland key habitats and production forests. As they got significant differences in other species groups such as lichens, vascular plants, bryophytes and polypores, the result for beetles was surprising. The woodland key habitats ought to have contained more species than the production forest, so Timonen *et al*. (2011) concluded that the sampling was the issue.

The reasons for the lack of differences in abundance and species richness in my study may be several. First, both Franc *et al*. (2007) and Økland *et al*. (1996) have discussed migration as a possible reason for the small differences between different types of forest. They relate this to the beetles' capability of moving across larger areas. Then the beetles will have the opportunity to find other sources of dead wood (Franc *et al.* 2007).

Second, the forest types were situated in a mosaic. Many of the sites were very close to each other, and to spot the differences was hard when we were out in the field. When the old natural and old managed forest sites are so close together and so similar, the beetles may easily spread to suitable substrates in the old managed forest and survive as long as they have viable populations in the old natural forest.

Third, I might have had too few sites to get an accurate result. The ALS-study, which had 60 sites *did* find differences in habitat characteristics, so if this study had 60 sites as well, differences in species richness and abundance may have been detected.

4.1 Elevation and variance in age of trees separate the forest types

The two forest stands differed in both the variance in age of trees and the elevation. The natural forest has significantly higher variance in age of trees than the old managed, as a natural consequence of the less intense management (selective felling). The old managed forest is more homogenous because of the more intense forestry. The old natural forest is situated higher than the old managed forest (on average 100 meters higher than the sites in the managed forest). This should mean slightly lower temperatures in the old natural forest, leading to fewer species and fewer individuals. Lower temperatures often require species that are adapted to such conditions, and at higher elevation, both wind and temperature will be harsher (Krebs 2009). The study confirmed this, as I found that abundance and species richness decreases with higher elevation. In addition, one should have expected higher species richness and abundance in an old natural forest, as the age of trees varied more. However, species richness and abundance were similar in the two forest types. One explanation may be that elevation together with few cut stumps and high amounts of dead wood have countered this effect, and that the variance in age of trees thus did not have an effect on neither species richness nor abundance.

4.2 Young mature forest explains species richness and abundance

In general, sites with forest development class 4 (young mature forest) had larger species richness and abundance than old mature forest (class 5). These results are the opposite of Irmler *et als*. (2010) study of deciduous woodlands of different sizes and ages. They found that large and older woods have twofold the species richness of young and small woods. On the other hand, Similä *et al*. (2002) who studied a boreal pine forest suggests that saproxylic species need all stages of succession, which includes younger stands. Both the old natural forest and the old natural forest had equal numbers of both development classes (4 and 5). Therefore, the results may indicate an evenness between the forest types, and that there are other factors influencing the species richness. Several areas had large amounts of dead wood, or a very small number of cut stumps, which again might influence the result.

4.3 Dead wood explains species richness and abundance

Dead wood was significant in explaining both species richness and abundance. This is supported by the findings of Martikainen *et al*. (2000) in a study of mature managed and old-growth boreal forests. They found that species richness of saproxylic beetles had a positive relationship with dead wood. Ina addition, Seibold *et al*. (2015) in a review of experimental dead wood-studies, say that dead wood has a positive relationship with all saproxylic taxa.

However, other researchers find that amount of dead wood might not be the most important factor influencing the saproxylic beetle diversity. For example, Fayt *et al*. (2006) only found a near significant correlation with dead wood on longhorn beetles in a deciduous forest. They used tree different trap methods in a yearlong study, but they only sampled from 22 sites and only caught species that were not specialized on dead wood. This may have affected their result. Siitonen (1994) who did a similar study in two old spruce forests found no correlation at all between species richness and the amount of dead wood near the traps (100 m^2). He concludes that the swarming individuals are distributed across larger areas, and not necessarily around the traps. In addition, he only used window traps. He might have caught more saproxylic species by having pitfall traps as well. Similä *et al.* (2003) state that it is rather the continuity of dead wood and not the total amount of dead wood that is important for the survival of saproxylic beetles. Gossner *et al*. (2013a) who did a dead wood-enrichment experiment in the canopy and on the forest floor in mature stands of Norway spruce state that explaining factors of species richness is temperature, precipitation, tree species and vertical stratum.

It seems that these researchers focused more on the type of dead wood, and not the amount of dead wood as I did in my thesis. However, the conclusion of many authors (Martikainen *et al*. 2000, Kaila *et al*. 1997, Økland *et al.* 1996, Gibb *et al*. 2005, Gossner *et al*. 2013a) is that enrichment of dead wood is an important contribution to the maintenance of saproxylic beetle diversity.

4.4 A denser forest increases species richness and abundance

The results show that where the forest is denser (higher basal area), the largest number of species are found. This may be surprising, as many authors have found that saproxylic beetles often tend to thrive in sun-exposed gaps (Bouget 2005, Sverdrup-Thygeson & Ims 2002, Kaila *et al*. 1997). Sverdrup-Thygeson & Ims (2002) in a boreonemoral forest-study found that sun-exposure is an important factor influencing saproxylic beetles. When they are dispersing, the beetles will rather choose substrates in open areas, and not where the forest is dense. On the other hand, other studies focus on the fact that certain saproxylic species performs best in shaded conditions (Lindhe *et al.* 2005), or is indifferent to shade or sun-exposure (Jonsell *et al*. 1998). However, a more open forest may have frequent change in the abundance of species between each site (pers. comm. T. Birkemoe 15.03.2016) due to the species dispersal opportunities in an open forest.

4.5 Beetle size does not differ between the two forest types

The results show that the beetle size does not differ between the old natural and the old managed forest. This is surprising as Seibold *et al.* (2014) found that large beetle species (6.04 mm in average) tend to stay within old natural forests. The reason is that the natural forest have provided long-lasting conditions, supporting larger beetles without the need for dispersal. In addition, it is where the amount of dead wood is higher. Reflecting this is the need for large pieces of dead wood for the larvae of large beetles. Because of their size they need a stable environment, which the large dead wood can provide (Foit 2010). In support of this, Gossner *et al*. (2013b) found that the body size of the beetles increased significantly with increased amount of dead wood. In contrast, my study shows that there are no differences between the two forest types in regard to beetle size. Nor can any of the environmental variables explain the variation in size of beetles between the sites. This is also contradictory to what I predicted. The two forest types have only a slight, non-significant difference in amount of dead wood, which might be the reason why the size of the beetles does not differ.

4.6 Generalists are affected by the amount of dead wood

Results in this thesis show that there are no differences in the preference for tree species between the two forest types. Since I expected the old natural forest to contain more broadleaved trees (Abrahamsson *et al.* 2009, Seibold *et al*. 2014, Rolstad *et al.* 2002, Stokland *et al*. 2012), one could assume that there would be more species specialized on broadleaved trees in the old natural forest (Similä *et al.* 2003). The most surprising result is that the number of conifer-specialists does not differ between the two forest types either, as I would have expected to find conifer-generalists in a conifer-dominated boreal forest. However, results from this thesis does not support that prediction. As earlier stated, the two forest types are situated in a mosaic, so the tree species and beetle species may be evenly distributed in both forests.

Some of the environmental variables, however, could explain the variation in tree preference. The richness of generalist species increases with larger amounts of dead wood. As stated earlier, many researchers find that species richness increases with larger amounts of dead wood (Martikaninen *et al*. 2000, Seibold *et al.* 2015, Kaila *et al.* 1997, Økland *et al.* 1996, Gossner *et al*. 2013a), but Müller *et al.* (2010) found the same as I, that the amount of dead wood has a positive relationship with generalist species. They also found that conifer-specialists had a positive relationship with dead wood, which I did not find. With larger amounts of dead wood, the competition for resources may be smaller as the dead wood increases the amount of niches, including successional stages. This may be why the generalist species is significantly correlated with dead wood.

'Other' species decreases with a higher elevation and an older forest and increases with a denser forest. My conclusion is that more research on beetles' tree preference is necessary to get more accurate results.

4.7 Few red-listed species were found

The capture of red-listed species in this thesis were so low that statistical analysis on red-listed species were excluded. I found only three red-listed species in the old natural forest and one in the old managed forest. Martikainen & Kouki (2003) describe the capture of threatened species as "challenging", and that "catches containing less than 200 trapped species (or less than 2000 individuals) are almost useless in surveying threatened and NT beetle species in boreal forests".

Supporting the fact that there are more red-listed species in the old natural forest, Bergman *et al*. (2012) found that the richness of red-listed saproxylic oak beetles was higher in old near-primeval forests than in previously managed forest. This was the same as Kouki *et al*. (2012) found comparing an intense managed forest with a less intense managed forest that still had characteristics similar to a natural forest. Sverdrup-Thygeson *et al.* (2014) found that species richness of red-listed species in a woodland key habitat and an old managed forest was larger than both a nature reserve and a retention patch, while Djupström *et al.* (2008) found that the woodland key habitat had more red-listed species than the old managed forest. In Sverdrup-Thygesons study from 2001, 6.2 % (7 of 109) of the sampled beetles were red-listed. This was done in the same area as my study. In addition to using trunk window traps, she sampled saproxylic beetles from fruiting bodies attached to logs and snares. Still she found a low number. The analysis showed that the red-listed species had a correlation with geographic location, forest type, trapping method and sampling effort. Sverdrup-Thygeson concluded that she should have increased the sampling effort by using free-hanging window traps.

I expected that the old natural forest had more red-listed species than the old managed forest due to a longer continuity and more dead wood-substrate. However, due to the small number of observations, the results are far from conclusive. Martikainen & Kouki (2003) state that to get enough information about threatened species, you have to have sampled approximately 300-400 species (>4000 individuals). In addition, they consider pitfall-traps to be a poor method for sampling threatened and near-threatened species based on results they gathered from other studies of threatened species. Trunk-window traps together with direct searching seems to be the most effective method for sampling threatened species, according to Martikainen & Kouki (2003) while free-hanging window traps catch a very few number, which were what I used.

4.8 Methodological remarks

4.8.1 Pitfall traps vs. window traps – both are important

Two types of trap methods were important to use to make the study more robust. Thirty species out of the 168 found were exclusively caught in pitfall traps. This is interesting, as nearly 20 % of the species sampled would not have been caught if I only used window traps, which is very usual in saproxylic beetle-studies. Most of the studies I have referred to in this thesis, only use window traps (either free-hanging or attached to a tree trunk). As many as 56.7 % (17) of the 30 species are in the group that has unknown tree preference (‘other’). It could mean that they in fact are generalists, and can survive on more than one tree species.

My conclusions are that more than one type of trap method is necessary to get a more accurate result.

4.8.2 Twigs did not attract more saproxylic beetles

I tested the use of twigs on half of the pitfall traps to see if this attracted more saproxylic beetles in search of a hiding place. There were no significant differences between pitfall traps without twigs and those with twigs. I would have expected there to be some differences, as some species are specialized on dead twigs (Stokland *et al*. 2012). Gossner *et al.* (2013a) placed out freshly cut wood of different sizes in the canopy (the smallest being 0-5 cm and 0.2 cm^3) and left it there for two years. The number of species caught increased significantly after they placed the cut wood out. I, however, did not get the same result in spite of having twigs that differed somewhat in size. Nonetheless, I only left the twigs there for a short amount of time. In addition, I may have obtained a more positive result if I used newly dead twigs, as was what Gossner *et al*. (2013a) used. However, they state that “the amount of ground dead wood is by itself not a sufficient measure for the local diversity of saproxylic beetles. While both Gossner *et al*. (2013a), Abrahamsson *et al*. (2009) and Fridman & Walheim (2000) focus on large logs as the important saproxylic attractant, Jonsell *et al*. (1998) state that they believe that twigs are important for many saproxylic insects and that the removal of these in nature reserves will have a negative impact. Nonetheless, Stokland *et al.* (2012) say that very few species specialize on twigs that small (1-4 cm), which may be why there were no differences. Nevertheless, even if this experiment did not prove that twigs work as an attractant, they may be important substrates regardless of this.

4.8.3 Limitations

When it comes to sampling effort, we could have included more sites, but the limit of time and the conditions of roads made it impossible.

4.9 Conclusions

The two forest types did not differ significantly in either abundance or species richness. Nor did the forests have differences in tree preference among beetles. The size of the beetles was insignificantly different between the two forest types, while red-listed species gave an inconclusive result. Twigs did not attract more saproxylic beetles in spite of the success other researchers have had in doing almost similar experiments. However, some environmental variables separate the two forest, though not the ones I would expect the most. Elevation and the variance in age of trees differed, while the amount of dead wood was statistically not different, which is contradictory to the expectations. Both the amount of dead wood, forest development class, basal area and elevation influence the species richness and abundance.

These results indicate several things. First, the beetles may have such a good dispersal ability, that they move across the area making it hard to detect differences. Second, due to the mosaic of old natural and old managed forest stands, suitable substrate may be found in both forest types. As long as the beetles have a viable population in the old natural forest, movement around in the mosaic will not cause problems. However, if the old natural forest are cut, these viable populations will disappear. Third, my study might have had too few sites to get accurate results.

4.9.1 Future prospects

This thesis did have some important findings that can help in guiding the future management. Dead wood, forest development class, basal area and elevation influences species richness and abundance. These are all factors important in management because forestry alters several forest characteristics. The most important factor is the amount of dead wood. To secure the survival of saproxylic beetles, management should be done in such a way that viable populations are not lost. With a proper management strategy, the differences between a managed forest and an unmanaged forest may be reduced if measures are taken to preserve the remaining forest species. By using the old natural forest as a reference, old near-natural forests and old managed forests can obtain viable habitats for forest species. The remaining old natural forests should be preserved in nature reserves, and the old managed forests should be allowed to grow to obtain more of the characteristics an old natural forest have. Dead wood of all sizes and decay stages ought to be placed out in the old managed forests, and retention forestry should leave even more trees to die and decay to create some corridors between managed and unmanaged forest stands. This thesis has shown that the species richness and abundance does not differ between the two forest types. However, my thesis may have inaccurate result due to too few sites, but it may also show that if cutting is to be practised, old managed forest and old managed forest should be situated in a mosaic to allow dispersal between suitable habitats. With that in mind, it is important that future management obtain knowledge about the spatial distribution of suitable habitats (e.g. dead wood) for saproxylic beetles. Further investigation in this particular area should be done including more sites over a longer period time.

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6 Appendix

Table 1: Environmental variables, species richness and abundance per site

Site	Forest type	Forest dev.	M.a.s.l	No. of cut stumps	Basal area	Dead wood	Age of trees (var)	Species richness	Abundance
K3	Old Managed	4	636	0	39	160	100,33	46	165
K4	Old Managed	4	632	30	19	248	226,33	29	90
K9	Old Managed	4	527	11	20	1947	39	51	163
K10	Old Managed	4	417	19	24	330	22,33	37	115
K11	Old Managed	4	392	20	19	1249	22,33	40	95
K12	Old Managed	4	395	12	23	1899	1	44	104
K13	Old Managed	4	519	16	27	0	19	24	47
K15	Old Managed	4	434	12	27	2407	30,33	43	146
K16	Old Managed	5	644	12	28	1790	1089,33	28	74
K17	Old Managed	5	685	40	25	513	33,33	27	66
K18	Old Managed	5	697	19	18	898	408,33	21	54
K21	Old Managed	5	544	36	38	240	27	36	119
K23	Old Managed	5	690	31	15	0	24,5	23	39
K25	Old Managed	5	691	11	9	845	350,33	24	42
N1	Old Natural	4	519	23	15	700	991	39	88
N2	Old Natural	4	734	18	17	668	1125,33	23	50
N3	Old Natural	4	720	8	14	975	661,33	32	49
N4	Old Natural	4	740	2	11	503	834,33	31	56
N5	Old Natural	4	538	21	32	1257	101,33	39	135
N6	Old Natural	4	567	37	32	953	93	41	170

N8	Old Natural	4	705	2	23	1132	156,33	40	185
N9	Old Natural	4	711	4	20	2338	2092	41	100
N11	Old Natural	4	500	16	19	0	3545,33	25	71
N12	Old Natural	5	666	20	19	6667	229,33	33	67
N13	Old Natural	5	774	4	34	1528	457,33	22	67
N16	Old Natural	5	665	1	18	6096	331	39	89
N19	Old Natural	5	534	19	28	1310	305,33	40	87
N20	Old Natural	5	674	17	21	1908	5262,33	28	72
N21	Old Natural	5	682	16	19	1308	1552	32	73

Table 2: Correlation test between explanatory variables

Explanatory variables	*M.a.s.l*	*Cut stumps*	*Basal area*	*Dead wood*	*Age of trees(var)*
M.a.s.l	**1.0000**	-0.2295	-0.2415	0.0968	0.1960
Cut stumps	-0.2295	**1.0000**	0.1425	-0.2819	-0.1314
Basal area	-0.2415	0.1425	**1.0000**	-0.1138	-0.2144
Dead wood	0.0968	-0.2819	-0.1138	**1.0000**	-0.0053
Age of trees (var)	0.1960	-0.1314	-0.2144	-0.0053	**1.0000**

Table 3: Overview of species and families with abundance, tree preference, beetle size and species only caught in pitfall traps

Species	**Family**	**Forest type**	**Abundance, old natural**	**Abundance, old managed**	**Tree preference**	**Body Size**	**Pitfall trap**
Acrulia inflata	Leiodidae	Old managed	0	3	Generalist	2,25	
Agathidium atrum	Leiodidae	Both	2	3	Other		X
Agathidium badium	Leiodidae	Both	2	2	Generalist	2,45	
Agathidium rotundatum	Staphylinidae	Old natural	1	0	Generalist	2,5	
Agathidium varians	Cerambycidae	Old managed	0	1	Generalist	2,75	
Aleochara moerens	Elateridae	Old managed	0	1	Other		X
Alosterna tabacicolor	Elateridae	Old managed	0	1	Generalist	7	
Ampedus balteatus	Elateridae	Old managed	0	1	Generalist	8,75	
Ampedus nigrinus	Scraptiidae	Both	6	9	Generalist	7,5	
Ampedus tristis	Scraptiidae	Old natural	1	0	Generalist	8	
Anaspis marginicollis	Leiodidae	Old natural	2	0	Generalist	3,5	
Anaspis rufilabris	Leiodidae	Both	8	6	Generalist	3	
Anisotoma castanea	Coccinellidae	Both	2	1	Generalist	3,5	
Anisotoma humeralis	Staphylinidae	Both	2	1	Generalist	3,35	
Aphidecta obliterata	Staphylinidae	Old managed	0	1	Generalist	4	
Atheta brunneipennis	Staphylinidae	Both	9	10	Other		X
Atheta corvina	Staphylinidae	Old managed	0	1	Other		X
Atheta crassicornis	Staphylinidae	Old managed	0	2	Other	3	
Atheta diversa	Staphylinidae	Old managed	0	1	Other		X
Atheta euryptera	Staphylinidae	Old natural	1	0	Other	3	
Atheta gagatina	Staphylinidae	Old natural	1	0	Other		X
Atheta hypnorum	Staphylinidae	Both	44	35	Other	4,25	
Atheta paracrassicornis	Staphylinidae	Both	16	22	Other		X
Atheta sodalis	Staphylinidae	Both	4	6	Other	2,75	
Atheta subtilis	Elateridae	Both	2	10	Other	1,8	
Atheta vaga	Cryptophagidae	Old natural	3	0	Generalist	2,4	
Athous subfuscus	Cryptophagidae	Both	18	20	Generalist	9,15	

Atomaria affinis	Cryptophagidae	Both	2	4	Broadleaf	2	
Atomaria ornata	Staphylinidae	Both	29	23	Conifer	2	
Atomaria pulchra	Staphylinidae	Both	1	1	Conifer	1,5	
Atrecus longiceps	Staphylinidae	Old natural	1	0	Generalist	6,25	X
Atrecus pilicornis	Staphylinidae	Both	1	9	Generalist	6	
Bibloporus bicolor	Staphylinidae	Both	8	10	Generalist	1,3	
Bisnius puella	Staphylinidae	Both	1	3	Other	8	
Bolitochara pulchra	Ptinidae	Both	1	1	Generalist	4	X
Bryaxis puncticollis	Oedemeridae	Old natural	1	0	Other		X
Cacotemnus thomsoni	Cerylonidae	Old natural	1	0	Conifer	4,7	
Calopus serraticornis	Ciidae	Both	1	1	Generalist	19	
Cerylon histeroides	Ciidae	Both	1	1	Generalist	2,05	
Cis boleti	Ciidae	Old natural	1	0	Broadleaf	3	
Cis castaneus	Ciidae	Old natural	1	0	Generalist	1,8	X
Cis dentatus	Ciidae	Both	1	1	Generalist	2,3	
Cis festivus	Ciidae	Both	9	13	Broadleaf	2,1	
Cis micans	Latridiidae	Both	1	1	Generalist	2,55	
Cis punctulatus	Curculionidae	Old natural	7	0	Generalist	2,5	
Corticaria rubripes	Cryptophagidae	Old natural	2	0	Generalist	1,9	
Cryphalus asperatus	Cryptophagidae	Both	13	14	Conifer	1,55	
Cryptophagus dentatus	Cryptophagidae	Both	2	1	Broadleaf	2,4	
Cryptophagus lapponicus	Cryptophagidae	Both	4	2	Generalist	2,45	
Cryptophagus scanicus	Curculionidae	Both	8	2	Generalist	2,3	
Cryptophagus setulosus	Curculionidae	Both	17	10	Broadleaf		X
Crypturgus cinereus	Nitidulidae	Both	8	6	Conifer	1,3	
Crypturgus hispidulus	Nitidulidae	Both	9	11	Conifer	1,25	
Cychramus luteus	Staphylinidae	Both	4	6	Generalist	4,3	
Cychramus variegatus	Staphylinidae	Old managed	0	3	Generalist	6	
Dadobia immersa	Silvanidae	Both	2	1	Generalist	1,75	
Deliphrum tectum	Lycidae	Old natural	1	0	Other	3,25	X
Dendrophagus crenatus	Staphylinidae	Old natural	1	0	Generalist	6,5	

Dictyoptera aurora	Curculionidae	Both	3	2	Generalist	10,5	
Dinaraea arcana	Lymexylidae	Both	2	2	Generalist	2,65	
Dryocoetes autographus	Latridiidae	Both	38	42	Conifer	3,85	
Elateroides dermestoides	Latridiidae	Both	14	13	Generalist	12	
Enicmus fungicola	Latridiidae	Both	13	16	Generalist	1,85	
Enicmus planipennis	Nitidulidae	Old natural	3	0	Generalist	1,6	
Enicmus rugosus	Nitidulidae	Old managed	0	1	Generalist	1	
Epuraea aestiva	Nitidulidae	Both	5	14	Other	3,15	
Epuraea angustula	Nitidulidae	Old managed	0	2	Generalist	2,45	X
Epuraea binotata	Nitidulidae	Old natural	1	0	Broadleaf	2,25	
Epuraea boreella	Nitidulidae	Old managed	0	7	Generalist	2,35	
Epuraea laeviuscula	Nitidulidae	Old managed	0	3	Conifer	3,2	
Epuraea marseuli	Nitidulidae	Both	2	11	Generalist	3	
Epuraea muehli	Nitidulidae	Both	2	1	Conifer	2,4	
Epuraea oblonga	Nitidulidae	Both	1	1	Conifer	3	
Epuraea pygmaea	Staphylinidae	Both	10	13	Conifer	2	
Epuraea rufomarginata	Staphylinidae	Both	6	5	Generalist	3	
Euconnus claviger	Staphylinidae	Old managed	0	2	Generalist	1,6	
Euryusa castanoptera	Staphylinidae	Old natural	1	0	Broadleaf	3	
Gabrius splendidulus	Nitidulidae	Old managed	0	1	Generalist	5	
Geostiba circellaris	Nitidulidae	Both	3	25	Other	2,25	X
Glischrochilus hortensis	Staphylinidae	Old natural	5	0	Broadleaf	5,5	
Glischrochilus quadripunctatus	Staphylinidae	Both	18	25	Generalist	4,75	
Gyrophaena boleti	Curculionidae	Old managed	0	4	Generalist	1,1	
Haploglossa villosula	Curculionidae	Both	7	2	Generalist	3	
Hylastes cunicularius	Curculionidae	Both	439	236	Conifer	3,85	
Hylobius abietis	Curculionidae	Both	9	10	Generalist	10,25	
Hylobius piceus	Curculionidae	Both	1	5	Conifer	14,4	
Hylobius pinastri	Curculionidae	Both	50	46	Conifer	7	X
Hylurgops glabratus	Curculionidae	Both	2	5	Conifer	4,75	
Hylurgops palliatus	Staphylinidae	Both	5	10	Conifer	2,85	

Ips typographus	Cerambycidae	Old natural	1	0	Generalist	4,85	X
Ischnoglossa prolixa	Latridiidae	Both	1	2	Generalist	2,9	
Judolia sexmaculata	Staphylinidae	Old managed	0	1	Generalist	11	
Latridius minutus	Staphylinidae	Old natural	1	0	Generalist	1,8	X
Leptusa pulchella	Staphylinidae	Both	7	13	Generalist	2,95	
Leptusa ruficollis	Staphylinidae	Both	11	22	Broadleaf	2,4	
Lordithon lunulatus	Cantharidae	Old managed	0	1	Generalist	6	
Lordithon thoracicus	Cantharidae	Both	13	1	Generalist	3,5	
Malthodes brevicollis	Staphylinidae	Old managed	0	1	Broadleaf	2,4	
Malthodes fuscus	Elateridae	Both	9	3	Other	3,9	
Megarthrus depressus	Cryptophagidae	Both	6	9	Other	2,65	
Melanotus castanipes	Staphylinidae	Both	14	7	Generalist	17	
Micrambe abietis	Mycetophagidae	Both	10	5	Conifer	2,3	
Mniusa incrassata	Staphylinidae	Both	3	1	Generalist	2,75	X
Mycetophagus populi	Staphylinidae	Old natural	1	0	Broadleaf	4,25	
Mycetoporus clavicornis	Staphylinidae	Both	24	16	Other		X
Mycetoporus lepidus	Staphylinidae	Both	28	25	Other	4,5	
Nevraphes Coronatus	Staphylinidae	Both	5	1	Generalist		X
Omalium rugatum	Melandryidae	Both	10	19	Other	3	
Omalium strigicolle	Corylophidae	Old managed	0	1	Other		X
Orchesia minor	Cerambycidae	Old natural	1	0	Generalist	3,5	
Orthoperus atomus	Staphylinidae	Old managed	0	1	Generalist	0,9375	
Oxymirus cursor	Staphylinidae	Old natural	1	0	Generalist	23	
Oxypoda alternans	Staphylinidae	Both	15	3	Other	3,5	
Oxypoda bicolor	Staphylinidae	Both	2	1	Generalist	1	X
Oxytelus laqueatus	Staphylinidae	Old managed	0	2	Other	4,4	
Philonthus addendus	Staphylinidae	Old managed	0	1	Other	10,5	X
Philonthus decorus	Staphylinidae	Old managed	0	7	Other	12	X
Philonthus marginatus	Staphylinidae	Old natural	3	0	Other		
Philonthus succicola	Staphylinidae	Old managed	0	6	Other	11,5	X
Phloeonomus punctipennis	Staphylinidae	Old managed	0	1	Generalist	2	

Phloeonomus pusillus	Curculionidae	Old natural	1	0	Generalist	2	
Phloeopora testacea	Curculionidae	Both	1	1	Generalist	2,75	
Phloeotribus spinulosus	Curculionidae	Old natural	1	0	Conifer	2,05	
Pissodes harcyniae	Curculionidae	Old managed	0	1	Conifer	5,75	
Pissodes pini	Curculionidae	Old natural	1	0	Conifer	7,35	
Pityogenes bidentatus	Nitidulidae	Old managed	0	1	Conifer	2,5	
Pityogenes chalcographus	Curculionidae	Both	37	99	Conifer	2,15	
Pityophagus ferrugineus	Lucanidae	Both	4	4	Conifer	5	
Pityophthorus micrographus	Cantharidae	Old managed	0	2	Conifer	1	
Platycerus caraboides	Curculionidae	Old natural	1	0	Broadleaf	11	
Podistra schoenherri	Staphylinidae	Both	13	17	Generalist	8,5	
Polygraphus poligraphus	Ptiliidae	Both	6	13	Conifer	2,6	
Proteinus brachypterus	Cryptophagidae	Both	4	1	Other		X
Ptenidium formicetorum	Ptinidae	Old managed	0	1	Other	0,925	
Pteryngium crenatum	Staphylinidae	Both	1	1	Generalist	1,9	
Ptinus subpillosus	Staphylinidae	Both	12	5	Generalist	2,4	
Quedius brevis	Staphylinidae	Both	2	3	Other	6	
Quedius fuliginosus	Staphylinidae	Both	9	23	Other		
Quedius mesomelinus	Staphylinidae	Old managed	0	1	Broadleaf	9	
Quedius plagiatus	Salpingidae	Both	5	5	Generalist	7,5	
Quedius xanthopus	Cerambycidae	Both	7	1	Generalist	8,5	
Rabocerus foveolatus	Monotomidae	Both	18	22	Broadleaf	3,3	
Rhagium inquisitor	Monotomidae	Old managed	0	1	Generalist	15,5	
Rhizophagus depressus	Monotomidae	Old managed	0	1	Broadleaf	3,4	
Rhizophagus dispar	Monotomidae	Both	12	10	Generalist	3,5	
Rhizophagus fenestralis	Monotomidae	Old managed	0	2	Broadleaf	2,4	
Rhizophagus ferrugineus	Curculionidae	Both	6	3	Conifer	3,75	
Rhizophagus nitidulus	Salpingidae	Both	4	6	Generalist	3,65	
Rhyncolus ater	Staphylinidae	Both	4	2	Generalist	3,75	
Salpingus ruficollis	Staphylinidae	Both	36	36	Generalist	3,9	
Scaphisoma agaricinum	Elateridae	Old managed	0	1	Generalist	2,2	

Sepedophilus littoreus	Silvanidae	Both	5	5	Generalist	4,5	
Sericus brunneus	Nitidulidae	Both	7	4	Conifer	8,5	
Silvanoprus fagi	Staphylinidae	Both	4	2	Conifer	2,7	
Soronia grisea	Latridiidae	Old natural	1	0	Broadleaf	4,5	
Stenichnus bicolor	Curculionidae	Old natural	1	0	Generalist	1,3	
Stephostethus rugicollis	Staphylinidae	Both	1	8	Conifer	1,8	
Strophosoma capitatum	Cerambycidae	Old managed	0	1	Generalist	4,1	X
Syntomium aeneum	Trogossitidae	Both	2	1	Broadleaf	2,5	X
Tetropium castaneum	Erotylidae	Both	4	1	Conifer	13,5	
Thymalus limbatus	Curculionidae	Old natural	2	0	Generalist	6	
Triplax aenea	Curculionidae	Both	4	3	Broadleaf	3,8	
Trypodendron domesticum	Staphylinidae	Both	11	44	Broadleaf	3,35	
Trypodendron lineatum	Curculionidae	Both	33	44	Conifer	3,1	
Xantholinus tricolor	Melandryidae	Both	21	22	Other	10	X
Xylechinus pilosus	Staphylinidae	Both	4	2	Conifer	2,35	
Xylita laevigata	Melandryidae	Old natural	1	0	Generalist	8,25	
Zyras lugens	Staphylinidae	Both	4	4	Generalist	4,25	

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