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Herbivorous insect diversity in boreal forest

A comparison between old near-natural forest and old managed forest in south-eastern Norway

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Management of Natural Resources

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Preface

This thesis is part of the project "Sustainable utilization of forest resources in Norway". I am grateful for the financial support from the project, and I hope that my study can be helpful in future planning of extraction of forest resources.

I will like to thank my supervisors, Anne Sverdrup-Thygeson and Tone Birkemoe, for all their help and guidance they have given me during the whole of last year. I am also very grateful for their financial support to our fieldwork. Thanks to Sindre Ligaard for species identification of the beetles. Thanks to Mathiesen Eidsvold Værk for letting us having traps in their forest holdings.

Thanks for the great nature experience with species such as *Tetrao urogallus, Alces alces*, *Bos taurus, Ovis aries* that were watching our steps through the woods, and a special thanks to the thousands of Simuliidae for sucking my blood and making our skin itch whenever we stopped in the forest to empty the traps; this speeded up our work considerably and made us even more effective!

I will thank Charlotte Norseng, for making the field work a great experience, for being a good driver, and for being a great support during the whole year. Thanks to my friend Håvard Hageberg for helping out in the field, carrying down our traps and telling jokes to makes us feel better in the rain. I will thank my dad for correcting my English and helping me with financial support when I crashed his car during fieldwork, and my mom for baking hundreds of buns and bringing me nuts to keep my energy level up. Thanks to my fellow students at Ås for making the last five years a great experience. Lastly, thanks to Jon Peder, who have been a great support and given me good advice and making incredible dinners when I had been in the forest for a week at the time.

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Abstract

Forestry has changed the forest structure and modified the associated ecosystems throughout time. With increasing extraction of forest resources in the future, there is a risk that most of the natural forests in Norway will have disappeared within 30 to 40 years. The decline of natural forests is a concern for the forest dwelling species that prefer the variety of habitats. Herbivorous insects play an important role in the forest ecosystems.

The purpose of this study was to investigate the importance of forests structure for herbivorous insects, and whether the associated diversity differs between old near-natural and old managed forest sites in south-eastern Norway. Window traps and pitfall traps were used to catch flying and ground-dwelling herbivorous insects in 29 study plots. Compared to old managed forests, old near-natural forests are characterized by more variation in age and trunk diameter, and on average a higher elevation.

This study found no significant difference in species richness nor abundance of herbivorous insects between the old near-natural and old managed forest. However, several environmental variables related to forest age, forest structure and elevation was found important for the associated herbivorous insects. Species richness and abundance of herbivorous beetles increased with lower elevation, and that abundance increased with fewer cut stumps and more variation in crown height. In contradiction to this, the abundance of other herbivorous insects increased with higher elevation, more cut stumps, and more variation in trunk diameter. None of the explanatory variables were able to describe any difference in the abundance of wood ants.

The investigated forest area contains a mosaic of old near-natural and old managed forest, which may make it difficult to detect differences in herbivorous insect diversity. Many forest dwelling species have a wide habitat range and will therefore be found in both old near-natural and old managed forests stands. The near-natural forest stands will eventually turn into true natural forest and might then potentially contain important characteristics favourable for many herbivorous insects. A larger number of study plots, and a survey over several years, would increase the robustness of the results.

Keywords: Biodiversity, forest management, herbivorous insects, phytophagous insects, entomology, boreal forest, forest structure, near-natural forest, managed forest

Sammendrag

Skogsdrift har i tidens løp modifisert skogstrukturen og de tilhørende økosystemene. Med økende hogst i framtiden er det fare for at de fleste naturskogene i Norge har forsvunnet innen 30 til 40 år. Tilbakegangen av naturskog kan få betydelige konsekvenser for de artene i skogen som foretrekker varierende habitat. Planteetende (herbivore) insekter spiller en viktig rolle i økosystemene i skogen.

Hensikten med denne studien er å undersøke hvor viktig skogstrukturen er for planteetende insekter, og om det tilhørende mangfoldet er forskjellig i gammel nær-naturskog og gammel kulturskog i Sørøst-Norge. Vindusfeller og fallfeller ble brukt til å fange flygende og bakkelevende planteetende insekter i 29 studieområder. Sammenliknet med gammel kulturskog var gammel nær-naturskog karakterisert ved mer varierende alder og stammediameter, samt gjennomsnittlig høyere beliggenhet.

Denne studien fant ingen signifikant forskjell mellom gammel nær-naturskog og gammel kulturskog med hensyn til artsrikdom og tallrikhet av planteetende insekter. Imidlertid ble det funnet flere miljøvariable relatert til skogens alder, struktur og elevasjon som hadde betydning for de tilhørende planteetende insektene. Artsrikdommen og tallrikheten av planteetende biller økte med lavere elevasjon, og tallrikheten økte med færre hogststubber og mer varierende trekronehøyde. I motsetning til dette økte tallrikheten av andre planteetende insekter med høyere elevasjon, flere hogststubber og mer varierende stammediameter. Ingen av de forklarende variablene kunne beskrive forskjeller i tallrikheten av skogsmaur.

Det undersøkte skogsområdet omfatter en mosaikk av gammel nær-naturskog og gammel kulturskog, noe som kan være årsaken til at var vanskelig å finne ulikheter i mangfoldet av planteetende insekter. Mange arter i skogen har et bred utbredelse i ulike habitat, og vil derfor finnes i bestander både av gammel nær-naturskog og gammel kulturskog. Bestandene av nær-naturskog vil før eller siden bli til ekte naturskog, og kan da potensielt ha viktige karakteristikker som er gunstige for mange planteetende insekter. Et større antall studieområder, og en undersøkelse som strekker seg over flere år, vil kunne gi resultatene økt robusthet.

Nøkkelord: biomangfold, skogforvaltning, planteetende insekter, herbivore insekter, entomologi, boreal skog, skogstruktur, nær-naturskog, kulturskog

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1 Introduction

1.1 Forest biodiversity

The Norwegian forests are part of the world's largest terrestrial biome, *the boreal forest zone* (Esseen et al. 1997). The boreal forest ecosystems are located at high latitudes (56°N to 69°N) throughout Norway, Sweden, Finland and Russia, and through Canada and Alaska. In addition to containing half of the world's remaining intact forests, the boreal forest zone also stores one of the biggest carbon reserves on earth (Luyssaert et al. 2008; Read et al. 2001; Society. 2001).

The forests provide a vast number of ecosystem services, benefits that the human society obtains for free. Among the most important are carbon storage, wood production, protection against floods and erosion, places for hunting and fishing, outdoor recreation and nature experience (Cardinale et al. 2012; Lindhjem & Magnussen 2012). Biodiversity, including variation among genes, species and functional traits is the key for providing these ecosystem services (Cardinale et al. 2012; NOU 2013:10). Biodiversity is essential for the production of biomass, and for decomposing and recycling of nutrients. It is also fundamental for the resilience of the forest ecosystems (Cardinale et al. 2012). Approximately 60 % of 44 000 species found in the Norwegian terrestrial environments are associated with forest (Gundersen & Rolstad 1998; Henriksen & Hilmo 2015). The major species groups found are arthropods (insects and arachnids dominate), lichens, mosses and fungi (Gundersen & Rolstad 1998).

1.2 Herbivorous insects

About half of all existing insect species on earth are herbivores feeding on living plants (Schoonhoven et al. 2005; Strong et al. 1984). Based on their biology, herbivorous (synonymous with phytophagous) insects can be roughly separated by the parts of plants they feed on: living plant tissue, plant fluids, stems, leaf-litter, nectar and pollen, and those forming galls and mines (Strong et al. 1984). Saproxylic beetles feeding on dead and decaying wood (Speight 1989) are not included in this definition. The majority of the herbivorous insect fauna are butterflies and moths (Lepidoptera), grasshoppers and locusts (Orthoptera), thrips (Thysanoptera), gnats and flies (Diptera), beetles (Coleoptera), wasps, bees and ants (Hymenoptera), bugs and leaf-hoppers (Hemiptera) (Schoonhoven et al. 2005; Stokland et al. 2012).

Insect herbivory play an important role in natural communities, affecting plant performance and plant population dynamics (Crawley 1989). A great number of the insects in the orders Hymenoptera and Lepidoptera are essential as pollinators for flowering plants (Angiosperms)

(Crawley 1989). Furthermore, a great part of the herbivorous beetles and ants play a crucial role as decomposers of leaf-litter and recyclers of nutrients back to the forest soil (Gullan & Cranston 2014; Strong et al. 1984). Seed harvesting by ants benefits as seed dispersal for plants (Gullan & Cranston 2014). In addition, herbivorous insects are important as food source for other predators (Strong et al. 1984). On the other hand, plant suckers, such as leaf-hoppers and aphids, feed on the plant's vascular system and may hurt the plant by spreading plant viruses as they feed (Schoonhoven et al. 2005). However, these herbivores may increase the plant diversity by controlling potentially dominant plants (Crawley 1989).

The number of host plants that insects feed on depends on whether the insects are host specific on one (monophagous) or a number of species (oligophagous) within a single plant family, or generalists (polyphagous) on many different plant families (Schoonhoven et al. 2005). In addition, specialization on a particular part of plants such as leafs, seeds, stems, roots and fruits, are common (Bernays & Chapman 1994). A majority of the herbivore insects are host specific, with over 80 % of Hemiptera, Diptera, Hymenoptera and Lepidoptera being monophagous or oligophagous (Bernays & Chapman 1994). The host specialization is mainly due to plant chemistry, either the level of organic nitrogen available in the plant as food, or plant defences, such as physical or chemical defences (Strong et al. 1984).

The boreal forest landscape provides a variety of habitats, structures and suitable environments that differ from other nature types (Gjerde et al. 2010). The plant architecture that describes size, spread of plant tissues in space and variety of plant structures, influences the insect diversity (Lawton & Schroder 1977; Strong et al. 1984). Larger and more complex plants provide a greater range of microhabitats and therefore more niches for insects to colonize. Hence, trees host a higher proportion of herbivorous insects than bushes and herbs (Strong et al. 1984). Thunes et al. (2003) suggest that the canopy of Scots pine (*Pinus sylvestris* L.) provides a place for resting and swarming sites for the less mobile herbivore species groups, such as Thysanoptera and Heteroptera. Furthermore, older trees with wider and more voluminous canopies have a higher species richness, than younger trees with narrow canopies (Thunes et al. 2003).

1.3 Forestry and structural changes

Forestry has modified ecosystems and changed the forest structure throughout history (Esseen et al. 1997). In Norway, only 1,3 % of the total forest area remains as natural forests (Tomter & Dalen 2014), and the proportion of old growth forest (>160 years old) has declined to 2,4 % of the total forest area (Stokland et al. 2014). With increased extraction of forest resources in the future, there is a risk that most of the natural forests will have disappeared within 30 to 40 years (Rolstad & Storaunet 2015). The decline of natural forests is a concern for the forest dwelling species that prefer this variety of habitats (Esseen et al. 1997).

From the end of the 19th century, the forest management has been dominated by selective dimension felling, taking out the large-diameter trees (Sippola et al. 2001). Even though the timber volume was largely reduced (Esseen et al. 1997; Siitonen 2001), the selectively logged forests were still able to maintain a diverse heterogonous forest composition, with variation in age and size (Lie et al. 2012). Since the middle of the 20th century, clear-cutting and high density planting has been the dominant logging regime (Storaunet et al. 2005). As much as 75 % of the Norwegian natural forest area has been logged by modern stand-replacing methods (Rolstad & Storaunet 2015). Forest stands are harvested at an age of between 70 and 120 years, depending on the site productivity, which is long before their natural life span is reached (Framstad & Sverdrup-Thygeson 2015). Norway spruce (*Picea abies*) has a maximum life span of 500 years, and Scots pine of 800 years (Vennesland et al. 2006). This management has resulted in forests with biologically young stands of Scots pine and Norway spruce that are homogenous, even-aged and denser, and of similar sizes (Lie et al. 2012). In addition, this might lead to fewer ecological niches of dead wood and old trees (Gjerde et al. 2010), and may indicate a loss of forest dwelling species (Bakke 1994; Linder & Östlund 1998). On the other hand, natural forest ecosystems formed by long forest continuity, fire disturbance and gap disturbance, provide a heterogeneous tree composition with variation in age and size, deciduous trees, old trees and large amounts of coarse woody debris (Andersson & Bohlin 1998; Esseen et al. 1997; Franklin et al. 2002; Rolstad et al. 2002; Siitonen 2001). Natural forests are effected by small-scale disturbances, where one or few canopy trees will die or get injured, making opening in the forests, called “gaps” (Watt 1947; Yamamoto 2000). This creates special microclimates of temperature, moisture and light which gives more trees the possibilty to grow (Yamamoto 2000).

Even though the old managed forests planted in the 1950’s are now reaching maturity, the truly mature stands are largely remnants from the selective logging period (Storaunet et al. 2005). Studies show that forests that are intensively selective logged are able to develop old-growth stand structures, with variation in size and age, and increasing levels of diverse dead wood after 100 to 150 years of harvest (Groven et al. 2002; Jönsson et al. 2009; Storaunet et al. 2000). Without the interference of humans, these remaining old near-natural forests stands are now developing into the characteristics of natural forest ecosystems, and may function as important areas for specialized species associated with old-growth forest (Sverdrup-Thygeson et al. 2016; Vandekerkhove et al. 2012).

1.4 Forest management

Forestry is considered to be the main threat to biodiversity in forests, resulting in fragmentation and loss of forest habitats (Gjerde et al. 2010; Kålås et al. 2010). A severe consequence is the reduction of coarse woody debris and loss of old forest (Esseen et al. 1997; Siitonen 2001). Approximately 48 % of the endangered and near threatened species are associated with forest (according to the 2015 Norwegian Red List), a majority being insect species (Henriksen & Hilmo 2015; Kålås et al. 2010). 84% of the endangered species are connected with old-growth forest, especially forest that is old and with low interference of harvest (Henriksen & Hilmo 2015).

“The prime cause of insect declines and extinctions, at least of local populations if not whole species, is the loss of their natural habitat” (Gullan & Cranston 2014, pp.14). To maintain healthy insects populations there is a need to maintain large habitats with good quality and reduced isolation of habitats (Gullan & Cranston 2014). In Norway, only a small proportion (2,9 %) of the productive forest area is protected by nature reserves (Regjeringen 2015), although 9,3 % has been recommended to secure species diversity (Framstad et al. 2002). Establishing protected forest reserves can create habitats for insects with limited distribution, including rare and habitat-demanding species. Such reserves can also be important for the natural dynamic and development of a diverse forest (Framstad et al. 2002). Framstad and Sverdrup-Thygeson (2015) emphasize that remaining old forests, which are not yet clear-cut, should be protected to secure forest biodiversity in the future.

In order to maintain species richness in managed boreal forests, there is a need to mimic natural forest dynamics (Gustafsson et al. 2010; Gustafsson et al. 2012; Similä et al. 2003). Hence, keeping in mind stands with long continuity, old trees and coarse woody debris (Bengtsson et al. 2000; Similä et al. 2003). Thus, smaller habitat patches appropriate for many threatened species, so called “woodland key habitats”, may be conserved within the managed forests, serving as life-boats for old forest species (Direktoratet for naturforvaltning 2007; Timonen et al. 2010). Furthermore, at the time of harvest, it is essenstial to keep structures to ensure continuity of habitats (Stokland et al. 2012). Examples of such structures are single trees or groups of trees, buffer zones bordering lakes or bogs, and dead wood (Gustafsson et al. 2012; Stokland et al. 2012; Sverdrup-Thygeson et al. 2014). Continuity, meaning “forest with long, uniterrupted presence” (Yamamoto 2000), is especially important for species that are disperal-limited and dependent on a certain substrate (e.g dead wood of late decay age) (Nordén et al. 2014; Sverdrup-Thygeson & Lindenmayer 2003). These aspects are highly important to keep in mind for maintaining viable insects population when increasing extraction of forest resources.

1.5 Aim of the study

This study is part of a larger research project “Sustainable utilization of forest resources in Norway” (KPN BIONÆR) for assessment of the environmental challenges of increasing forest extraction. The project contains three sub-projects, one of them focusing on the investigation of differences between forest structures in old near-natural versus old managed forest using airborne laser scanning (ALS). The ALS-study conducted by Sverdrup-Thygeson et al. (2016) showed clear differences in the forest structures between old near-natural and old managed forest. The old near-natural forests differ from old managed forests by a lower canopy, more variation in crown size, fewer trees per area and fewer, but larger gaps.

This thesis is part of the subproject and is based a survey of the herbivorous insect diversity within the same study area. The old near-natural forests are remnants from selectively logged forests, and the old managed forests are the results of extensive logging around the 1950's (Sverdrup-Thygeson 2000; Sverdrup-Thygeson et al. 2016). Despite comprehensive mapping of the biodiversity in Hurdal, Gran and Nannestad municipalities, the insect diversity has previously been given limited attention, and there is a need for further survey in the older forest at higher elevation (Blindheim 2003; Gaarder & Larsen 2002; Larsen et al. 2004).

The past few years, many studies have investigated saproxylic beetles in boreal forests (see e.g. Siitonen 2001; Similä et al. 2003; Sippola et al. 2002; Stokland et al. 2012). However, how differences in forest structure affect herbivorous insect diversity in boreal forest is little investigated, in spite of being an important issue in the assessment of future forest extraction in old forests.

In this thesis I raise these questions: (1) Does the number of associated herbivorous insects differ between old near-natural and old managed forest? (2) Does the number change due to differences in forest structure?

I predict that there will be greater species richness and abundance of herbivorous insects in the old near-natural forest compared to old managed forests. Due to longer continuity, a forest structure with more gaps, older trees with wider and more voluminous canopy, and more vegetation on the forest floor, will provide a greater number of niches for the herbivore insects to colonize. Hence, differences in the forest structure change the associated herbivorous insect diversity.

2 Methods

2.1 Study area

The study area was contained within a 17 000 ha forested area, located in Mathiesen Eidsvold Værk's forest holdings in the Hurdal and Nannestad municipalities (Akershus county) and the Gran municipality (Oppland county), in south-eastern Norway (Figure 1). The study area is situated in the boreal vegetation zone, approximately 100 kilometres north of Oslo (N60° 23′, E10° 55′). The elevation ranges between 392 and 775 metres above sea level. A total of 29 sample plots were used in this study, 15 sample plots where selected in old near-natural forest and 14 in old managed forest (Figure 1). The size of each forest plot was 750 m^2 with radius of 15.45 metres.

The dominant tree species in the area is Norway spruce, and subdominants are Scots pine, with infrequent occurrences of birch (*Betula pubescens*) and aspen (*Populus tremula)* (Sverdrup-Thygeson 2000). The forest floor vegetation consists mainly of Bilberry spruce forest (*Vaccinium myrtillus*) and small elements of low-fern spruce forest, swamp spruce forest and heath forest (*Calluna vulgaris*). The forested area contains an intertwined mosaic of both old near-natural and old managed forest. The forest development class ranges from 4 (young mature) to 5 (old mature forest).

The sample plots were chosen based on a combination of current digital forest maps and scanned georeferenced historical maps from 1954 and 1964 with previously logging history indicated (Sverdrup-Thygeson et al. 2016). From the current digital maps only forest stands categorized as old (age >60 years) were included. The forest stands were divided into two categories:

> (1) Old near-natural forests (called old natural below)
> Classified as the oldest age class in 1954. Some degree of selective logging have occurred, but the forest has not been subjected to clear felling.
>
> (2) Old managed forest
> Either classified as young in 1954, or was cut during the 1950's and then changed the stand into the youngest age class according to the 1964 map. The forest stands are now reaching maturity, with age more than 60 years.

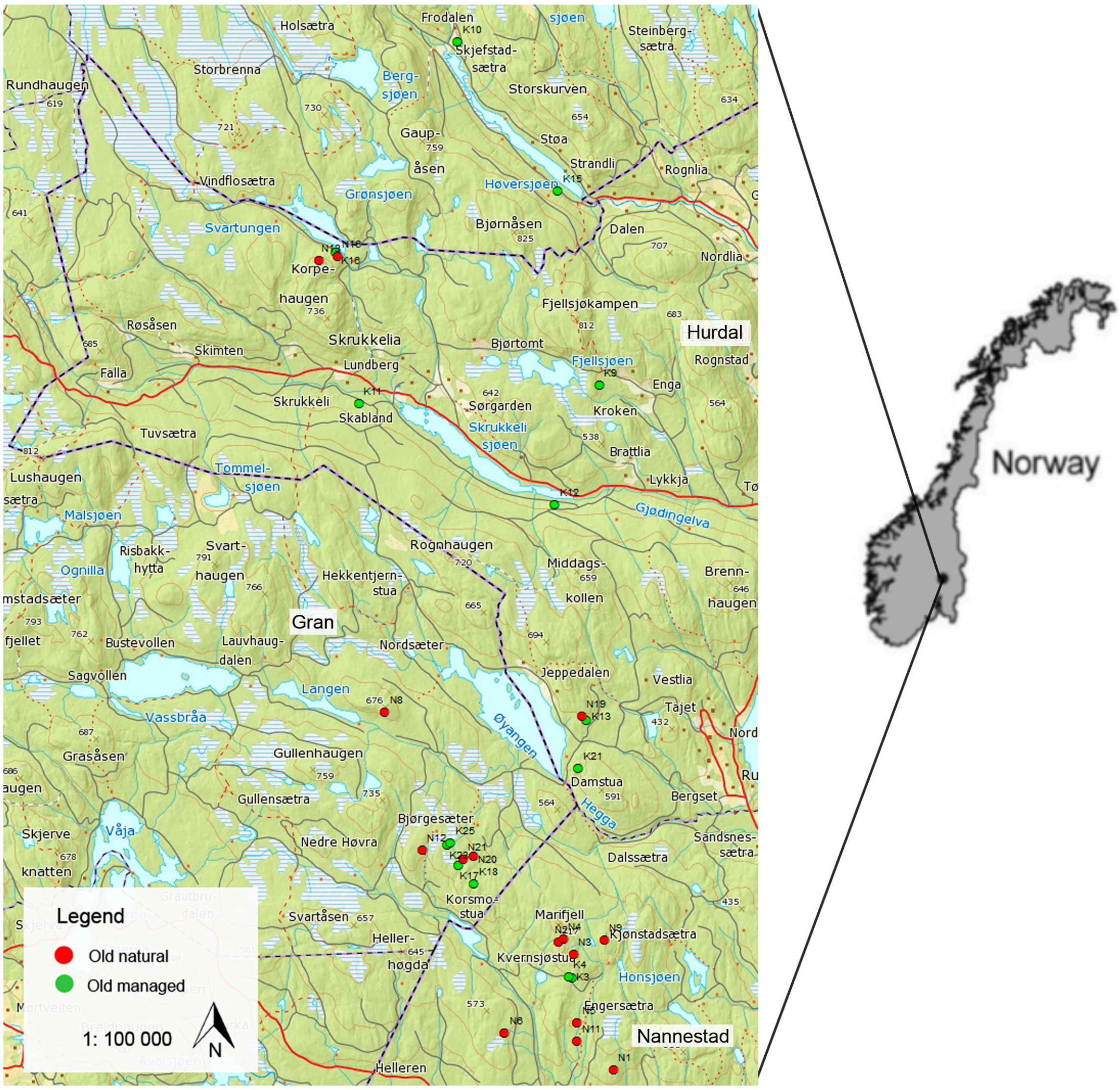

Figure 1: Overview of the study area, with the 29 study plots. The geographical position of the study is also indicated.

2.2 Experimental design

The insects were sampled by using window traps and pitfall traps. The window traps were used to collect flying insects, and were able to catch a large number of species and individuals within the area (Birkemoe & Sverdrup-Thygeson 2015). Pitfall traps were used to catch ground-dwelling insects which are likely to have colonies within the type of habitat (Punttila et al. 1996). These types of traps are easy and quick to operate, as well as being inexpensive (Southwood & Henderson 2009). However pitfall traps are dependent on population density and movement of species, the supply of food, and of weather conditions (Southwood & Henderson 2009; Westerberg 1977). In addition to forage, herbivorous insects need shelter and oviposition sites, and twigs are of great importance for these purposes (Lawton 1983). In this survey, twigs were used on half the pitfall traps.

Two window traps were used per site (Figure 2). Each trap consisted two transparent 40 cm x 22 cm acrylic panes, arranged crosswise, with a funnel located below, leading into a 0,5 litre sampling bottle containing a solution of 70 % propylene glycol, water and a small amount of dishwasher detergent (to break the surface tension). The bottle had drainage holes to avoid overflow of water. The ratio between propylene glycol and water changed with rainfall. The traps were hanging with the lower edge approximately 1,5 metre above ground, between two tree trunks within 5 to 10 metres from the centre of the plot (Figure 4). The total number of window traps was 58 (2x14 + 2x15).

Figure 2: Window trap hanging between two tree trunks.

In addition, four pitfall traps were used per site to catch insects moving on the surface of the ground (Figure 3). Each trap consisted of a 9,5 cm x 6 cm plastic cup with iron wire holding 15 cm x 15 cm acrylic lid above. The cup was filled with a solution of 70 % propylene glycol, water and a small amount of dishwater detergent. Two of the traps per site had a pile of approximately 4 twigs (about 10 cm long and 0.5-1 cm in diameter) above the cup. The traps were placed in the ground at the corners of a 2 m x 2 m square, with the centre of the square located approximately at the middle of the plot (Figure 4). The total number of pitfall traps used was 116 (4x14 + 4x15).

Figure 3: Pitfall traps without twigs (left) and with twigs (right).

The traps were operating from the 2th of June to the 8th of August 2015, and were emptied every third week (24.-27. June, 13.-17. July and 4.-8. August). When we emptied the traps, we separated the insects from the collecting solution by pouring the contents into a plastic cup with a net in the bottom. The insects were stored in a solution of propylene glycol and kept in a freezer before sorting. In the lab, the insects were identified and transferred into vials with 70 % rectified alcohol.

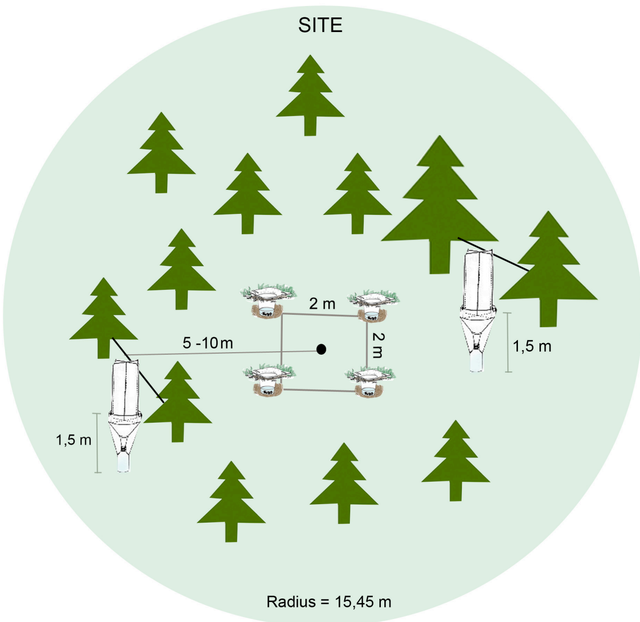

Figure 4: Overview of the experimental design at each plot. The black dot is the centre of the plot. Four pitfall traps were placed in the ground in a square with centre approximately 2 metres from the centre of the plot and 2 metres apart. Two window traps were mounted 1,5 metres above the forest floor between two tree trunks located 5 to 10 metres from the centre of the plot.

2.3 Study organisms and grouping

Insects collected by window traps and pitfall traps were classified into 9 taxonomical groups (Table 1). Further divided into herbivorous beetles (Table 4), non-beetle herbivorous insects (Table 7) and wood ants. Identification of non-beetle herbivorous insects was based on Sømme (1998) and Douwes (1997). Sindre Ligaard classified the herbivorous beetles to species level (Table 4). Threatened beetle species were identified using the Norwegian 2015 Red List for species (Henriksen & Hilmo 2015).

Species richness (the number of species) and abundance (the number of individuals) was further studied. For insects that were not classified to species level, only abundance was studied.

*Table 1: Taxonomic classification of the composition of study organisms. Bold indicates the lowest order of classification. *See table 4 for further specification.*

Insect order	Suborders	Family	Subfamily	Genus
Coleoptera*				
Lepidoptera				
Hymenoptera	Apocrita	Apidae	Apinae	**Bombus**
Hymenoptera	Apocrita	**Vespidae**		
Hymenoptera	Apocrita	Formicidae	Myrmicinae	**Formica**
Hymenoptera	**Symphyta**			
Hemiptera	**Heteroptera**			
Hemiptera	Homoptera	**Aphididae**		
Hemiptera	Auchenorrhyncha	**Cicadellidae**		

2.4 Environmental variables

At each site environmental variables related to forest age, forest structure, vegetation type, and elevation, were recorded in a field study in the autumn of 2014 (unpublished data) (Table 2).

Table 2: Abbreviation and description of the environmental variables used in the analysis.

Abbreviation	Description	Unit
Elevation	Metres above sea level	m
TrunkDiam (Var)	Variance in trunk diameter at breast height (1,3m above the forest floor)	cm
TrunkDiam (Mean)	Mean trunk diameter at breast height (1,3m above the forest floor)	cm
CutStumps	Number of logging traces in the form of cut stumps	1-40
Age (Var)	Variance in age of three sample trees per site	years
CrownHeight (Var)	Variance in height of crown base of sample tree per site	cm
TreeHeight (Var)	Variance in height of sample tree	m
Basal area	Density of the forest, measured with a Relascope	m^2/ha
ForestDev	Forest development class - Development class 4 (young mature forest) Development class 5 (old mature forest)	4 or 5
ForestType	Old natural or Old managed	

2.5 Data management & statistical analysis

Data management was carried out using Microsoft Excel (2010). All statistical analyses were conducted in JMP 12.1.1 (SAS Institute Inc. 2015). Significance level used was $\alpha = 0.05$.

Analysis was conducted separately for herbivorous beetles and non-beetle herbivorous insects. The data samples from the window traps and pitfall traps were pooled, and the categories “Total abundance” and “Total species richness” (Appendix, Table 14-15) were established.

Pooled species richness and abundance of the different herbivorous insect groups were used as response variable (Y). Forest type, forest development class, number of cut stumps, elevation, variance in trunk diameter at breast height (dbh), variance in height of sample tree, variance in age of trees, variance in crown height of sample trees, and basal area, were used as explanatory variables (X).

The Shapiro-Wilk test was used to check for normality of the response variables. The response variables were log-transformed if necessary to fulfil the requirements for normal distribution. I applied a Pearson multicollinearity test on explanatory variables creating a correlation table (Appendix, Figure 11). It revealed a strong relationship between TrunkDiamVar (0.75) and TrunkDiamMean (0.75), both exceeding 0.5 (as a threshold level) .To avoid collinearity among the explanatory variables in the final model, TrunkDiamMean was not included. Since the dominating vegetation type was bilberry spruce forest and small variation in vegetation types, the variable “vegetation types” were rejected from the model (Appendix, Figure 14).

One-way ANOVA was used to test for differences in species richness and abundance among forest types. To test which of the environmental variables that could best explain the variation in species richness and abundance in the two forest types, I used Standard Least squares (Linear regression) with all the environmental variables as explanatory variables, and abundance or species richness as response. Backward stepwise multiple regression was performed to get the best subset. The model with the lowest corrected Akaike information criterion (AICc) value was selected. Only the best models are presented in the results. For results showing weak results in Backward elimination, step by step linear regression was used to give a more realistic result (Table 8). The model with the closest R^2 adjusted to 1 was used.

Wood ants were studied as a categorical variable with three levels, based on volumes ”small” (1), ”medium” (2), or ”large” (3) (Appendix, Figure 13). The mean from each site was used in the model (Appendix, Table 15). A contingency analysis was conducted on the wood ants, to explore the distribution of two categorical variables.

3 Results

A total of 388 individuals of herbivorous beetles, belonging to 20 different species, were caught in the traps (Table 4). The most dominant species, *Otiorhynchus scaber,* comprised almost 63% of the total catch. One red-listed species was sampled, *Bagous brevis*. This species is categorized as endangered (EN) in the Norwegian 2015 Red list for species.

In total 973 individuals of non-beetle herbivorous insects were caught (Table 7), divided into Bombus (43), Vespidae (10), Symphyta (20), Lepidoptera (39), Heteroptera (68), Aphididae (695) and Cicadellidae (98). Aphididae was the dominating group, making up 71.4 % of all individuals of non-beetle herbivorous insects caught.

3.1 Habitat characteristics in old managed and old natural forest

The structural changes between the forest plots showed that old natural forests on average are situated at higher elevation, have greater variation in trunk diameter, and have greater variation in age structure, compared to old managed forests (Table 3 and Figure 5).

Table 3: Results from ANOVA. Structural changes between forest types. Significant p-values are given in bold. Var= variance. N=14 in Old managed and N=15 in old natural.

Variable	**Managed**		**Natural**			
	Mean	**Std.Error**	**Mean**	**Std.Error**	**F-ratio**	**p-value**
Elevation	564.5	28.486	648.474	27.520	4,631	**0.040**
Basal area	23.642	2.023	21.466	1.954	0,598	0.446
No. of Cut Stumps	19.214	2.857	13.866	2.760	1,811	0.189
Crown Height (var)[a]	0.277	0.021	0.51	0.146	1,480	0.234
Trunk Diameter (var)[a]	1.484	0.085	1.978	0.083	17,048	**0.0003**
Age of trees (var)[a]	1.71	0.755	2.78	0.536	19,704	**0.0001**
Height of tree (Var)[a]	0.777	0.083	0.889	0.080	0,929	0.343
Forest Development[b]	8 (4), 6 (5)	-	9 (4), 6 (5)	-	0,024[c]	0.881

[a] Log-transformation of CrownHeightVar, TrunkDiamVar, AgeVar and TreeHeightVar was done to achieve normality
[b] Total number of forest development classes per forest type (4=young mature forest, 5=old mature forests)
[c] ChiSquare

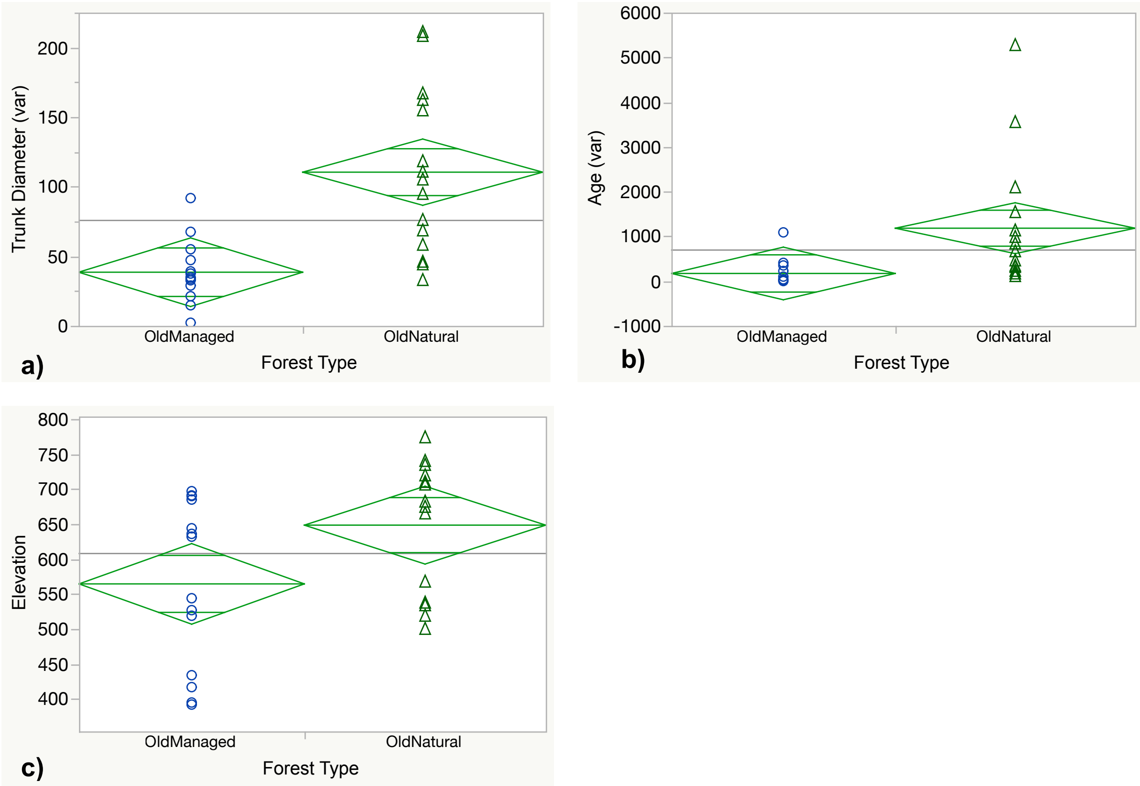

*Figure 5: Differences between old managed and old natural forest by variation in trunk diameter **(a)**, variation in age **(b)** and elevation **(c)**. The mean line across the middle of each diamond represents the group mean, whereas the lines above and below illustrate the 95 % confidence interval. The data points illustrate the observations from each site. (N=29).*

3.2 Herbivorous beetles and effect of forest types

There is no significant difference in species richness (R^2 Adj= 0.04, *p*=0.15) or abundance (R^2 Adj= -0.017, *p*=0.48) of herbivores beetles between the old managed and old natural forest (Figure 6).

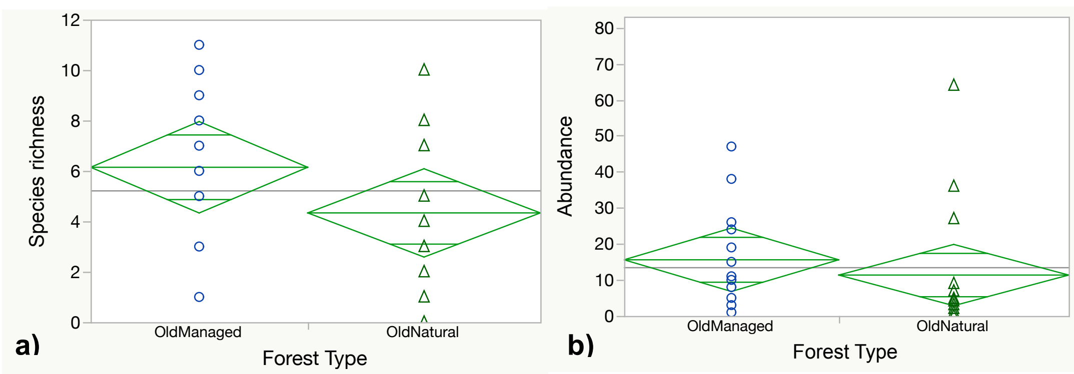

*Figure 6: Results from ANOVA. Relationship between the number of beetle species by **(a)** and number of beetle individuals **(b)** in old managed and old natural forest. The mean line across the middle of each diamond represents the group mean, whereas the lines above and below illustrate the 95 % confidence interval. The data points illustrate the observations from each site.*

In total, 218 individuals were caught in old managed forest and 170 individuals in old near-natural forest (Table 4). The distribution of species showed that 11 species (374 individuals) were common for both forest types, 6 species (11 individuals) was only present in old managed forest, and 3 species (3 individuals) were present only in old near-natural forest (Table 4).

*Table 4: Total number of individuals of herbivorous beetle species distributed in old natural or old managed. *red listed species (EN)*

Family	**Species**	**Old managed**	**Old natural**
Curculionidae:	*Bagous brevis** (Gyllenhal 1836)	1	-
	Otiorhynchus lepidopterus (Fabricius 1794)	6	-
	Otiorhynchus nodosus (O.F. Muller 1764)	43	33
	Otiorhynchus scaber (Linnaeus 1758)	135	109
	Polydrusus pilosus (Gredler 1866)	3	3
	Polydrusus undatus (Fabricius 1781)	1	-
Chrysomelidae:	*Lochmaea suturalis* (Thomson 1866)	-	1
	Lythraria salicariae (Paykull 1800)	1	-
	Syneta betulae (Fabricius 1792)	4	5
Nitidulidae:	*Meligethes aeneus* (Sturm 1845)	1	1
	Meligethes denticulatus (Heer 1841)	-	1
Byrrhidae:	*Byrrhus arietinus* (Steffahny 1842)	5	7
	Byrrhus pilula (Linnaeus 1758)	1	-
	Cytilus sericeus (Forster 1771)	1	-
Scirtidae:	*Cyphon coarctatus* (Paykull 1799)	1	3
	Cyphon padi (Linnaeus 1758)	1	1
	Cyphon variabilis (Thunberg 1787)	1	1
Byturidae:	*Byturus tomentosus* (De Geer 1774)	12	2
Kateretidae:	*Heterhelus scutellaris* (Heer 1841)	-	2
Staphylinidae:	*Megarthrus nitidulus* (Kraatz 1857)	1	1

3.2.1 Effect of environmental variables

Species richness of herbivorous beetles

The species richness of herbivorous beetles increased with lower elevation (Table 5 and Figure 7).

Table 5: The optimal model based on stepwise regression with backward elimination based on the lowest AIC-criteria explaining the species richness of all herbivore beetle species. Significant p-values are given in bold.

Variable	**Estimate**	**Std.Error**	***p-value***
Intercept	13.136	3.091	**0.0002**
Elevation	-0.012	0.005	**0.0252**
Variance in Age	-0.0008	0.0004	0.0904

*p= **0.011**, df=28, n=29, R^2 Adj=0.238*

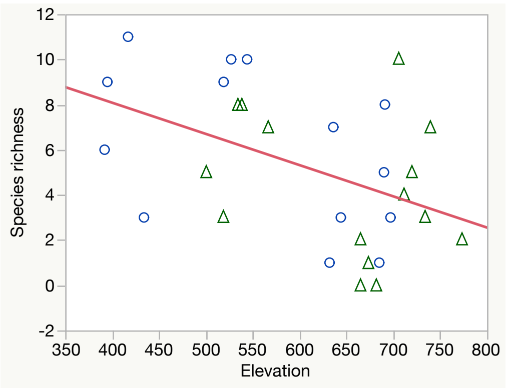

Figure 7: Distribution of species by elevation in old near-natural (triangles) and old managed forest (circles). The line is a linear regression.

Abundance of herbivorous beetles

The number of herbivorous beetles increased by greater variation in height of crown height, lower elevation and fewer cut stumps (Table 6 and Figure 8). Variation in age was near significant (*p*=0.058) and abundance increases with less variation in age (Figure 8).

Table 6: The optimal model based on stepwise regression with backward elimination based on the lowest AIC-criteria explaining the number of herbivore beetles. Significant p-values are given in bold. Log-transformation of abundance was needed to achieve normality.

Variable	**Estimate**	**Std.Error**	***p-value***
Intercept	4.511	1.137	**0.0007**
Elevation	-0.003	0.001	**0.0372**
No. of CutStumps	-0.037	0.014	**0.0209**
Variance in CrownHeight	0.165	0.059	**0.0103**
Variance in Age	-0.0002	0.0001	0.0589

*p= **0.0001**, df= 26, N=27, R^2 Adj=0.56*

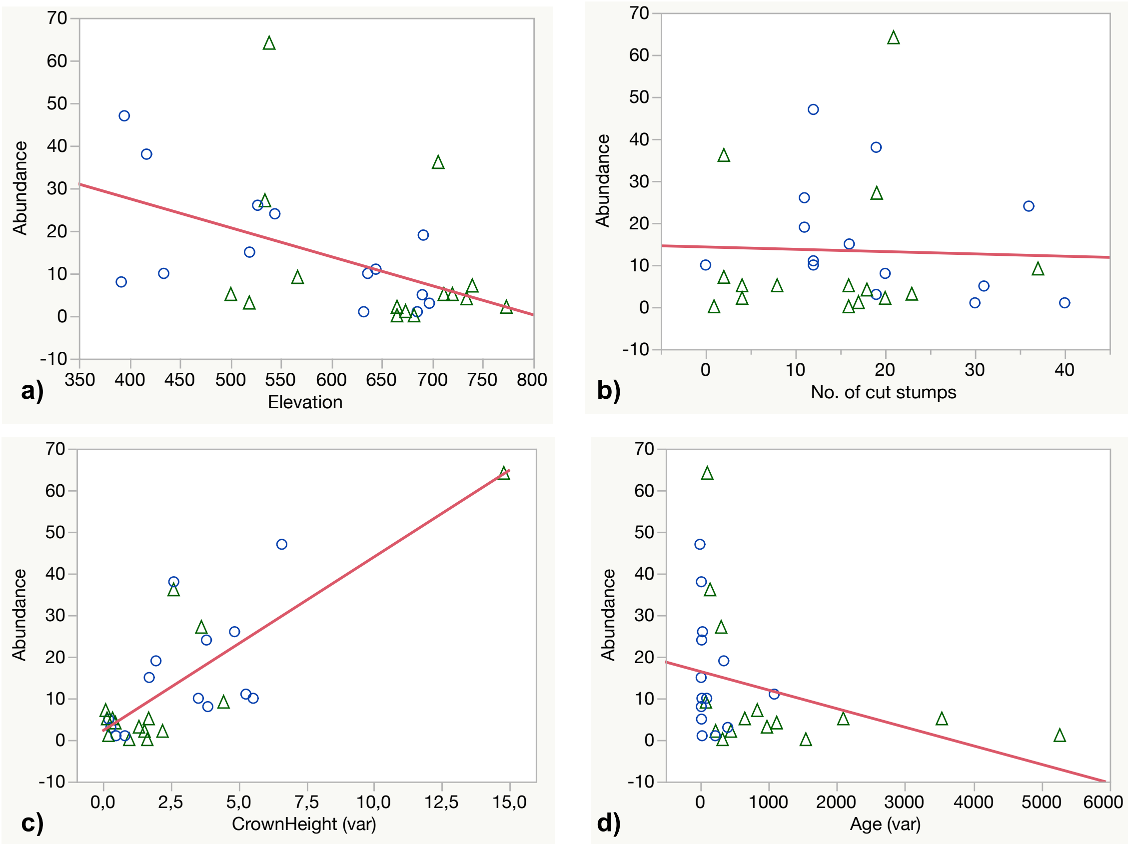

*Figure 8: Distribution of abundance by **(a)** elevation, **(b)** number of cut stumps **(c)** variation inn crown height **(d)** variation in age. The triangles are abundance in old near-natural sites and circles are individuals in old managed forests sites. All lines are based on linear regression.*

3.3 Abundance of non-beetle herbivores and effect of forest types

There was no significant difference between old managed forest and old natural forest in abundance (R^2 Adj= 0.004, *p*=0.30, n= 29, df=27) (Figure 9).

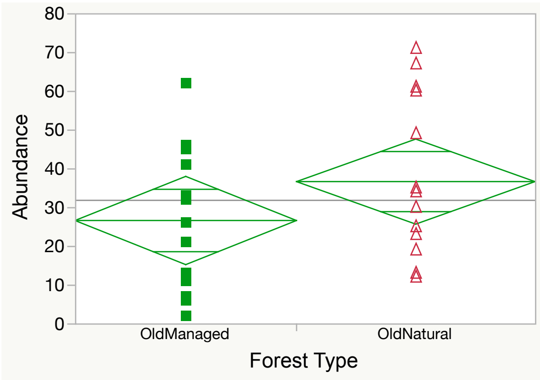

Figure 9: Results from ANOVA. The relationship between the number of insect individuals and forest type. The mean line across the middle of each diamond represents the group mean, whereas the lines above and below illustrate the 95 % confidence interval. The data points illustrate the observations from each site.

In total, 562 individuals were found in old natural forest and 411 individuals were found in old managed forest (Table 7).

Table 7: Total number of individuals of each group caught.

Group	Old Managed	Old Natural
Bombus	22	21
Vespidae	5	5
Symphyta	8	12
Lepidoptera	20	19
Heteroptera	32	36
Aphididiae	256	439
Cicadellidae	68	30

3.3.1 Effects of environmental variables

The abundance of herbivorous insects, beetles not included, increased by number of cut stumps, higher elevation, more variation in trunk diameter. Forest development class 4 (young mature) was near-significant (*p*=0,054) (Table 8 and Figure 10).

Table 8: Parameter estimates from Linear Regression of abundance of herbivore insects. Significant p-values are given in bold. One outlier was rejected from the model to make a better subset.*

Variable	Estimate	Std.Error	p-value
Intercept	-29.945	26.894	0.278
ForestType[OldNatural-OldManaged]	-7.146	9.076	0.44
Forest Development [5-4]	-17.469	8.381	0.054
Elevation	0.096	0.036	**0.017**
No. of CutStumps	0.881	0.356	**0.022**
Basal area	-0.618	0.457	0.192
Variance in TrunkDiameter	0.196	0.086	**0.034**
Variance in CrownHeight	-0.116	0.122	0.353

p= ***0.0361****, Df= 27, n=28,* R^2 *Adj = 0.31*

*The site was affected by clear cutting next to the centre of the site and therefor the pitfall traps were placed in the forest edge. With all the sites included the model had a R^2 adjusted of 0.21 and a p-value of 0.09. 88 show the better subset where the R^2 adjusted is 0.31 and with a significant p-value 0.03.

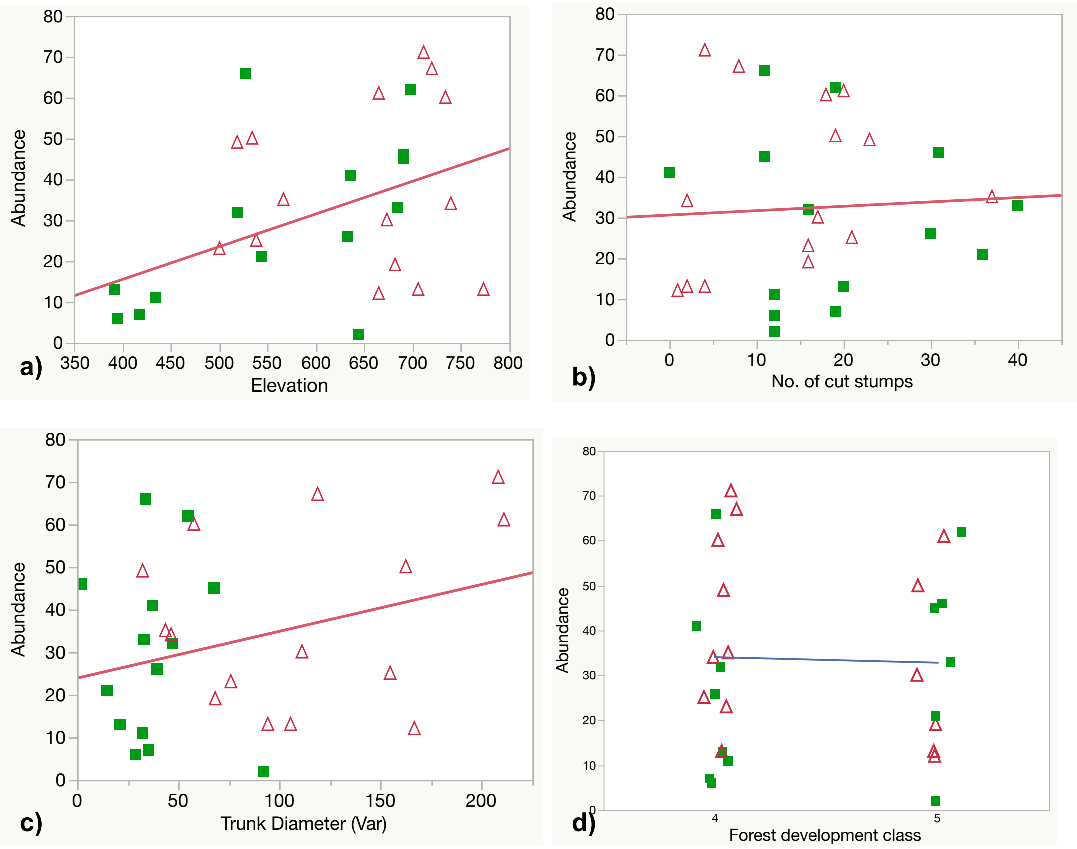

Figure 10: Distribution of abundance by ***(a)*** *elevation,* ***(b)*** *number of cut stumps and* ***(c)*** *variation in trunk diameter* ***(d)*** *forest development class. The triangles are abundance in old near-natural sites and squares are individuals in old managed forests sites.*

A further study using simple linear regression, to investigate which insect group (Appendix, Table 16) was most affected by the significant environmental variables in Table 8, showed a significant relationship for aphids and true bugs. Aphids had a significant positive relationship with elevation and variation in trunk diameter (Figure 11). This indicates that the number of aphids increases with higher elevation and with more variation in trunk diameter. True bugs had a near-significant relationship with variation in trunk diameter (p=0.06), and there is a trend where the abundance of true bugs decreases with more variation in trunk diameter (Figure 11).

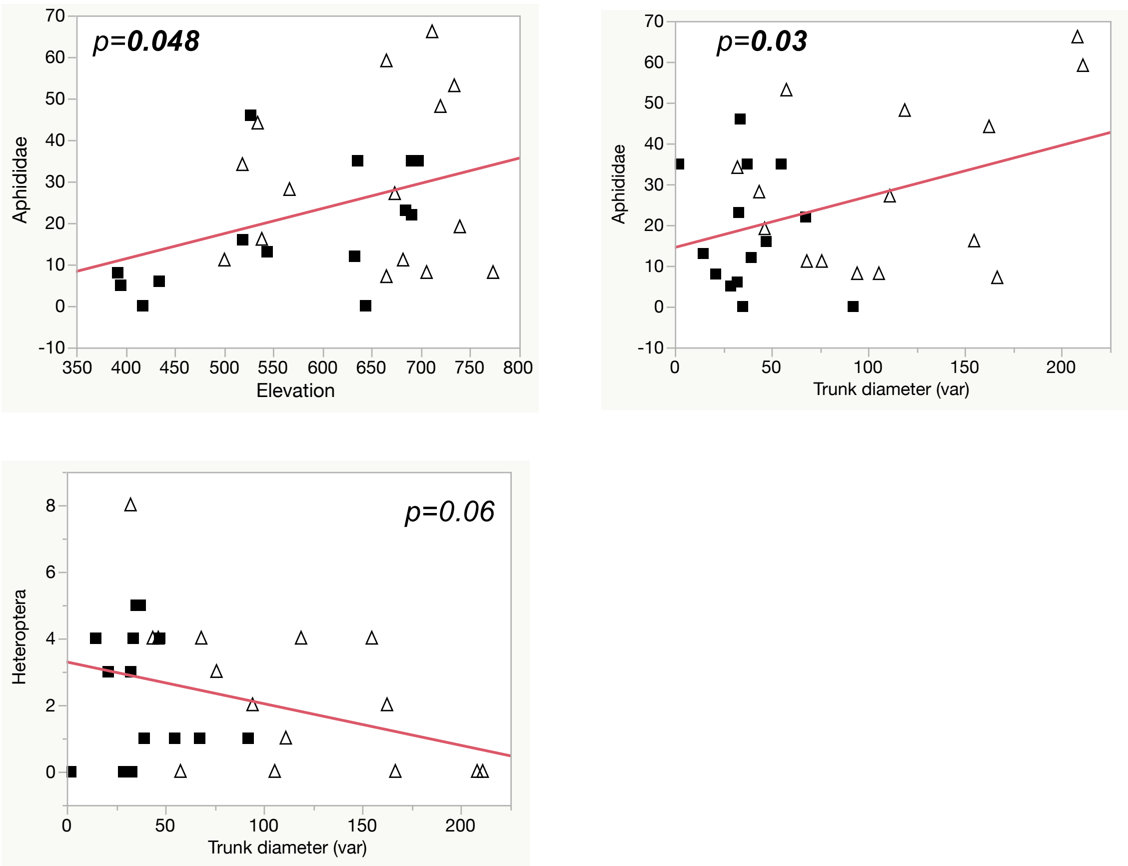

Figure 11: Parameter estimates from Simple Linear Regression of the abundance of groups of herbivorous insects and significant environmental values. Significant p-values are given in bold.

3.4 Distribution of Wood ants (Formica) and effect of forest types

The distribution of wood ants were categorised into mean volumes of small (1), medium (2) and large (3) (Figure 12). The model shows that there is no significant difference in distribution of ants in different forest types (p=0.78). The majority of forest types fall into the small and medium (volume of ant categories) (Figure 12).

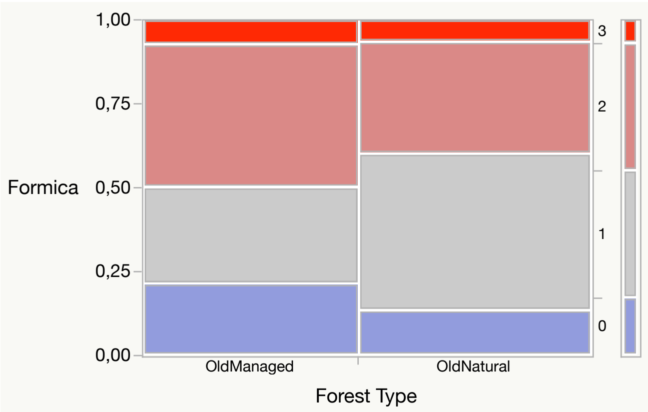

Figure 12: Contingency analysis of Formica (y) by forest type (x). The y-axis at right represents the overall proportion of small (1), medium (2) and large (3) volume of Formica of the combined levels (Old managed and old natural). The y-axis at left represents the probability of Formica being in the forest types.

3.4.1 Effect of environmental variables

None of the explanatory variables were able to predict the distribution of Formica (Table 9).

Table 9: The optimal model based on stepwise regression with backward elimination based on the lowest AIC-criteria explaining the volume of Formica. Significant p-values are given in bold.

Variable	Estimate	St.Error	Prob>ChiSq
Intercept[0]	-1.568	0.491	**0.0014**
Intercept[1]	0.207	0.373	0.5782
Intercept[2]	2.602	0.732	**0.0004**
AICc= 77.88, N=29, RSquare = 0.00			

4 Discussion

The focus of this study is to investigate the importance of forests structure for herbivorous insects, and whether the associated diversity differs between old near-natural and old managed forest.

In the present study I have shown that species richness and abundance of herbivorous beetles increased with decreasing elevation, and that abundance increased with fewer cut stumps and more variation in crown height. In addition, the number of beetles was almost near significant with less variation in age (p=0.058). In contradiction to this, the abundance of non-beetles herbivorous insects increased with increasing elevation and more cut stumps, and also increased with more variation in trunk diameter. In addition, the number of non-beetles was near significant with forest development class (young mature) (p=0,054). None of the explanatory variables were able to describe any difference in the number of wood ants. The associated herbivorous insect diversity did not differ between the old near-natural and old managed forest.

I expected that insect diversity would increase in old near-natural forests due to longer continuity, a forest structure with more gaps, older trees with wider and more volume in the canopy (Thunes et al. 2003), and more vegetation on the forest floor, providing a greater number of niches for the herbivore insects to colonize (Edwards & Wratten 1980; Strong et al. 1984). Contrary to my prediction, there was no significant difference between old managed forest and old near-natural forest in abundance and species richness of herbivorous beetle, nor non-beetle herbivorous insects. However, the number of individuals and species caught was different in the two forest types (Tables 4 and 7).

According to Sverdrup-Thygeson et al. (2016) airborne laser scanning revealed that old near-natural forests have more variation in tree height and canopy distribution. Furthermore, that old near-natural forests has less uniform spatial distribution of trees, and has more gap areas and more variation in gap size, in addition to having a more developed shrub-layer relative to the old managed forest. In the present study, the old near-natural forests sites on average are situated higher, with more variation in trunk diameter, and more variation in age. Since this study is a subplot of the larger ALS-project, this study will not fully reflect the differences in forest structure compared to the larger study.

Elevation

Most insects are poikilothermic (having surrounding dependent body temperature). Temperature and productivity of plants are closely related to elevation and will decrease at higher elevations. The distribution of insects can be explained by the different elevation of sites and corresponding temperature differences. It is expected that the temperature will drop with 0,6 ºC every 100 meters (Børset 1985).

The species richness and abundance of herbivorous beetles showed a continuous decrease with higher elevation. This is supported by Röder et al. (2010), who studied species richness in mature canopies (age 80-120 years) of Norway Spruce in Germany and found a clear negative relationship between herbivorous species richness and elevation ranging from 300 to 1300 metres above sea level. Their study showed that species richness decreased with higher elevations, and that the herbivorous insects were the most influenced. They found similar herbivorous beetle species to this study, *Otiorhynchhus lepidopterus, Polydrusus undatus, Meligethes aeneus, Cyphon coarctatus, Cyphon padi* and *Byturus tomentosus.* The species were found in low numbers, similar to this study. In contrast they found that both beetle and true bugs specialist on spruce doubled at elevation at 1000 metres above sea level. I expected to find more specialists in the old-near natural forests due to lower temperatures and longer continuity. However, beetle specialist and generalists are not widely investigated in this study.

In this study I found that the abundance of herbivorous non-beetles did not decrease with increasing elevation, while other studies have found that species richness and abundance decline with elevation (Hoiss et al. 2012; MacArthur 1972; Rahbek 1995; Sydenham et al. 2015). The dominating group was Aphids, being most abundant at the highest elevation of the old near-natural forest sites. This might control the pattern of an increase towards higher elevation and might not reflect every insect group. Increased abundance of Aphids at higher elevations is supported by Mühlenberg and Stadler (2005) who studied aphids in 10-year-old spruce canopies. They found that aphids first infested forests at lower elevation (500 m.a.s.l), but 3 weeks later, when the temperature increased, the aphids moved to higher elevations (765 m.a.s.l). Stadler et al. (1998) studied aphids on 1-2 years old spruce shoots and 10-15 years old Norway spruce trees, and found that the most important parameters for abundance of aphids are temperature and the nutritional status of the host plant. Of special importance was the development stage of the host plant. Plants with different sizes and ages will have differences in their microclimate, and mature trees are expected to have greater niches to colonize. This might be the reason why aphids are found in greater numbers in old near-natural forests. In addition, mutualism between wood ants and aphids was studied by Kilpeläinen et al. (2009) in Finland who found that 60- and 100 years old forest stands did not have any effect on growth by aphids infestation. Ants are protecting aphids against natural enemies. This issue is not investigated in my study, however it would be interesting to do a study of the relationship between ants and aphids in this environment.

Effect of environmental variables

Old near natural forests are under the influence of small-scale natural disturbances that create a multi-layered forest with trees of different ages in several successive stages (Rolstad et al. 2002). A combination of young and old trees will have variation in trunk diameter and variation in canopy height. In contrast, a cut and planted managed forest will be homogeneous, with trees with the same age and less variation in trunk diameter (Lie et al. 2012). From the ALS-study we know that the old managed forest is denser, with smaller gaps and less light. A forest with disturbances maximizes the species richness of plants (Hobbs & Huenneke 1992).

Herbivorous beetles

My study showed a negative relationship between the abundance of beetles and the number of cut stumps. This indicates that the number of beetles increases with less cut stumps. Beetles are often “sturdy, compact and heavily sclerotized or armoured, with fore wings modified as rigid elytra covering folded membranous hind wings” (Gullan & Cranston 2014, pp.594). Hence, their design makes them better protected against predators and environmental hazards, such as excessive heat or aridity (Harde & Severa 2000). In addition, they are able to fly and disperse widely in new habitats without the risk of being crushed as softer bodied insects, and thus can crawl into cracks, soil and wood (Harde & Severa 2000). This may be the reason why herbivorous beetles are found in both types of forest.

Overall there was an overall large proportion of beetle species occurring only once (Table 4). A study by Sverdrup-Thygeson and Birkemoe (2008) shows that a higher proportion of single species, so called ”singletons”, was found in the free-hanging traps, rather than in traps hanging on the tree trunk of aspen. Some studies have criticized the use of window traps, as these may catch transient species that lack real association with the immediate surroundings, so called “tourists” (Saint-Germain et al. 2006). Niemelä (1997, pp.602) emphasized that “because many forest-dwelling arthropods are wide-ranging species, stragglers may be found in habitats where they are not able to reproduce”. In this study, some of the stands are located in a mosaic. This is because several of the plots were located less than 1000 metres apart, with short distances for the beetles to disperse to suitable forage. Not all beetle species are good at dispersal, but are depended on a continuous habitat. Short distances may favour ground dwelling beetles.

Otiorhynchus scaber (Coleoptera: Curculionidae) was the most dominating species (Table 4). *O. scaber* are to be found on conifers, shrubs and herbaceous plants (Harde & Severa 2000), but are mostly found underground the whole year (Stenberg et al. 2003). The larvae mainly live on blueberry roots, but can also be found on spruce roots (Stenberg et al. 1997). Weevils have asexual reproduction, similarly to aphids (Stenberg & Lundmark 2004). However, are flightless and have poor dispersal abilities, but have good populations where they are found (Stenberg & Lundmark 2004). Hence, *O. scaber* are considered as a minor forest pest (Stenberg & Lundmark 2004). This supports the high distribution found. Their reproduction adaptation and high distribution on blueberry and spruce in both forest types, are a good indicator of their presence at these sites.

The abundance of beetles was near-significant with variation in age. There is a negative relationship with variation in age, indicating that the number of individuals increases with lower variation in age. In contrast, the number of beetles showed a positive relationship with variation in crown height. Older trees with wider and more voluminous canopy have a higher species richness compared to younger trees with narrow canopies (Thunes et al. 2003). This supports that larger and more complex plants provide larger microhabitats and more niches for insects to colonize (Edwards & Wratten 1980; Strong et al. 1984). Old managed forests have taller and more even canopies, a result of spruce planting in a dense and systematic pattern (Sverdrup-Thygeson et al. 2016). A study investigating the structure of canopies in gaps, found that in depth facing gaps the canopies were larger than on forest-facing sides (Bazzaz 2002). However, gaps were found to be more important for young succecional trees than for later succecional trees and conifers (Bazzaz 2002). This supports that trees with more variation in age provide more gaps for light forage.

A similar study comparing beetle diversity in old growth forests and regeneration areas in Lapland, found that the species composition of non-saproxylic species (probably many herbivorous species) was similar in the various forest types (Sippola et al. 2002). The species richness of non-saproxylics had a positive relationship (but not significant) with productivity of the site, including the volume of living stand and cover of eutrophic plants (Sippola et al. 2002). Non-saproxylics were able to inhabit both old-growth forests and areas regenerated 15 years ago, especially in pine forests, since the forests had been relatively open even before cutting (Sippola et al. 2002). This indicates that the beetles favour gap areas with more sun-exposure (Haila et al. 1994). Many beetle species are highly thermophilic, and ongoing densification of suitable forest habitats is negative for the species (Ødegaard et al. 2015a).

Non-beetle herbivorous insects

A positive relationship was found between the number of cut stumps and the other insect groups. This indicates that the non-beetle herbivores show a pattern different from beetles when the quantity of cut stumps is increased. On average, there are more cut stumps in the old managed forests compared to old near-natural forests (Table 3). However, there is not a significant difference between old managed or old near-natural forests sites. This indicates that there are gaps in the homogenous old managed forests as well. In addition, sun-loving insects may be favoured by the gaps. It is known from the ALS-study that old near-natural forests have more variation in gap size and larger gaps. This might indicate that some of the non-beetle herbivorous insects favour larger gaps. When gaps are created, and thus more light is provided, plants and shade intolerant trees are favoured by higher temperature and moisture (Yamamoto 2000). In addition, sun-loving insects may be favoured. More light exposure will give rise to more biomass on the forest floor, and may be of importance for pollinators and insects searching for forage (Ødegaard et al. 2015b).

The number of non-beetle herbivorous insects was shown to increase with more variation in trunk diameter. Investigation of each group with significant environmental variables (Figure 11) showed that the number of true bugs (Heteroptera) was near significant with variation in trunk diameter. Many herbivorous true bugs species are associated with trees and bushes, where they suck the sap from foliage or flowers (Ødegaard & Coulianos 1998). True bugs are frequently more abundant in buffer zones and openings than in dense shady forests, since true bugs are sun-loving (Ødegaard & Coulianos 1998). This supports that forest structures with more gaps are suitable for herbivorous true bugs. Since the old managed forest sites are beginning to reach maturity, the forests are not so dense as when they were younger, and gaps will be present. For this reason, in both forest types, it is expected to find biomass that is important as forage.

Vegetation types were not included in the statistical analysis, due to small variation of vegetation types in the forests investigated, where Bilberry spruce forest dominated. However, we know from the ALS-study that old near-natural forests have a more developed shrub-layer, providing more niches on the forest floor. According to Lawton (1983), Strong et al. (1984) and Lewinsohn et al. (2005), species richness increases with complexity of plants. Thus, trees inhabit more species than bushes and herbs, while shrubs inhabit more species than herbs.

The majority of herbivorous insect orders are host specific, in particular Hymenoptera, Hemiptera, and Lepidoptera. Since old near-natural forests are more open and have a more developed shrub-layer, it would be expected to find more specialized species in the gap-habitats with younger biomass in several successional stages. Young shots and leaves, are the most defended by plants because of the high nutritional value (Gullan & Cranston 2014). Hence, the insects feeding on young shots are to be the most specialized because of the high levels of toxic secondary plant substances than mature leaves (Schoonhoven et al. 2005). Polyphagous species prefer mature leaves of their various host plants (Schoonhoven et al. 2005). Therefore, it would be expected to find more polyphagous insects in old managed forests. For many species of butterflies living on annual plants, it is especially important that the host plant returns every year (Ehnström & Waldén 1986). Particularly during the larval development resource availability is crucial. More openness will provide more biomass on the forest floor, and in forests with long continuity of forest biomass, gaps will be important for some species of butterflies, except for butterflies that are not sun-loving.

However, butterflies living in the forest habitats mostly forage on leaves and needles, not being dependent on the age of the forest (Aarvik 2015), but a small group is dependent on old growth forest (Aarvik 2015). In young mature forest, with near-significant forest development class, it is known that trees are under growth, while for trees in old mature forest the growth has culminated (Solbraa 2001). These might favour species favouring trees in different successional stages. A clear connection with the other environmental variables (Figure 10) implies that a combination of several environmental factors explains the presence of herbivorous insects, and that the forest development class alone is not able to explain the increase of herbivorous insects in these areas.

Data quality and further studies

The present study, being a subplot of 60 study sites, is not wide enough to detect the difference in herbivorous insect diversity between the two forest types. A larger number of sites, and a survey over several years, would probably show a clearer difference, and would increase the robustness of the results.

Aphids, which are among the most abundant insects on plants, always will have a higher number of individuals because of their asexual reproduction. An analysis without this response variable would increase the robustness. However, there is limited information about the superfamily Aphidoidae living in boreal forest, and there is a need of further studies on the influence of Aphids.

None of the environmental variables were able to predict the abundance of wood ants. Pitfall traps do not provide a convenient way to compare the forest types with respect to the abundance of wood ants. Registration of wood ants may be heavily influenced by the location of the pitfall traps, for example if traps were located in the pathway to an ant colony. Counting the number of ant colonies at every site may be a better way in further studies for calculation of the abundance of wood ants.

In this study, species requirements were partly unknown, since identification mostly was limited to family level and not to species level for non-beetle herbivorous insects. I would recommend to identify all herbivorous insects to species level.

In this study sample data of ground-dwelling and flying insects was pooled. A further, separate, study on ground-dwelling insects and their forage requirements is needed. Herbivorous insects need places to lay and hide eggs, and to feed. The availability of twigs may be important. In this study I did not separate results in this respect, but investigation of the aspects of twigs can be of interest.

Interesting field methods for further investigation of species on living trees would be to test beating technique on branches (Porcel et al. 2013), and to use a vacuum aspirator on branches, trunks and canopy of trees (Henderson & Whitaker 1977).

5 Conclusion and management implications

In this study, no significant difference in herbivorous diversity between old near-natural and old managed forest was found. However, the following environmental variables were identified as being important for herbivorous insects: elevation, number of cut stumps, variation in crown height, variation in trunk diameter, variation in age and forest development class, young mature. None of the explanatory variables were able to describe any difference in the number of wood ants. A larger number of sites, and a survey over several years, would increase the robustness of the results. The forest area contains a mosaic of old near-natural and old managed forest, which may make it difficult to detect differences in herbivorous insect diversity. Many forest dwelling species have a wide habitat range and will therefore be found in both old near-natural and old managed forests stands. The near-natural forest stand will eventually turn into true natural forest might potentially contain important characteristics favourable for many herbivorous insects.

Management implications

Remnants of selectively cut forest stands will develop into true natural forest ecosystems with important structures for old-growth forest species (Jönsson et al. 2009; Vandekerkhove et al. 2012). In Norway, there is only 1,3 % of natural forests remaining, and most of these forests are expected to disappear within the next 30-40 years (Rolstad & Storaunet 2015). It is therefore especially important to protect these natural forests habitats for forest dwelling species which prefer continuous forest habitats in the future. The establishment for additional nature reserves might be helpful in preserving natural dynamics and developing diverse forests.

There is a need to mimic natural forest dynamics in future extraction of forest resources. Canopy gaps are expected to inhabit many herbivorous insect species and taking this into account in forest management is therefore important. Furthermore, an increasing establishment of woodland key habitats within the managed forests can serve as life-boats for old forest species.

There is still a need for better knowledge about insect diversity in boreal forest. There are many species groups of which there is little knowledge about and a further study about the occurrence of species, habitat requirements and taxonomy is needed to value forest biodiversity.

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7 Appendix

Table 10: One and one variables ANOVA of herbivorous insects group by significant environmental variables. + = positive relationship, green = significant values

Variable	Bombus	Vespidae	Symphyta	Lepidoptera	Aphididae	Cicadellidae	Heterotera
Elevation	NS	NS	NS	NS	+	NS	NS
CutStumps	NS	NS	NS	NS	NS	NS	NS
TrunkDiam	NS	NS	NS	NS	NS	NS	+

Table 11: Multicollinarity test of the environmental variables. The threshold level for collinarity was >0,5.

	DevelopmentClass	Elevation	CutStumps	Basal area	TrunkDiameter (mean)	TrunkDiameter (var)	TreeHeight (var)	CrownHeigh (var)	Age (var)
DevelopmentClass	1,0000	0,4149	0,1880	0,0170	0,0993	0,2235	0,2248	-0,2295	0,1057
Elevation	0,4149	1,0000	-0,2296	-0,2411	0,2230	0,3384	0,1133	-0,4607	0,1960
CutStumps	0,1880	-0,2296	1,0000	0,1425	-0,4650	-0,3674	-0,2310	0,0128	-0,1314
Basal area	0,0170	-0,2411	0,1425	1,0000	-0,1053	-0,0333	-0,1360	0,5507	-0,2144
TrunkDiameter (mean)	0,0993	0,2230	-0,4650	-0,1053	1,0000	0,7521	0,2898	0,1779	0,2843
TrunkDiameter (var)	0,2235	0,3384	-0,3674	-0,0333	0,7521	1,0000	0,2496	0,0650	0,2584
TreeHeight (var)	0,2248	0,1133	-0,2310	-0,1360	0,2898	0,2496	1,0000	0,2543	-0,0418
CrownHeigh (var)	-0,2295	-0,4607	0,0128	0,5507	0,1779	0,0650	0,2543	1,0000	-0,3014
Age (var)	0,1057	0,1960	-0,1314	-0,2144	0,2843	0,2584	-0,0418	-0,3014	1,0000

Table 12: The distribution of ants. The three periods we emptied the traps are pooled into "mean".

Site	**Forest Type**	**Mean**
N1	OldNatural	2
N2	OldNatural	3
N3	OldNatural	1
N4	OldNatural	1
N5	OldNatural	1
N6	OldNatural	1
N8	OldNatural	1
N9	OldNatural	2
N11	OldNatural	1
N12	OldNatural	2
N13	OldNatural	0
N16	OldNatural	1
N19	OldNatural	2
N20	OldNatural	2
N21	OldNatural	0
K3	OldManaged	2
K4	OldManaged	1
K9	OldManaged	1
K10	OldManaged	1
K11	OldManaged	0
K12	OldManaged	2
K13	OldManaged	2
K15	OldManaged	0
K16	OldManaged	0
K17	OldManaged	2
K18	OldManaged	2
K21	OldManaged	1
K23	OldManaged	3
K25	OldManaged	2

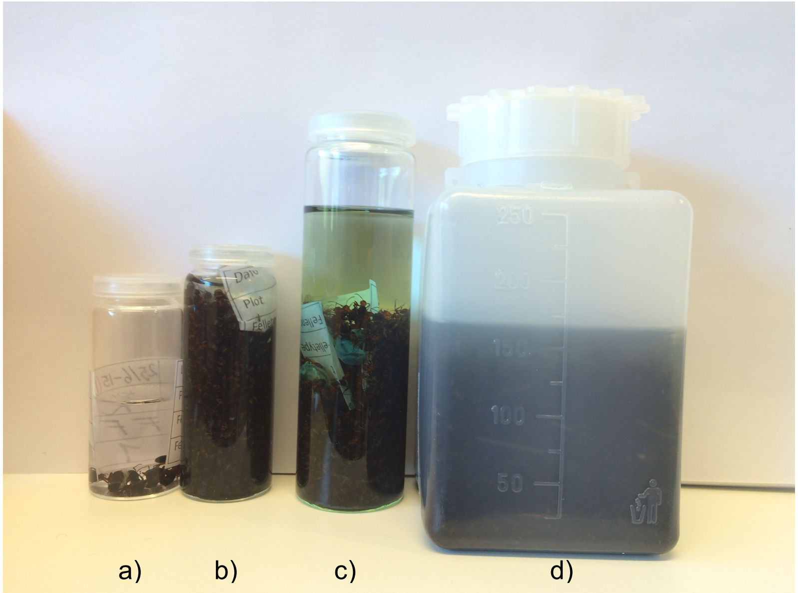

Figure 13: Number of ants estimated by volume. Small (a) Medium (b) and (c), and Large (d)

The forest floor vegetation in old near-natural forests consisted of two forest types: Blueberry spruce forest (14 stands) and heath forest (one stand). Four forest types represented the old managed forests: Blueberry spruce forest (9 stands), swamp spruce forest (one stand), low-fern spruce forest (two stands) and heath forest (one stand).

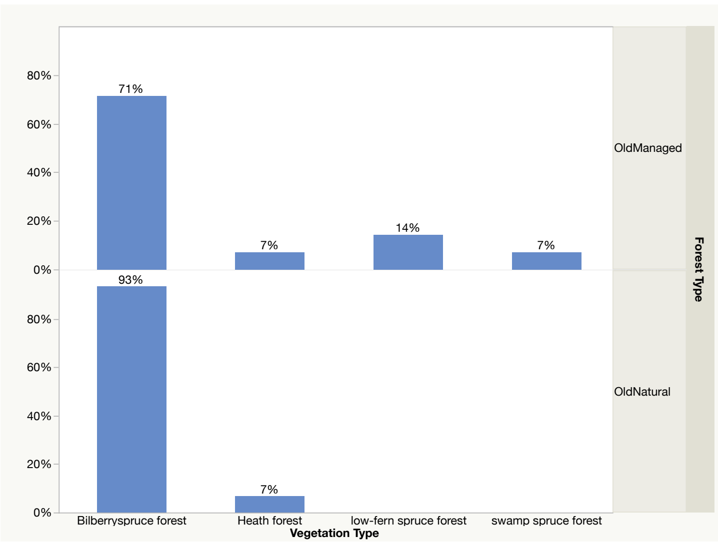

Figure 14: Vegetation types in old managed and old natural forest sites. The percentage is how much of the forest type is represented of each vegetation type.

Table 13: Environmental variables used in the statistical analysis

Site	Forest Type	Vegetation Type	Forest Dev	Elevation	Cut stumps	Basal area	TrunkDiam Var	TrunkDiam Mean	TreeHeight Var	CrownHeight Var	Age Var
N1	OldNatural	Bilberryspruceforest	4	518,6939	23	15	32,42	23,36	5,72	1,3	991
N2	OldNatural	Bilberryspruceforest	4	734	18	17	57,95	22,4	5,57	0,42	1125,33
N3	OldNatural	Bilberryspruceforest	4	719,7871	8	14	118,53	25,86	5,53	0,15	661,33
N4	OldNatural	Heathforest	4	739,5809	2	11	46,41	25,03	6,78	0,09	834,33
N5	OldNatural	Bilberryspruceforest	4	537,9334	21	32	154,56	30,41	14,7	14,82	101,33
N6	OldNatural	Bilberryspruceforest	4	566,7582	37	32	43,63	23,32	11,79	4,44	93
N8	OldNatural	Bilberryspruceforest	4	705,4359	2	23	94,27	27,69	7,18	2,6	156,33
N9	OldNatural	Bilberryspruceforest	4	710,8817	4	20	207,91	29,11	9,49	0,31	2092
N11	OldNatural	Bilberryspruceforest	4	499,9643	16	19	76,26	23,52	10,17	1,66	3545,33
N12	OldNatural	Bilberryspruceforest	5	665,5799	20	19	210,74	33,98	7,84	1,54	229,33
N13	OldNatural	Bilberryspruceforest	5	773,9393	4	34	105,14	27,83	6,9	2,17	457,33
N16	OldNatural	Bilberryspruceforest	5	664,6814	1	18	166,85	27,82	14,01	1,59	331
N19	OldNatural	Bilberryspruceforest	5	534,2993	19	28	162,17	24,66	14,77	3,6	305,33
N20	OldNatural	Bilberryspruceforest	5	674,0449	17	21	111,03	29,57	3,35	0,18	5262,33
N21	OldNatural	Bilberryspruceforest	5	681,5268	16	19	68,13	24,69	4,08	0,95	1552
K3	OldManaged	Lowfernspruceforest	4	636	0	39	37,58	22,55	8,02	5,54	100,33
K4	OldManaged	swampspruceforest	4	632	30	19	39,18	22,01	4,35	0,46	226,33
K9	OldManaged	Bilberryspruceforest	4	527	11	20	33,82	23,57	12,37	4,85	39
K10	OldManaged	Bilberryspruceforest	4	417	19	24	34,89	26,77	3,76	2,6	22,33
K11	OldManaged	Bilberryspruceforest	4	392	20	19	21,31	22,85	4,77	3,86	22,33
K12	OldManaged	Bilberryspruceforest	4	395	12	23	28,96	23,99	6,47	6,6	1
K13	OldManaged	Bilberryspruceforest	4	519	16	27	47,24	17,37	6,12	1,69	19
K15	OldManaged	Lowfernspruceforest	4	434	12	27	32,44	24,25	3,69	3,51	30,33
K16	OldManaged	Bilberryspruceforest	5	644	12	28	91,78	30,42	28,61	5,27	1089,33
K17	OldManaged	Bilberryspruceforest	5	685	40	25	32,72	20,45	5,16	0,79	33,33
K18	OldManaged	Bilberryspruceforest	5	697	19	18	55,02	25,5	4,28	0,27	408,33
K21	OldManaged	Bilberryspruceforest	5	544	36	38	14,77	15,37	1,46	3,81	27
K23	OldManaged	Bilberryspruceforest	5	690	31	15	2,26	17,27	1,74	0,19	24,5
K25	OldManaged	Heathforest	5	691	11	9	67,56	24,47	41,83	1,94	350,33

Table 14: Distribution of herbivore beetles caught.

Site	ForestType	Total Species richness	Total Abundance	Species/Window	Species/Pitfall	Abundance/Window	Abundance/Pitfall
N1	OldNatural	3	3	2	1	2	1
N2	OldNatural	3	4	1	2	1	3
N3	OldNatural	5	5	1	4	1	4
N4	OldNatural	7	7	4	3	4	3
N5	OldNatural	8	64	0	8	0	64
N6	OldNatural	7	9	4	3	4	5
N8	OldNatural	10	36	2	8	4	32
N9	OldNatural	4	5	1	3	1	4
N11	OldNatural	5	5	2	3	2	3
N12	OldNatural	2	2	0	2	0	2
N13	OldNatural	2	2	1	1	1	1
N16	OldNatural	0	0	0	0	0	0
N19	OldNatural	8	27	0	8	0	27
N20	OldNatural	1	1	0	1	0	1
N21	OldNatural	0	0	0	0	0	0
K3	OldManaged	7	10	2	5	2	8
K4	OldManaged	1	1	0	1	0	1
K9	OldManaged	10	26	2	8	2	24
K10	OldManaged	11	38	3	8	4	34
K11	OldManaged	6	8	4	2	6	2
K12	OldManaged	9	47	4	5	7	40
K13	OldManaged	9	15	0	9	0	15
K15	OldManaged	3	10	0	3	0	10
K16	OldManaged	3	11	0	3	0	11
K17	OldManaged	1	1	0	1	0	1
K18	OldManaged	3	3	0	3	0	3
K21	OldManaged	10	24	1	9	1	23
K23	OldManaged	5	5	3	2	3	2
K25	OldManaged	8	19	1	7	1	18

Table 15: Total number of non-beetle herbivore insects (Bombus, Vespidae, Symphyta, Lepidoptera, Heteroptera, Aphididae and Cicadellidae) caught per site.

Site	Forest Type	Abundance/window	Abundance/pitfall	Total abundance
N1	OldNatural	40	9	49
N2	OldNatural	57	3	60
N3	OldNatural	57	10	67
N4	OldNatural	17	17	34
N5	OldNatural	17	8	25
N6	OldNatural	28	7	35
N8	OldNatural	10	3	13
N9	OldNatural	55	16	71
N11	OldNatural	19	4	23
N12	OldNatural	60	1	61
N13	OldNatural	12	1	13
N16	OldNatural	12	0	12
N19	OldNatural	20	30	50
N20	OldNatural	28	2	30
N21	OldNatural	19	0	19
K3	OldManaged	38	3	41
K4	OldManaged	22	4	26
K9	OldManaged	44	22	66
K10	OldManaged	6	1	7
K11	OldManaged	10	3	13
K12	OldManaged	6	0	6
K13	OldManaged	19	13	32
K15	OldManaged	9	2	11
K16	OldManaged	2	0	2
K17	OldManaged	28	5	33
K18	OldManaged	52	10	62
K21	OldManaged	19	2	21
K23	OldManaged	46	0	46
K25	OldManaged	34	11	45

Table 16: The distribution of each group of non-beetle herbivorous insects.

Site	Bombus	Vespidae	Symphyta	Lepidoptera	Heteroptera	Aphididae	Cicadellidae	Forest Type	Vegetation type	Elevation
N1	3	0	0	2	8	34	2	OldNatural	Bilberryspruceforest	518,6939
N2	0	1	0	2	0	53	4	OldNatural	Bilberryspruceforest	734
N3	0	0	0	5	4	48	10	OldNatural	Bilberryspruceforest	719,7871
N4	4	0	0	0	4	19	7	OldNatural	Heathforest	739,5809
N5	1	0	0	3	4	16	1	OldNatural	Bilberryspruceforest	537,9334
N6	1	1	0	1	4	28	0	OldNatural	Bilberryspruceforest	566,7582
N8	0	1	1	0	2	8	1	OldNatural	Bilberryspruceforest	705,4359
N9	4	0	1	0	0	66	0	OldNatural	Bilberryspruceforest	710,8817
N11	3	1	4	0	3	11	1	OldNatural	Bilberryspruceforest	499,9643
N12	0	0	1	0	0	59	1	OldNatural	Bilberryspruceforest	665,5799
N13	1	1	3	0	0	8	0	OldNatural	Bilberryspruceforest	773,9393
N16	2	0	0	3	0	7	0	OldNatural	Bilberryspruceforest	664,6814
N19	1	0	1	1	2	44	1	OldNatural	Bilberryspruceforest	534,2993
N20	1	0	0	1	1	27	0	OldNatural	Bilberryspruceforest	674,0449
N21	0	0	1	1	4	11	2	OldNatural	Bilberryspruceforest	681,5268
K3	1	0	0	0	5	35	0	OldManaged	lowfernspruceforest	636
K4	7	0	0	0	1	12	6	OldManaged	swampspruceforest	632
K9	1	0	2	2	4	46	11	OldManaged	Bilberryspruceforest	527
K10	0	0	0	2	5	0	0	OldManaged	Bilberryspruceforest	417
K11	0	0	0	0	3	8	2	OldManaged	Bilberryspruceforest	392
K12	1	0	0	0	0	5	0	OldManaged	Bilberryspruceforest	395
K13	0	0	2	1	4	16	9	OldManaged	Bilberryspruceforest	519
K15	1	0	0	0	3	6	1	OldManaged	lowfernspruceforest	434
K16	0	0	0	0	1	0	1	OldManaged	Bilberryspruceforest	644
K17	2	0	1	2	0	23	5	OldManaged	Bilberryspruceforest	685
K18	5	4	1	10	1	35	6	OldManaged	Bilberryspruceforest	697
K21	0	0	1	0	4	13	3	OldManaged	Bilberryspruceforest	544
K23	1	0	0	1	0	35	9	OldManaged	Bilberryspruceforest	690
K25	3	1	1	2	1	22	15	OldManaged	Heathforest	691

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