Preface

Insects have fascinated me from an early age, and I have used countless of hours chasing butterflies, collecting beetles and digging in the muddy bottom of the pound in my parents garden, hunting for new discoveries. My fascination and curiosity for the diversity and complexity of insect communities has increased during my studies at the Norwegian University of Life Sciences (NMBU), and has led me to choose a topic within entomology for my master thesis.

My work is based on a study that was started in 2014 by Leonie Gough, and is a collaboration with the *Habitat fragmentation and Pathways to Extinction in dead-wood dependent fungi* (PATHEXT) by Jenni Nordén and Karl-Henrik Larsson at the University of Oslo. The purposes of this study was to use the fungi and dead wood data from the PATHEXT to explain patterns of species richness and resource preferences of saproxylic insects.

I would like to thank my supervisors, Tone Birkemoe and Anne Sverdrup-Thygeson, for all the help and guidance they have given me. They have followed the development of the work from an early point, and have sheared of their knowledge at all stages of the process. Our discussion group, with master student Ranjeni Sivasubramaniam, has helped me to collect my thoughts, and the feedback from Ranjeni has encourage me during the writing. I would also like to thank Jenni Nordén, for sharing her data from the PATHEXT project with me. Thanks to Leonie Gough and Adrian Rasmussen for their contribution in the collection of data, and Sindre Ligaard, Lars Ove Hansen and Csaba Thuroczy for the species identification of the beetles and parasitoid wasps.

Lastly, I would like to thank my family and friends who have corrected my English, and put up with me during this past year.

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Abstract

Many saproxylic insects are threatened by extinction, and a decline in the saproxylic species has been observed since the 1800s. The loss of areas of old-growth forest, fragmentation and the decline in volume of dead wood in managed boreal forests, have been found as important reasons for the observed decline.

The purpose of this study was to investigate whether or not the size of old-growth forest fragments affects the species richness of different saproxylic insect groups, and to find what environmental variables best explain the species richness of these different insect groups. Such information is important for further conservation work.

The insects were collected by window traps and by rearing of insects from sporocarps of *Fomitopsis pinicola*. The collected insects were divided into the different insect groups; saproxylic beetles, fungivorous beetles (a subset of the saproxylic beetles), reared beetles species, parasitoid wasp species and hyperparasitoid wasp species. The parasitoid and hyperparasitoid wasps represented higher trophic level than the other insect groups.

The study showed that the species richness of the saproxylic insect groups was either the same or higher in the small forest fragments, compared to the large forest fragments.

The species richness of each insect groups was best explained by different environmental variables: The number of saproxylic beetle species increased with an increase in volume of dead wood, while at the same time it decreased with an increase in polypore diversity. The species richness of the fungivorous beetle subset increased with the polypore hymenophore area. The number of beetle species was highest in the most decomposed sporocarps, compared to the least decomposed ones. The species richness of parasitoid wasps was higher in decomposition class II sporocarps, compared to decomposition class I sporocarps. The species richness of parasitoid wasps also increased with the number of beetles present in the sporocarps.

It was concluded that large and continuous old-growth forests should be prioritizes in the conservation of threatened saproxylic insects. Forests with a high diversity of dead wood substrates and wood-decomposing fungi supports a high diversity of saproxylic insects, and should also hold a high value for the conservation of saproxylic insects.

Sammendrag

Mange saproxyle insekter er truet med å dø ut, og en nedgang i disse artene har vært observert siden 1800-tallet. Tap av arealer med gammel skog, fragmentering og nedgangen i mengde død ved i skogbruksområder er noen av grunnene til denne nedgangen.

Hensikten med denne studien var å undersøke om størrelse på gammelskogområder har en påvirkning på artsrikheten av ulike grupper av saproxyle insekter, og å finne hvilke miljøvariabler som er viktigst for å beskrive artsrikheten til disse ulike gruppene.

Insektene ble samlet inn fra vindusfeller og fra fruktlegemer av *Fomitopsis pinicola*. De innsamlede insektene ble delt inn i de ulike insektsgruppene; saproxyle biller, soppspisende biller (en undergruppe av de saproxyle billene), klekkede biller, snylteveps og hyperparasitoide snylteveps. Snyltevepsen og de hyperparasitoide snyltevepsene representerte høyere trofiske nivåer enn de øvrige artsgruppene.

Studien viste at det var like mange eller flere billearter per arealenhet i de små skogsområdene. I forhold til i de store.

Antallet av arter i de ulike insektsgruppene ble best beskrevet ved hjelp av ulike miljøvariables: Antall arter av saproxyle biller økte med mengde død ved, og på samme tid sank med økende polypore diversitet. Antall arter av fungivore biller økte med økende pore-overflate-areal av polypore sopper. Det var flere arter av biller i de sterkest nedbrutte fruktlegemene, i forhold til de minst nedbrutte. Det var flere arter av snylteveps i fruktlegemer i nedbrytningsfase II, sammenlignet med nedbrytningsfase I. Antall arter av snylteveps økte også med mengden av biller til stede i fruktlegemene.

Det ble konkludert at store sammenhengende skogsområder av gammel skog burde prioriteres ved videre bevaringstiltak for truede saproxyle insekter. Skogsområder med en høy diversitet av død ved og råtesopp har en høy diversitet av saproxyle insekter, og har en høy verdi for videre bevaring av disse artene.

Contents:

1. Introduction

The purpose of this study was to investigate the effect of size of old-growth forests on the species richness of beetles and parasitoid wasps, and to find what environmental variables best explain the species richness of different groups of these insects.

The size and design of nature reserves have been a common topic in conservation biology for several decades (Noss & Cooperrider 1994). A common question has been: What size is the optimal size of a reserve when the aim is to conserve the diversity of species within a specific ecosystem for the future? The development of the classic theory of island biogeography by MacArthur and Wilson (1967) and Richard Levins metapopulation theory in the 1970s (Hanski 1999) have contributed to the understanding of the relation between the size, quality and distribution of habitats, and the persistence and extinction of species and populations in a fragmented landscape.

Diamond (1975) used the classical island biogeography theory to form different geometric principles in evaluating the best shape and size of reserves. These principles suggest that large forest fragments would have a higher species richness per unit area than small forest fragments. The mechanism behind this is that large reserves are larger in size. The available resources in large reserves is higher, following the habitat heterogeneity hypothesis, and can support larger populations of species (He & Legendre 1996). Larger populations are less prone to stochastic and deterministic extinction. Larger reserves are also assumed to have a higher immigration rate and low emigration rate. This is because it is easier to reach a large reserve by chance, during migration. It is also easier to reach the edge when dispersing inside a small reserve. The degree of isolation, and distance between the reserves is important for the migration patterns between the reserves.

The metapopulation theory is further building on many of the same ideas from the island biogeography, but this theory focuses on the connections between, and the importance of, different local populations for the viability of the species richness on a landscape level (Hanski 1999; Hanski 2001). Habitat patches are often divided into "sinks" or "sources" to describe the function and quality of the habitats for the local populations, in a metapopulation. Small and isolated habitats are more likely to be a "sink" than a "source" in the metapopulation (Gustafson & Gardner 1996; Kindvall & Petersson 2000). Large reserves also have less edge effect, with a more stable microclimate, and are more robust against large natural disturbances (Berntsen et al. 2010; Noss & Cooperrider 1994; Primack 2010).

Arguments building on the theory from the island biogeography and metapopulation theory are commonly used to claim that large reserves have a generally higher conservation value, especially in a fragmented landscape (Berntsen et al. 2010; Noss & Cooperrider 1994; Soule & Simberloff 1986). The discussion about what size of forest reserves should be prioritized is still going on today, and there has been a resent increased acknowledge of the potential conservation value of small sized habitat fragments (Götmark & Thorell 2003; Schwartz & van Mantgem 1997).

How vulnerable a species is to fragmentation depends on different species-specific traits, as their habitat and niche preference, dispersion ability, competitive ability, population density and life strategy (Diamond 1975; Schwartz 1999; Shmida & Wilson 1985; Sverdrup-Thygeson & Lindenmayer 2003). Species that depend on patchy resources, with a low dispersal ability and low reproductive ability will be more vulnerable to fragmentation and have a higher extinction risk (Hanski 1999). It is also thought that the specialist species of higher trophic levels are more vulnerable to habitat changes and fragmentation, compared to generalist species at lower trophic levels (Holt et al. 1999; Jonsell et al. 1999; Kruess & Tscharntke 2000; Pimm 1991; Shaw & Hochberg 2001).

Saproxylic species are species that depend on dead wood, dying trees or other saproxylic organisms during one of their life stages (Stokland et al. 2012). The decline in saproxylic species in the boreal forests has been observed since the 1800s, and many of these species are now highly threatened (Davies et al. 2008; Siitonen 2012b). The main cause of the decline of saproxylic species are the loss of areas of old-growth forests, fragmentation and the decline in volume and size of dead wood in managed boreal forests (Bader et al. 1995; Esseen et al. 1997; Hottola & Siitonen 2008; Kouki et al. 2001; Penttilä et al. 2004; Schigel 2012; Siitonen 2001; Siitonen 2012b).

Today only 2.4 percentage of the total forest area in Norway are more than 160 years, and these forests are highly fragmented (Berntsen et al. 2010; Stokland et al. 2014). Almost half of the species in the Norwegian 2010 Red List for species are forest-dwelling species, and many of these are saproxylic insects (Berntsen et al. 2010; Økland et al. 1996). A national goal in Norway is to preserve all ecosystems, their ecosystem services and to hinder extinction of species (Prop. 1 S (2015-2016), p. 16). To preserve the saproxylic species and the forest ecosystems they are a part of, it is necessary to understand their habitat requirements and to evaluate which spatial scales these systems are dependent on.

The old-growth spruce forests, and species that live in and are dependent on these forests, are protected by creating forest reserves, or woodland key habitats (Blindheim et al. 2011; Direktoratet for naturforvaltning 2007). Areas of old-growth spruce forests are also included in several national parks and landscape protection sites (Blindheim et al. 2011). Woodland key habitats are a conservation tool used to conserve the biodiversity in productive forests. They are small set-asides (average size of 21.3 ha) of forest areas that are especially important for the biodiversity in the forest landscape, or areas with high species richness or presence of threatened species (Direktoratet for naturforvaltning 2007; Timonen et al. 2010).

Dead wood is a hotspot for biodiversity (Schigel 2012; Thunes et al. 2000), and an important resource for many organisms in the boreal forests (Komonen 2001; Kouki et al. 2001; Stokland et al. 2012). The volume and quality of dead wood changes both temporally and spatially in the forest landscape, where trees dies, decomposes and disappears (Esseen et al. 1997; Jonsson 2012). Dead wood is both a direct resource for organism groups like wood decaying fungi and detritivorous insects, and an indirect resource for the insects that are dependent on the wood decaying fungi (fungivorous insects). Many of the organisms in dead wood have their own predators, parasitoids and hyperparasitoids (parasitoids that parasitize other parasitoid species). This makes the community rich with many trophic levels and species that are dependent on each other. (A'Bear et al. 2014; Schigel 2012; Stokland 2012a).

Some of the most important structural wood decayers in boreal forests are the polypores, a group of fungi under the phyla Basidiomycetes (Boddy et al. 2008). The polypores contribute to the nitrogen cycle in the boreal forests, through their decomposition of woody material. This is an important ecosystem service because nitrogen is an limiting resource in the boreal forest ecosystem, and is mostly found bound in the vegetation (Tamm 1991). Different polypore species grow on different woody substrates, like different tree species, dimensions, tree parts and decomposition stages (Hottola & Siitonen 2008; Stokland & Siitonen 2012). They have different enzymatic ability for decomposition of woody substrates, like white rot or brown rot, and some are pathogenic while others only grow on dead trees (Kauserud et al. 2008; Stokland 2012b; Stokland & Siitonen 2012). The different requirements for growth substrates makes the richness and diversity of polypores in a forest depend on the diversity of dead wood within the forest (Hottola & Siitonen 2008; Penttilä et al. 2004; Similä et al. 2006; Sippola et al. 2001; Sippola et al. 2004). At the same time the polypores themselves is an important vector that contribute to the production and diversity of dead wood (Stokland & Siitonen 2012).

Sporocarps of polypores are an important food and habitat source for many fungivorous insects, especially beetles (Heilmann-Clausen et al. 2015; Kaila 1993; Komonen 2003; Stokland 2012a), and represent a much more nutrient rich food source than wood (Martin 1979). The production and persistence of sporocarps varies between different polypore species (Schigel 2009). The persistence of sporocarps differ from short lived annual sporocarps to long lasting perennial sporocarps (Stokland & Siitonen 2012). Perennial sporocarps produce a new spore producing layer (hymenophore area/hymenial layer) every year, and grow larger as they become older (Siitonen 2012a; Thunes et al. 2000).

The main decomposer of Norway spruce (*Picea abies*) in boreal forests is the brown rot polypore *Fomitopsis pinicola* (Penttilä et al. 2004). This is also the most abundant polypore species and it mainly grow on dead or weakened spruce (Hågvar 1999). The sporocarps of *F. pinicola* are perennial and can host several generations of species (Grove 2002). Many beetle species feed on the spores of *F. pinicola*, and beetles in the Ciidae family are commonly found in dead and decomposing sporocarps (Esseen et al. 1997).

Beetles constitutes a major part of the saproxylic insects (Franc et al. 2007). The species richness of the saproxylic beetles has been found to increase with the diversity, total volume and diameter of dead wood, and the richness of polypores (Martikainen et al. 2000; Ohlson et al. 1997; Similä et al. 2006; Økland et al. 1996). The saproxylic beetles belong to many different functional groups, like; detritivores, predators and fungivores (Stokland 2012a).

Saproxylic detritivorous beetles eat dead wood and the decomposing bacteria or fungi in the decaying wood. Bark- and wood-boring beetles are also included as detritivorous, even if they are species that may attack healthy trees (Stokland 2012a). Saproxylic predator beetles mainly hunt and eat larvae and pupae of other saproxylic species. They can be found in all parts of the tree, where detritivorous and fungivorous insects live. Some species have specialized on insects living under the bark, in galleries, or in sporocarps (Stokland 2012a). Fungivorous beetle species typically have their larvae development inside sporocarps (sporocarp feeders) but there are also mycelia feeders and spore feeders (Stokland 2012a).

The community composition and species richness of fungivorous beetle species in sporocarps changes over time, from species feeding upon the live spore-producing layers, to the more species rich communities in dead and decomposing sporocarps (Jonsell & Nordlander 2004; Siitonen 2012a; Thunes et al. 2000). Many fungivorous beetles are monophagous or oligophagous and are able to colonize live and recently dead sporocarps while the

polyphagous species are only able to colonize the sporocarps of polypores in later decay stages (Jonsell et al. 2001; Jonsell & Nordlander 2004; Stokland et al. 2012). This is most likely the result of the presence of secondary chemical compounds in the live sporocarps (Kukor and Martin (1987) as read in Jonsell & Nordlander 2004). Other factors like the hyphal structure, size, toughness and temporal durability, chemical composition, successional stage, moisture of fruiting body, and environmental conditions are also found to be important for the host selection by fungivorous species (Siitonen 2012a).

Common parasites of saproxylic insects are parasitoid wasps. Parasitoid wasps belong to one of the most species rich insect orders, the Hymenoptera (Gaston 1991). Many parasitoid wasps are host-specific and parasitize different types of invertebrates, at different live stages (Stokland 2012a). The occurrence of parasitoid wasps is believed to be dependent on the present and abundance of their host species and the habitat substrate of their hosts (Gibb et al. 2008; Hilszczański et al. 2005; Sullivan & Berisford 2004). Because many parasitoid wasps are specialized species at high trophic levels, they are believed to be sensitive to changes in their host species and might be more strongly affected by changes in the forest ecosystem (Holt et al. 1999; Roland & Taylor 1997; Shaw & Hochberg 2001).

There is a lot of studies focusing on the difference in saproxylic richness and species composition between old-growth and manged forests, and the environmental variables causing these differences (Grove 2002; Johansson et al. 2007). There has been less focus on the differences between old-growth forests of different sizes. There are few old-growth forests left in Fennoscandia (Esseen et al. 1997) and there are limited resources available for the conservation of saproxylic species. There is a need for more studies to widen our knowledge about the effect of forest size and the substrate requirement of different groups of saproxylic insects (Holt et al. 1999; Johansson et al. 2007; Jonsell et al. 2001; Similä et al. 2006). There is also a need to include higher trophic levels in these studies, because changes in the species community might only be detectable at the higher trophic levels. The presence of a high species richness of parasitoids might indicate a high diversity of other saproxylic species in the forest (Hilszczański et al. 2005; Jonsell et al. 1999; Komonen et al. 2000).

Knowledge about the effect of forest size and the effect of different environmental variables on the species richness of different functional groups of saproxylic insects would be useful in the selection of new conservation areas, and in the evaluation of the forests value for the conservation of threatened saproxylic insects.

In this study, I investigated the influence of size and forest structure of old-growth forests on the species richness of saproxylic insects. The influence of forest size was investigated by comparing the species richness of saproxylic insects between three large (> 50 hectare) and three small (< 50 hectare) Norway spruce (*Picea abies*) dominated old-growth forests in south-eastern Norway. The effect of forest structure on the species richness of saproxylic insects was evaluated by looking at the relationship between the species richness of saproxylic insects and several environmental variables reflecting different forest structures and resources.

I looked at five different saproxylic insect groups, where two insect groups were collected using window traps (window trap study), and the other three insect groups were reared from the sporocarps of *F. pinicola* (sporocarp study). The two different collection methods were chosen to be able to collect different functional groups of saproxylic insects and species at different trophic levels. The five different saproxylic insect groups were: Saproxylic beetles and fungivorous beetles (a subset of the saproxylic beetles) from the window trap study, and beetles, parasitoid wasps and hyperparasitoid wasps from the sporocarp study.

Figure 1 represent a conceptual framework of the relationship between the five different saproxylic insect groups and some of the different environmental variables included in this study.
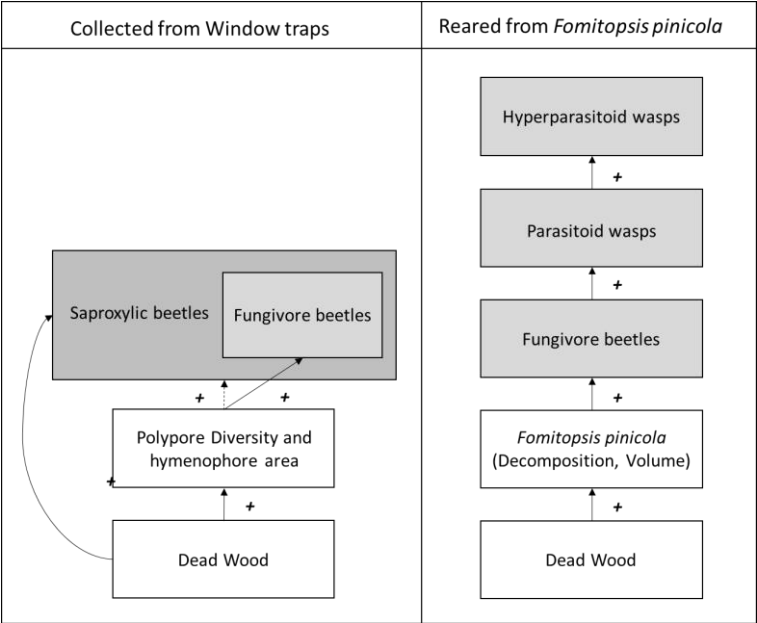
Figure 1: Conceptual framework of the two study systems. The figure at the left side show the system studied using window traps (window trap study) while the figure at the right side show the system studied by rearing insects from the sporocarps of F. pinicola (sporocarps study). The variables marked with grey colour are the different insect groups while the white variables are some of the environmental variables included in the study. The arrows and plus signs indicate the assumed relationships between the different variables in my two systems.

I will try to answer the two following research questions, for both the window trap study and the sporocarp study:

- Does the size of the old-growth forest fragments affect the species richness of the saproxylic insect groups?
- What environmental variables best explain the species richness of the saproxylic insect groups?

Concerning the first study question, I assume that the species community within the forest fragments follows the trends and mechanisms describe by the island biogeography and metapopulation theory (Diamond 1975; Hanski 1999; He & Legendre 1996; Rosenzweig 1995). I also assume that the species at higher trophic levels are more vulnerable to changes in the forests (Holt et al. 1999; Pimm 1991). Based on these hypothesis, the following predictions are made:

- There will be a higher species richness of saproxylic insects per unit area in the large forest fragments, compared to in the small forest fragments.
- The number of trophic levels will be lower in the small forest fragments, than in the large forest fragments.

For the second study question, I assume that the limiting factor for most saproxylic insects is related to their resource requirements (Jonsson 2012; Kouki et al. 2001). Different functional groups have different resource requirements, as described above. Based on this hypothesis the following predictions are made:

- The species richness of the different insect groups will be best describes by different environmental variables, and follow the relationships described in Figure 1.
- The volume of dead wood and the presence of polypores will affect the number of saproxylic beetles species present in the forests.
- The presence of polypores will affect the species richness of the fungivorous beetle subset.
- The quality and occurrence of *F. pinicola* sporocarps will affect the number of reared beetles present in the sporocarps.
- The abundance and presence of host species will affect the species richness of the parasitoid and hyperparasitoid wasps in the sporocarps.

2. Material and methods

2.1 Area description and study design

The study design was a block design with one large (>50 ha) and one small (<50 ha) old-growth forest situated near by each other in three different regions (2 forest sizes x three regions). The regions had an eastern, western and northern location in relation to the Oslo fjord, in the south-eastern part of Norway and the south-western part of Sweden (Table 1, Figure 2).

Table 1: Overview of the forest areas used in the study. The abbreviation, site name, location, forest size, set-aside type and establishment data is listed for each of the forest areas (Norwegian Environment Agency 2010; 1999; 2011; 2013; 2014; Swedish Forest Agency 2004).

Abbreviation	Site	Location	Size (ha)	Set-aside type	Date
EastLarge	Tjøstøl	Aremark, Østfold	432	Nature reserve	2013
EastSmall	Skee	Strömstad, Västra Götaland (SE)	5	Woodland key habitat	2004
WestLarge	Mørkvassjuvet	Drangedal, Telemark	2432	Nature reserve	2010
WestSmall	Sandalslia	Drangedal, Telemark	13	Woodland key habitat	1999
NorthLarge	Spålen-Katnosa	Jevnaker, Oppland	1844	Nature reserve	2014
NorthSmall	Rudskampen	Nannestad, Akershus	11	Woodland key habitat	2011

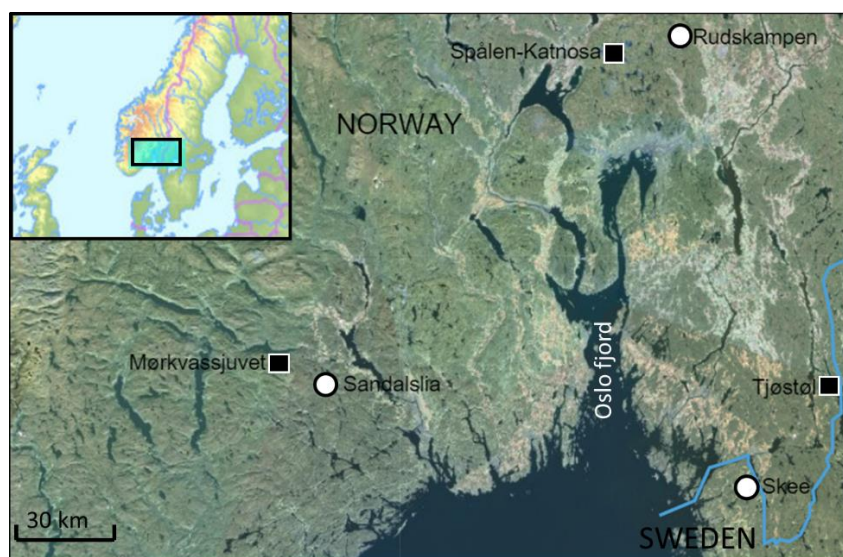

Figure 2: The geographical location of the six study sites; Tjøstøl, Skee, Mørkvassjuvet, Sandalslia, Spålen-Katnosa and Rudskampen. The large old-growth forest areas are marked with a black square, while the small old-growth forest areas are marked with a white circle. The study site Skee is located in Sweden, while the rest of the sites are in Norway (Norwegian Environmental Agency 2015).

The blocking for region was done to account for confounding factors and environmental differences between the regions. These forest pairs will be referred to as either the large or the small forest in the eastern, western or northern region, or by the abbreviations listed in Table 1, throughout this study. The vegetation zone was boreo-nemoral and middle boreal (Moen et al. 1998). All of the six forest areas were spruce dominated old-growth forests with a lot of dead wood (Norwegian Environmental Agency 2015; Svantesson 2012; Swedish Forest Agency 2004). All of the large forests were nature reserves, while the small forests were woodland key habitats (Table 1).

The data was collected from one 4 ha (200 x 200 meter) study plot in each of the forest. The same forests, and the same study plots, were also used in the *Habitat fragmentation and Pathways to Extinction in dead-wood dependent fungi* (PATHEXT) by Jenni Nordén and Karl-Henrik Larsson at the University of Oslo. The aim of PATHEXT is to identify the ecological processes of polypores and corticioids that determines their different reactions to forestry and fragmentation (Nordén 2012).

2.2. Sampling methods for the window trap study

The described sampling methods in the first paragraph was performed by Leonie Gough, while the part from the second paragraph until the end was performed by Marianne Hansen.

The collection of beetles in the forest landscapes was done using window traps. The window traps were made of two 40 x 60 cm plastic plates above a plastic funnel, and with a container filled with ethylene glycol and detergent mounted at the bottom of the trap. A total of five traps were evenly distributed within each of the 4 ha study plots. The traps were hanged in the vegetation approximately one meter above the ground, without direct contact with any trees. The traps were first put out in the field in mid May 2014 and emptied three times; mid June, mid July and mid August. The collected beetles were stored in collecting vials with 75% alcohol. It was not possible to place the window traps in the northern region in May, because of snow. In these two study plots the window traps were put out in the field in mid June, and emptied two times; mid July and mid August.

The collected beetles were identified to species by the expert Sindre Ligaard. The list of collected beetle species was divided into either saproxylic or non-saproxylic species using information collected from Dahlberg and Stokland (2004), Hyvärinen (2006), Köhler (2000) and the supplementary data from Seibold et al. (2014). The group of saproxylic beetle species was further divided into a subset of fungivorous beetle species based on the same databases.

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All development stages and feeding types were included in the grouping of species into saproxylic and fungivorous beetles. Threatened species were found using the Norwegian 2010 Red List for species (Kålås et al. 2010).

All of the beetle data from each trap was pooled for the analysis. This gave five independent measurements of the species richness of the saproxylic beetles and the fungivorous beetle subset, for each of the six study sites (5 traps x 6 sites).

2.2.1. Data adjustment

The traps in the northern region had a shorter time in the field with only two trapping periods, while the traps in the eastern and western regions had three trapping periods. The number of species of the saproxylic beetles and the fungivorous beetle subset from the northern region were adjusted to compensate for the data loss. This adjustment was done by calculating the percentage of species an extra trapping period would have contributed to in the dataset, based on the data set from the forest areas with three trapping periods:

First it was calculated how many more species in percentage was collected during three trapping periods, compared to two trapping periods. This was calculated for each trap in the eastern and western region, and the proportion was averaged across all traps. The data from EastSmall was excluded from the calculation as it represented an outlier. The average proportion of species was then used to calculate how many species was expected to be collected during three trapping periods for the traps in the northern region. This was done by dividing the number of species collected during two trapping periods on the calculated average proportion. The quality of this method was tested on the traps from the eastern and western regions. No significant difference between the predicted number of species and the original number of species was found (t-test, df = 8, p > 0,05), and the method was evaluated to be sufficient for the data adjustment.

The generated data was only used in the analysis, and in tables and figures showing the results of analysis. These generated data was not included when commenting on the forest sites total amount of beetles or beetle species.

2.3 Sampling methods for the sporocarp study

The described sampling methods in the first paragraph was performed by Leonie Gough and Adrian Rasmussen, while the part from the second paragraph until the end was performed by Marianne Hansen.

Beetles and parasitoid wasps were collected from dead sporocarps of *F. pinicola*. This was done by collecting as close to 40 dead sporocarps ($>20cm^3$) as could be found within the 4ha study plots. Several sporocarps were collected from the same log if only small sporocarps were found. These were then treated as one sporocarp throughout the study. The sporocarps were placed in individual rearing units made of cardboard cylinders with a plastic lid covering one of the ends and with fine mesh covering the other end. A collecting vial was fastened through the plastic lid (Figure 3). The rearing units were placed in a shed with natural outdoor climatic conditions (situated on Ås). The sporocarps were reared from the end of the summer 2014, until February 2015. The collecting vials were emptied once during October, and at the end of the rearing.
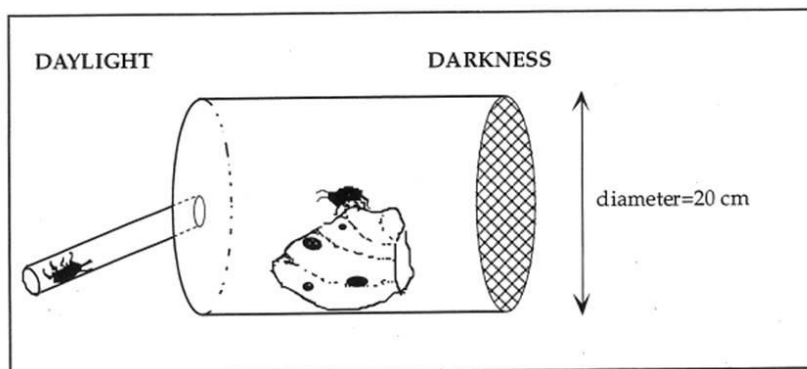
Figure 3: Illustration of a rearing unit used to collect emerging insects. The sporocarps are placed inside the dark cylinder. The emerging insects gets attracted by the daylight and ends up in the collecting vial (Sverdrup-Thygeson 1994).

After the rearing period, the sporocarps were brought to the lab. Here the sporocarps volume was measured using the formula: Volume = (length*width*hight) / 3 (Figure 4). The sporocarps degree of decomposition was estimated by dividing the sporocarps into three different classes (class I, II and III). Class I: Recently dead sporocarps with few signs of decomposition. Class II: Dead sporocarps with clear signs of insect activity, but still relatively complete. Class III: Heavily decomposed sporocarps, often with a darker colour (Figure 5). The different decomposition classes were modified from the description of polypore sporocarps five development stages by Graves (1960) as described by Siitonen (2012a). Lastly, the remaining insects (imago) in the sporocarps were collected by dissecting the sporocarps. The sporocarps were opened with the help of knife and axe.

Figure 4: Illustration of the measurements of the size of the sporocarps. From left to right: Length, Width and Height.

Figure 5: Examples of sporocarps representing the three different decomposition classes. From left to right: Decomposition class I, II and III.

The collected insects from the rearing and dissection of sporocarps were sorted in the lab and divided into beetles and parasitic wasps. The parasitic wasps were further divided into superfamily or family. The beetles and the parasitoid wasps were identified to species by the experts; Sindre Ligaard, Lars Ove Hansen and Csaba Thuroczy. The classification of threatened species was based on the Norwegian 2010 Red List for species (Kålås et al. 2010). The parasitoids were grouped into parasitoids or hyperparasitoids based on information collected from the Universal Chalciodidea Database (Nojes 2015) and the Norwegian biodiversity information centre (Artsdatabanken 2015).

There was too little data to treat the hyperparasitoid wasps as a separate group, so these were pooled together with the other parasitoid wasps for the analysis. The parasitoid wasps from NorthSmall were excluded from the final dataset, because many of the rearing units used on sporocarps from this forest area accidentally had nets with too large openings.

The number of collected sporocarps from the different forests was uneven, and ranging from 25 to 15 sporocarps. The final dataset used in the analysis was balanced by randomly choosing 15 sporocarps for each of the six forest areas. This gave 15 independent measurements of fungivorous beetle richness for each of the six study sites (15 sporocarps x 6 sites), and 15 independent measurements of parasitoid wasp richness for five of the study sites (15 sporocarps x 5 sites).

2.4. Environmental variables

Seven environmental variables at three different spatial levels were included in the analysis of the two study systems (table 2). These three different spatial levels were; the forest level, study plot level and sporocarps level.

The environmental variable at the forest level was the total size of the forest areas (ha). This data was collected from the Norwegian Environmental Agency (Naturbase) and the Swedish Forest Authority (Norwegian Environment Agency 2010; 1999; 2011; 2013; 2014; Swedish Forest Agency 2004).

The data used to calculate the variables at the study plot level was retrieved from the PATHEXT project. The PATHEXT fieldwork consisted of a dead wood survey and a sporocarp survey of the 4ha study plots. These surveys were done in October and November 2011. The volume of dead wood was measured within two 5x200m transects that crossed each other in the middle of the study plots in the dead wood survey (Nordén 2015). This data was used to calculate the volume of dead wood per ha of the study plots. All sporocarps on 60 spruce logs (diameter 20-40 cm) were recorded and their hymenophore area was measured within each plot in the sporocarp survey. All species that could be identified in the field were included in this study. The data from the sporocarp survey was used to calculate the variables; hymenophore area of polypores, hymenophore area of *F. pinicola*, and polypore diversity. The diversity of polypores was calculated using the Shannon's diversity index (H'):

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

where S is the species richness and p_i is the proportion of individuals belonging to the ith species, in the model.

The environmental variables at the sporocarp level describes the volume and decomposition class of the sporocarps, and the amount and richness of beetles in the sporocarps from the sporocarp study. How this was measured and estimated is described above, in the "Sampling methods for the sporocarp study".

Table 2: The environmental variables used in the analysis.Each variable is divided into spetial scale of the measurements, unit and study system.

Spatial scale	Variable	Unit	Variable in study system
Forest level	Total size of the forest	ha	Window trap and sporocarp study
Study plot level	Volume of dead wood per hectare	m^3/ha	Window trap and sporocarp study
	Polypore diversity	Shannon's H	Window trap
	Hymenophore area of polypores	cm^2/ha	Window trap
	Hymenophore area of *F. pinicola*	cm^2/ha	Sporocarp study
Sporocarp level	Volume of sporocarps	cm^3	Sporocarp study
	Degree of decomposition of sporocarps	I, II or III	Sporocarp study
	Number of beetle species per sporocarp	#species	Sporocarp study
	Number of beetles per sporocarp	#individuals	Sporocarp study

2.5 Statistical methods

The statistical analysis were performed using the statistical program JMP Pro 10.0 (SAS Institute Inc. 2012), and the significance level of all tests was $\alpha = 0.05$. The data was log-transformed if necessary to fulfil the requirements of normal distribution of the data.

The difference in species richness between the large and small sites within each region was tested using a t-test for equal or unequal variances. The data that did not follow a normal distribution was tested using a Chi Square test. The difference in richness of beetle and parasitoid wasp species between sporocarps of different decomposition classes was tested with a nonparametric comparison for each pair using a Wilcoxon test.

Generalized Linear Model (GLM; Poisson distribution, log link) was used to examine the relationship between the richness of species in the different insect groups and environmental variables in my study (Figure 1, Table 2). All combinations of variables were tested and significant models were found using the Pearson's Goodness-of-fit. The selection of the best model for each of the insect groups was based on the Akaike Information Criterion with a correlation for finite sample size (AICc), and only the best models were presented in the results. Correlations between the environmental variables used in the same GLM were tested using the Pearson's Product-Moment Correlation (r) (Appendix 2). It was a strong correlation ($r > 0.8$) between the polypore diversity and forest size (Appendix 2, Table 1), and these two

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variables were not used in the same regression models, to prevent collinearity. Alternative regression models to the GLM were tested to look for a better fit to the data, but these were rejected.

3. Results

3.1 Window trap study

In the window trap study a total of 1827 saproxylic beetles representing 158 different species were found. Of these saproxylic species a total of 50 species (298 beetles) were further classified as fungivorous. *Athous subfuscus* was the most abundant of all saproxylic beetle species (18%) while *Atomaria turgida* was the most abundant species within the subset of fungivorous beetle species (18%) (Appendix 4). Six of the saproxylic species were classified as near threatened (NT) in the Norwegian 2010 Red List for species, and three of these species were fungivorous (Kålås et al. 2010).

3.1.1. Difference in species richness between large and small old-growth forests

Opposite to the predictions, there was a higher species richness of saproxylic beetles in the small, compared to in the large forest in the eastern region (t = 3.23, df = 7.7, p = **0.013**) (Figure 6). The same pattern was indicated for the western region. No difference in species richness of the subset of fungivorous species was found between the forest areas within the three regions (Figure 7).
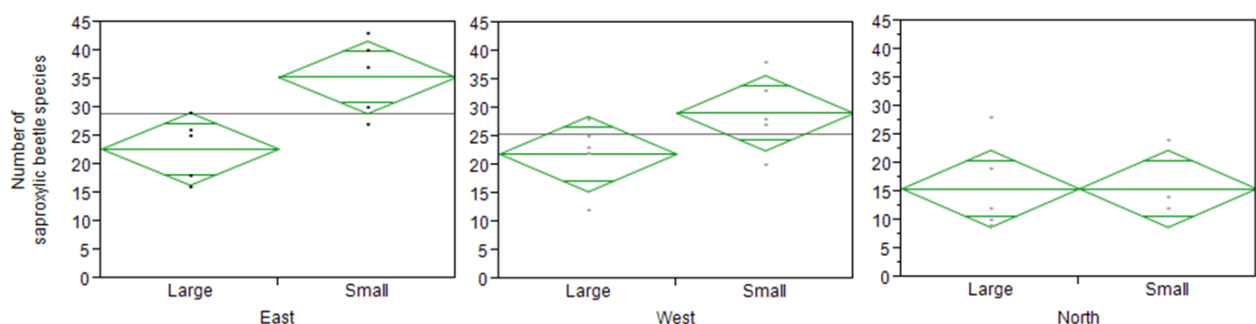

Figure 6: Difference in species richness of all saproxylic beetles between the large and small old-growth forests within the eastern, western and northern region respectively. The mean diamonds illustrates the sample mean and 95% confidence interval.
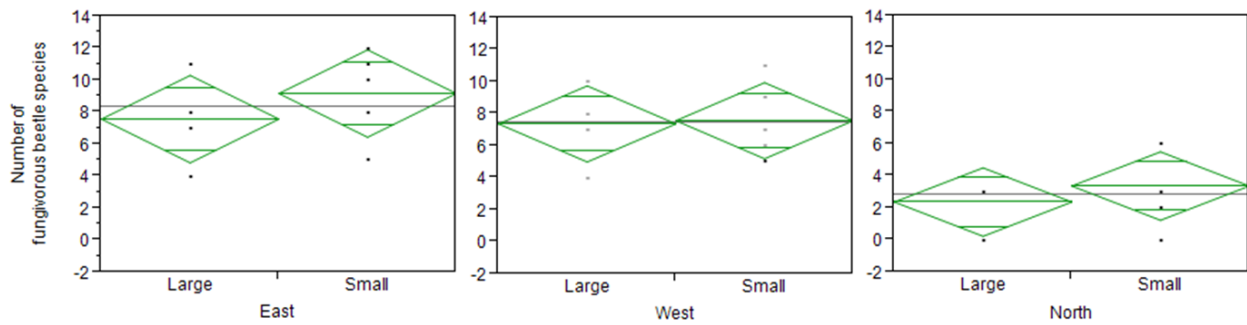
Figure 7: Difference in species richness of the fungivorous beetle subset between the large and small old-growth forests within the eastern, western and northern region respectively. The mean diamonds illustrates the sample mean and the 95% confidence interval.

3.1.2. Importance of environmental variables

A model using both the variables polypore diversity and dead wood best predicted the species richness of all saproxylic beetles (Table 3). The species richness had a positive relationship with the volume of dead wood, but at the same time a negative relationship with the polypore diversity (Table 3). The number of saproxylic beetle species increases with an increase in volume of dead wood, and decreases with an increasing polypore diversity. The species richness of the fungivorous beetle subset was best predicted by the hymenophore area of polypores (Table 4).

Table 3: The GLM that best explained the species richness of all saproxylic species. The total models p-value and df are listed at the top. The estimate, standard error, Chi Square-value and p-value are presented for each of the explanatory variables in the model. Significant p-values are in bold.

Variable	Estimate	Std. error	Chi Square	p-value
*Number of saproxylic beetles (Pearson Goodness-of-fit: **p = 0.001**, df = 26)*				
Polypore diversity	- 2.641	± 0.377	49.406	**<0.001**
Dead Wood	0.005	± 0.001	46.704	**<0.001**
Intercept	8.012	± 0.714	125.425	**<0.001**

Table 4: The GLM that best explained the species richness of the fungivorous beetle subset (lowest AICc). The total models p-value and df are listed for each of the presented models. The estimate, standard error, Chi Square-value and p-value are presented for each of the explanatory variables in the models. Significant p-values are in bold.

Variable	Estimate	Std. error	Chi Square	p-value
*Number of fungivorous beetles (Pearson Goodness-of-fit: **p = 0.045**, df = 28)*				
Hymenophore area of polypores	$1.3*e^{-5}$	$± 3.7*e^{-6}$	11.106	**<0.001**
Intercept	1.537	± 0.119	125.106	**<0.001**

3.2. Sporocarp study

A total of 2592 beetles from 25 species were reared from the sporocarps used in the analysis (n=90). *Cis glabratus* was the dominating species making up approximately 82% of all individuals. *Cis quadridens* was the second most abundant species (16%) and the only threatened beetle species collected from the sporocarps (NT) (Appendix 5). 11 species were represented by only one individual.

A total of 134 parasitoid wasps from ten different species emerged from the sporocarps. The most dominant species was *Cleruchus polypori,* which made up a total of 64% of all reared parasitoids (Appendix 6). One species, *Cyclogastrella simplex,* was classified as a hyperparasitoid wasp (Nojes 2015). The parasitoid species were not assessed in the Norwegian 2010 Red List for species (Kålås et al. 2010) and the threatened status of parasitoids could not be evaluated. The distribution of the total number of species of reared beetles, parasitoids and hyperparasitoids between the different forest areas can be seen in Table 5.

Table 5: Distribution of absolute numbers of reared species of beetles, parasitoids and hyperparasitoids between the different forest areas.

Forest	Beetle species	Parasitoid species	Hyperparasitoid species
EastLarge	9	5	
EastSmall	7	4	
WestLarge	6	1	
WestSmall	8	2	1
NorthLarge	10	6	
NorthSmall	8	-	

3.2.1. Difference in species richness between large and small old-growth forests

Contrary to the predictions, there was a higher species richness of reared beetles in the small forest, compared to the large forest in the western region (Chi Square = 5.72, df = 1, p = **0.017**) (Figure 8). There was not enough data to compare the species richness of parasitoid wasps between the large and small old-growth forest areas for the eastern and western region.
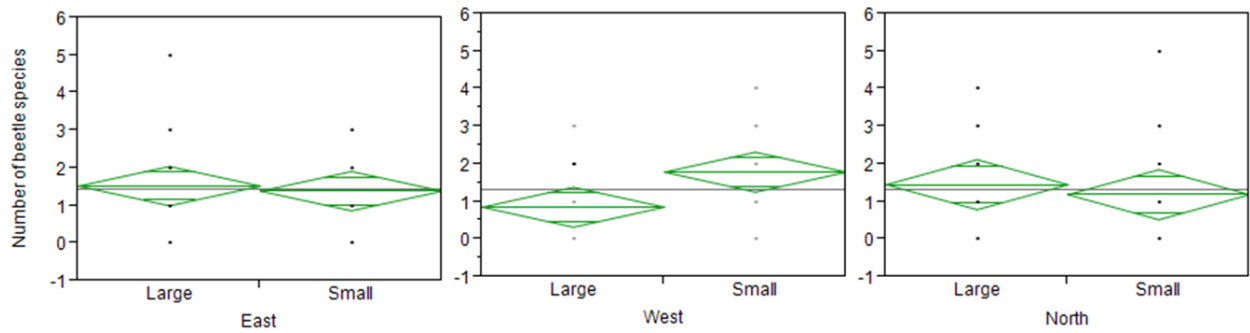
Figure 8: Difference in richness of beetles reared from F. pinicola between the large and small old-growth forests within the eastern, western and northern region respectively. The mean diamonds illustrates the sample mean and the 95% confidence interval.

3.2.2. Importance of environmental variables

None of the environmental variables on the forest stand level or study plot level were able to describe the richness of reared insect groups. On the sporocarp level, there was a higher richness of beetles reared from the sporocarps in decomposition class III compared to the sporocarps in decomposition class I (Z=2,368, p=**0,018**) (Figure 9A). There was also a higher species richness of reared parasitoids from the sporocarps in decomposition class II, compared to the sporocarps in decomposition class I (Z=2,010, p=**0,044**) (Figure 9B). The species richness of reared parasitoid wasps was higher from sporocarps with a high amount of beetles (Table 6).
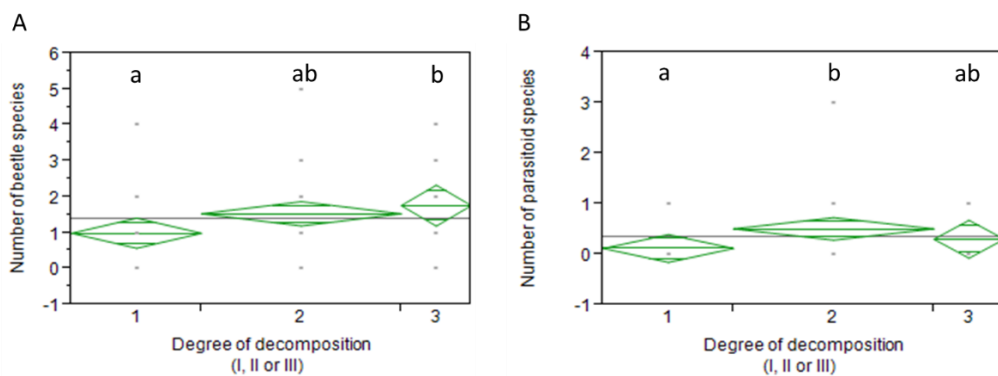
Figure 9: Difference in richness of species reared from F. pinicola between decomposition class I, II and III sporocarps, respectively. Graph A show the difference in species richness of beetles, while graph B show the difference in species richness of parasitoid wasps. Significant difference (p<0.05) between groups is marked with the letters a and b.

Table 6: The GLM that best explained the species richness of parasitoids wasps (Lowest AICc). The total models p-value and df are listed for each of the presented models. The estimate, standard error, Chi Square-value and p-value are presented for each of the explanatory variables in the models. Significant p-values are in bold.

Variable	Estimate	Std. error	Chi Square	p-value
*Number of parasitoid wasp species (Pearson Goodness-of-fit: **p = 0.049**, df = 72)*				
Amount of beetles	0.008	± 0.002	8.246	**0.004**
Intercept	-1.373	± 0.245	49.109	**<0.001**

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4. Discussion

The focus of this study was to investigate the habitat requirements of the different insect groups; the saproxylic beetles, the fungivorous beetle subset, and the reared beetles and parasitoid wasps. I wanted to find out if the size of old-growth forests had an effect on the species richness of the different insect groups, and what environmental variables best explained the species richness of these groups.

Contrary to my predictions about the effect of size of old-growth forests on the species richness, the species richness was either the same or higher per unit area in the small forests, compared to the large forests.

In accordance with my predictions about the effect of environmental variables on the species richness of the different insect groups, I found that the species richness of each insect group was best explained by different environmental variables. The number of saproxylic beetle species increased with an increase in volume of dead wood, and at the same time decreased with an increase in polypore diversity. The species richness of the fungivorous beetle subset increased with the polypore hymenophore area. The species richness of reared beetles was higher in decomposition class III sporocarps, than in decomposition class I sporocarps, while the species richness of parasitoid wasps was higher in decomposition class II sporocarps, than in decomposition class I sporocarps. The species richness of parasitoid wasps also increased with the number of beetles present in the sporocarps.

4.1 Effect of forest size on the species richness

The observation of a higher species richness per unit area in the small, contrary to the large forests, was found for both the saproxylic beetles and the reared beetles. This observation is not supported by the presented predictions, but there is support for these results when comparing to several other similar studies (Driscoll & Weir 2005; Halme & Niemelä 1993; Sverdrup-Thygeson et al. 2014; Webb & Hopkins 1984). Sverdrup-Thygeson et al. (2014) and Halme and Niemelä (1993) compared the species richness of aspen associated beetles and carabid beetles, respectively, between different sized forest fragments. Both of these studies divided the beetles into specialists and generalists, and found that there was a higher species richness of generalist species in the small, compared to the large forest fragments. They found no difference in the species richness of specialist species.

The different results between the generalist and specialist species could be compared to my own observations of the different respond between the different insect groups; all saproxylic beetles, the fungivorous beetle subset and the reared beetles. The species within the saproxylic beetle group belong to many different functional groups, with a large number of both generalists and specialists. The same goes for the species in the group of beetles reared from the sporocarps of *F. pinicola*. The fungivorous beetle subset represent a more specific functional group of the saproxylic beetles. I found a difference in species richness in the most diverse insect groups, while no difference was observed in the fungivorous beetle subset, which had a clearer functional role and habitat preferences.

A potential reason for why several studies have observed a higher species richness of generalist species in the small forests is a higher influx of matrix species into smaller forest fragments (Driscoll & Weir 2005; Halme & Niemelä 1993; Janzen 1983; Webb & Hopkins 1984). This observation is also supported by the results from Ås (1993; 1999). He observed no difference in the species richness of saproxylic beetles between different sized forest fragments of deciduous forest, but he did find a significant difference in the species composition. There was a higher amount of matrix species in the species pool from the small forest fragments, compared to in the larger forest fragments.

It is possible that the difference in species richness of saproxylic beetles and reared beetles also in my study is caused by a high influx of matrix species in the small old-growth forest fragments. It is not possible to evaluate whether or not this is true, based on the available information and scope of this study.

It was also not possible to evaluate the effect of forest size on the species richness of higher trophic levels because of sampling size. This indicate the need for a larger sample size in studies of species at higher trophic levels, which is also implied by the study of Komonen et al. (2000).

4.1.1 The importance of continuity

This study, and several other studies, have found that small old-growth forests have a higher conservation value than first expected, based in classical theories (Djupström et al. 2008; Franc et al. 2007; Götmark & Thorell 2003; Hottola & Siitonen 2008; Junninen & Kouki 2006). Even so, it is uncertain whether or not these forests are able to produce a continuous supply of resources, and preserve the observed species communities of saproxylic organisms, in the future.

It has been hypothesised that species communities and forest stand structure in recently fragmented forest patches represent an unbalanced system, which will change until it reaches the new equilibrium (Diamond 1975). These changes could both be caused by edge effects and extinction debt.

Small forest fragments have a higher proportion of edge, and would be more strongly affected by edge effects, like changes in the microclimatic conditions (sun exposure, temperature, wind speed and moisture), when the forest structure of the surrounding landscape changes (Murcia 1995). These changes could possibly affect the diversity and composition of forest structures utilized by saproxylic organisms. Peltonen and Heliövaara (1999) found that the speed of wood decomposition was higher in the edge of forests. Edge areas are more sunny and dryer than closed canopy forest fragments, and a change in the proportion of moist and shaded forest parts would affect the species richness and composition of wood-decaying fungi (Boddy et al. 2008).

Old-growth forest structures have a long persistence in the landscape and there will be a long time-lag from the fragmentation to a change in the forest structure caused by the fragmentation, and to an observed decrease in species of saproxylic insects in the forests. Junninen and Komonen (2011) suggested that it might take 100-150 years from fragmentation, until the species richness and composition of polypores in the forest fragment reaches the new equilibrium of that forest. This would further affect the species relying on both the direct and indirect resources these polypores represents.

Small populations and specialist species with low dispersal ability are more likely to go extinct in small old-growth forest fragments (Hanski et al. 1996; Jonsell et al. 1999; Komonen 2003; Sverdrup-Thygeson et al. 2014). This is because small populations have a higher risk of stochastic local extinction than larger more robust populations (Hanski et al. 1996). It is also because specialist species with short distance dispersal are more dependent on a continuous supply of specific substrates. A break in the substrate continuity could result in the species going locally extinct, without the species being able to recolonize the area when new suitable substrates appear (Jonsson et al. 2001).

All of the different forests in this study were relatively young (Table 1). I have not included any information about the landscape matrix in this study, but we do know that the forest surrounding the different woodland key habitats are managed forests. It is likely that the small old-growth forest fragments are still reflecting the original forest community, and that the

community will change until it reaches the new equilibrium of the forest (Penttilä et al. 2006). The observed effect of forest size on the species richness of saproxylic species in this study is therefor likely to change in the future. There is a need for additional studies which includes the time-since-fragmentation, to fully evaluate the value of small old-growth forests for the future conservation of threatened saproxylic species.

4.2 Effect of environmental variables on the species richness

The different insect groups; the saproxylic beetles, the fungivorous beetle subset, the reared beetles and the reared parasitoid wasps, were dependent on different environmental variables, which supports the hypothesis that different functional groups of saproxylic insect have different habitat and resource requirements (Jonsson & Jonsell 1999; Reid 1998; Similä et al. 2006). Heterogeneous forests with a high diversity of forest substrates should be able to support a high diversity of saproxylic insects.

4.2.1 Saproxylic beetles

The positive relationship between the species richness of saproxylic beetles and the total volume of dead wood in the forests is supported by the literature presented in the introduction. While the negative effect of the polypore diversity on the species richness was contrary to my prediction. This indicates that the polypore diversity in these forests was reflecting other type of forest characteristic than just the direct or indirect availability of resources used by the saproxylic beetles.

The negative relationship between the species richness of saproxylic beetles and the polypore diversity can be explained by the difference in species richness patterns of these two groups, in relation to decomposition stages of dead wood. The species richness of beetles has been found to be highest in the early decomposition stages of dead wood, when there is still a lot of inner bark left. The number of beetle species on the log decreases as the inner bark gets consumed and the wood becomes more decomposed (Stokland & Siitonen 2012). The species richness of polypores is highest in the median decomposition stages, and coincides with the decomposition phase with the highest fungal activity (Bader et al. 1995; Stokland & Siitonen 2012). The decomposition stage of the dead wood was not included in this study, and further studies is needed to evaluate whether or not this was the reason behind the observed negative relationship.

Old-growth forests with a high volume of dead wood have been found to have a high diversity of dead wood, with a high proportion of different decomposition stages of dead wood (Penttilä et al. 2004). Forests with a high volume of dead wood, distributed between different decomposition stages, would both support a high species richness of saproxylic beetles and a high polypore diversity (Bader et al. 1995; Penttilä et al. 2004). The positive correlation between the polypore diversity and the volume of dead wood in my analysis supports this relationship (Appendix 2, Table 1).

4.2.2 Fungivorous beetles

We were able to observe a positive relationship between the species richness of saproxylic beetles and the presence of polypores in the forest (as describe by the polypore hymenophore area), when the fungivorous beetle species were separated from the larger group of saproxylic beetles. This relationship is supported by the biology of the fungivorous beetles, but it has not been described before, as far as I know.

The polypore hymenophore area represents different types of resources used by many fungivorous beetles, like the sporocarp, the hymenophore surface area, spores and the presence of mycelia (Siitonen 2012a). Sporocarps represent discreet habitats which only persists for a limited amount of time, even if it is long enough to support several generations of sporocarp-dwelling species (Grove 2002; Siitonen 2012a). The species that are dependent on this resource are relatively good dispersers, and are adapted to trace this relatively ephemeral resource in the forest landscape (Grove 2002; Jonsson 2012; Rukke 2000; Siitonen et al. 2001).

The composition of volatile compounds differ between different polypore species, and between the different development stages of sporocarps, like during the sporulation and aging (Fäldt et al. 1999; Guevara et al. 2000a; Kahlos et al. 1994). Volatile compounds, released by sporocarps, have been found to be important ques used by fungivorous beetles to detect new resources during dispersal (Guevara et al. 2000ab; Jonsell et al. 2003; Jonsell & Nordlander 2004; Jonsson et al. 2003). Beetles have been found to even be able to distinguish different polypore species and level of decomposition, based on smell of sporocarps (Guevara et al. 2000a; Jonsell & Nordlander 1995). Jonsell and Nordlander (1995) found that both spore feeding and sporocarp breeding beetles were attracted to traps bated with chopped pieces of sporocarps of *F. pinicola*. Beetle species associated with the polypore species *Fomes fomentarius* did not show a high attraction towards traps bated with chopped pieces of *F.*

fomentarius, even if they were trapped in large numbers underneath *F. fomentarius* on logs. These beetle species might use other ques to find new hosts, like the use of sexual pheromones by female beetles to attract mates (Jonsson et al. 2003; White & Birch 1987).

Based on this, it is likely that the high number of fungivorous beetle species in forests with high levels of polypore hymenophore area is both caused by the high occurrence of required resources in these areas, and a stronger attraction of beetle species towards these areas, caused by the release of volatile compounds.

The possible importance of the hymenophore area on the species richness of fungivorous beetles in the forests is a new and interesting research topic that needs further investigation. It might represent a possible indicator variable that could be useful in future conservation work.

4.2.3 Reared beetles

The species richness of beetles present in sporocarps of *F. pinicola* was dependent on the quality of the different sporocarps; the degree of decomposition. The most decomposed sporocarps had a higher beetle species richness, compared to the least decomposed ones. This supports the hypothesis presented in the introduction; that the secondary chemical compounds present in sporocarps function as a defence against fungivores.

The size of the sporocarps has been found to be important for the species richness (Rukke & Midtgaard 1998; Thunes et al. 2000), but I was not able to describe this trend in my data, not even within the different decomposition classes. There was a high variability in number of species between similar sized sporocarps. This could be a sampling artefact, because several small sporocarps were pooled together to have a volume larger than 20 cm^3 (see material and methods). It could also been caused by the additional noise that is created in the dataset when pooling all beetle species, and all sporocarps from the different forests, into one group. Jonsell et al. (2001) found that the size of the sporocarp is only important for some polypore associated insect species, and Thunes et al. (2000) found that the volume of dead wood in the forest patch affected the species richness in similar sized sporocarps.

4.2.4 Parasitoid wasps

The species richness of parasitoid wasps increased with an increase in the amount of beetles present in the sporocarps, which is not surprising as many of the collected parasitoid wasp species parasitize beetles (Appendix 6). Jonsell et al. (2001) also found that the most

important factor for the occurrence of a parasitoid wasp species in a sporocarp of either the polypore species *F. pinicola* or *F. fomentarius*, was the occurrence of their host.

Even if Jonsell et al. (2001) mostly found that only the occurrence of the host species had an influence on the occurrence on the parasitoids, they also found that the decomposition class of the sporocarps had an influence on the parasitoid wasp species in the Eulophidae family. The Eulophidae are known to parasitize beetles of the Ciidae family, and both the Eulophidae and the Ciidae had a higher occurrence in most decomposed sporocarps.

I also observed that the species richness of parasitoid wasps was dependent on the decomposition class of sporocarps, with a higher species richness in the decomposition class II sporocarps than in the least decomposed sporocarps. Because the number of parasitoid wasp species was found to be increasing with the amount of beetles present in the sporocarps, it is likely to think that this pattern is seen as a result of the presence of host species. Contrary to this, I found that the amount of beetles followed the species richness of beetles, and was highest in the most decomposed sporocarps (Appendix 3). Not only the parasitoid wasp species with beetles as hosts were included in parasitoid wasp group, and the occurrence of for example Diptera (Appendix 6) could have contributed to the high presence of different parasitoid wasp species in the decomposition class II sporocarps.

Only the sporocarp-dwelling beetles were included in this study, and further studies are needed to full understand the habitat requirements of the highly diverse insects group that the parasitoid wasps represent (Gibb et al. 2008; Hilszczański et al. 2005).

4.3 Data quality and further studies

There was a time lag of three years between the PATHEXT fieldwork and the collection of insect species in the study plots. The environmental variables measure in 2011 all represent resources with a long persistence in the landscape, and these measurements should still be representative for the species richness of the different insect groups collected in 2014 (Berglund et al. 2005).

My models were not very robust, and small differences in the variable values changed the results of the analysis, and there were few significant models to choose from, when selecting the best model (based on AICc). Even so, I was able to find some significant results, which were supported by existing literature.

I would recommend using several study plots within each forests, when comparing the species richness and effect of environmental variables, between different forests. This would cover a larger part of the variability of both saproxylic beetles, parasitoid wasps and environmental variables present in the forests (Junninen & Komonen 2011; Thunes et al. 2000; Økland et al. 1996). This would probably both increase the robustness of the analysis and increase the number of collected threatened species and specialist species at higher trophic levels.

It is also important to compensate for the species richness variability, caused by environmental variables at smaller spatial scales, when comparing the difference in species richness between forests, at larger spatial scales. This was not done in this study, and might have influenced some of the observed species richness patterns between the small and larger old-growth forest fragments (Götmark & Thorell 2003). The effect the sporocarps degree of degradation had on the species richness of reared beetles, might for example have contributed to the collection of a higher species richness of reared beetles in WestSmall, than in WestLarge. No degradation class I sporocarps were collected from the study patch of WestSmall, while the proportions of different degradation classes was close to average from WestLarge (Appendix 1).

There is a need of more knowledge about the effect of forest size, and the relationships between the species richness of specific saproxylic insect groups and environmental variables. Some further research topics were mentioned in the text above, but I would like to mention some of these once more, because these topics are especially important for further research. The effect of time-since-fragmentation on the saproxylic insect species composition, specialist insect species richness and forest structure of old-growth forest fragments needs more attention. There is also a need for a better understanding of the habitat requirements of parasitoid wasps, and how these insects are affected by the size of forest reserves. The relationship between the fungivorous beetles and the polypore hymenophore area has not been describes before, and definitely needs further investigation.

5. Conclusion

I found that the small forest fragments had a higher species richness of saproxylic beetles and beetles associated with *F. pinicola* per unit area, than the large old-growth forest areas. Even so, it is uncertain what type of beetle species were contributing to this difference, and it is uncertain how well these small forest fragments will be able to support the observed species richness in the future. Based these uncertainties, large and continuous old-growth forests should be prioritized in the conservation of threatened saproxylic insects.

I also found that the species richness of different groups of saproxylic insects was mostly explained by these insect groups' specific substrate requirements. It is important to divide the saproxylic insect species into different clearly defined functional groups when studying the saproxylic insects habitat requirements. Forests with a high diversity of dead-wood substrates, and a high diversity of wood-decomposing fungi supports a high diversity of saproxylic insects, and should also hold a high value for the conservation of saproxylic insects.

References

A'Bear, A. D., Jones, T. H. & Boddy, L. (2014). Size matters: What have we learnt from microcosm studies of decomposer fungus–invertebrate interactions? *Soil Biology and Biochemistry*, 78: 274-283.

Artsdatabanken. (2015). Available at: http://www.artsdatabanken.no/ (accessed: 16.09.2015).

Bader, P., Jansson, S. & Jonsson, B. (1995). Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biological conservation*, 72 (3): 355-362.

Berglund, H., Edman, M. & Ericson, L. (2005). Temporal variation of wood-fungi diversity in boreal old-growth forests: implications for monitoring. *Ecological Applications*, 15 (3): 970-982.

Berntsen, B., Hågvar, S. & Bjørndalen, J. E. (2010). *Norsk natur - farvel? : en illustrert historie*. 2. utg. ed. Oslo: Unipub.

Blindheim, T., Thingstad, P. G. & Gaarder, G. (2011). Naturfaglig evaluering av norske verneområder. Dekning av naturtyper og vern. *NINA Rapport 539*.

Boddy, L., Frankland, J. C. & West, P. v. (2008). *Ecology of Saprotrophic Basidiomycetes*. Amsterdam: Elsevier. 372 pp.

Dahlberg, A. & Stokland, J. N. (2004). Vedlevande arters krav på substrat. *Skogsstyrelsen, rapport*, 7: 1-74.

Davies, Z. G., Tyler, C., Stewart, G. B. & Pullin, A. S. (2008). Are current management recommendations for saproxylic invertebrates effective? A systematic review. *Biodiversity and Conservation*, 17 (1): 209-234.

Diamond, J. M. (1975). The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. *Biological conservation*, 7 (2): 129-146.

Direktoratet for naturforvaltning. (2007). *Kartlegging av naturtyper : verdisetting av biologisk mangfold. DN-Håndbok 13*. 2. utg. 2006, oppdatert 2007. ed. Trondheim: Direktoratet for naturforvaltning.

Djupström, L. B., Weslien, J. & Schroeder, L. M. (2008). Dead wood and saproxylic beetles in set-aside and non set-aside forests in a boreal region. *Forest Ecology and Management*, 255 (8): 3340-3350.

Driscoll, D. A. & Weir, T. (2005). Beetle responses to habitat fragmentation depend on ecological traits, habitat condition, and remnant size. *Conservation Biology*, 19 (1): 182-194.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins*: 16-47.

Franc, N., Götmark, F., Økland, B., Nordén, B. & Paltto, H. (2007). Factors and scales potentially important for saproxylic beetles in temperate mixed oak forest. *Biological Conservation*, 135 (1): 86-98.

Fäldt, J., Jonsell, M., Nordlander, G. & Borg-Karlson, A.-K. (1999). Volatiles of bracket fungi Fomitopsis pinicola and Fomes fomentarius and their functions as insect attractants. *Journal of chemical ecology*, 25 (3): 567-590.

Gaston, K. J. (1991). The magnitude of global insect species richness. *Conservation Biology*: 283-296.

Gibb, H., Hilszczański, J., Hjältén, J., Danell, K., Ball, J., Pettersson, R. & Alinvi, O. (2008). Responses of parasitoids to saproxylic hosts and habitat: a multi-scale study using experimental logs. *Oecologia*, 155 (1): 63-74.

Graves, R. C. (1960). Ecological observations on the insects and other inhabitants of woody shelf fungi (Basidiomycetes: Polyporaceae) in the Chicago area. *Annals of the Entomological Society of America*, 53 (1): 61-78.

Grove, S. J. (2002). Saproxylic insect ecology and the sustainable management of forests. *Annual review of ecology and systematics*: 1-23.

Guevara, R., Rayner, A. D. & Reynolds, S. E. (2000a). Effects of fungivory by two specialist ciid beetles (Octotemnus glabriculus and Cis boleti) on the reproductive fitness of their host fungus, Coriolus versicolor. *New phytologist*, 145 (1): 137-144.

Guevara, R., Rayner, A. D. & Reynolds, S. E. (2000b). Orientation of specialist and generalist fungivorous ciid beetles to host and non-host odours. *Physiological Entomology*, 25 (3): 288-295.

Gustafson, E. J. & Gardner, R. H. (1996). The effect of landscape heterogeneity on the probability of patch colonization. *Ecology*, 77 (1): 94-107.

Götmark, F. & Thorell, M. (2003). Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. *Biodiversity & Conservation*, 12 (6): 1271-1285.

Halme, E. & Niemelä, J. (1993). *Carabid beetles in fragments of coniferous forest*. Annales Zoologici Fennici: JSTOR. 17-30 pp.

Hanski, I., Moilanen, A. & Gyllenberg, M. (1996). Minimum viable metapopulation size. *American Naturalist*: 527-541.

Hanski, I. (1999). *Metapopulation ecology*: Oxford University Press.

Hanski, I. (2001). Spatially realistic theory of metapopulation ecology. *Naturwissenschaften*, 88 (9): 372-381.

He, F. & Legendre, P. (1996). On species-area relations. *American naturalist*: 719-737.

Heilmann-Clausen, J., Barron, E. S., Boddy, L., Dahlberg, A., Griffith, G. W., Nordén, J., Ovaskainen, O., Perini, C., Senn-Irlet, B. & Halme, P. (2015). A fungal perspective on conservation biology. *Conservation Biology*, 29 (1): 61-68.

Hilszczański, J., Gibb, H., Hjältén, J., Atlegrim, O., Johansson, T., Pettersson, R. B., Ball, J. P. & Danell, K. (2005). Parasitoids (Hymenoptera, Ichneumonoidea) of saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biological Conservation*, 126 (4): 456-464.

Holt, R. D., Lawton, J. H., Polis, G. A. & Martinez, N. D. (1999). Trophic rank and the species-area relationship. *Ecology*, 80 (5): 1495-1504.

Hottola, J. & Siitonen, J. (2008). Significance of woodland key habitats for polypore diversity and red-listed species in boreal forests. *Biodiversity and Conservation*, 17 (11): 2559-2577.

Hyvärinen, E. (2006). Green-tree retention and controlled burning in restoration and conservation of beetle diversity in boreal forests. *Dissertationes Forestales*, 21: 1-55.

Hågvar, S. (1999). Saproxylic beetles visiting living sporocarps of Fomitopsis pinicola and Fomes fomentarius. *Norwegian Journal of Entomology*, 46: 25-32.

Janzen, D. H. (1983). No park is an island: increase in interference from outside as park size decreases. *Oikos*: 402-410.

Johansson, T., Hjältén, J., Gibb, H., Hilszczanski, J., Stenlid, J., Ball, J. P., Alinvi, O. & Danell, K. (2007). Variable response of different functional groups of saproxylic beetles to substrate manipulation and forest management: Implications for conservation strategies. *Forest Ecology and Management*, 242 (2–3): 496-510.

Jonsell, M. & Nordlander, G. (1995). *Field attraction of Coleoptera to odours of the wood-decaying polypores Fomitopsis pinicola and Fomes fomentarius*. Annales Zoologici Fennici: JSTOR. 391-402 pp.

Jonsell, M., Nordlander, G. & Jonsson, M. (1999). Colonization patterns of insects breeding in wood-decaying fungi. *Journal of Insect Conservation*, 3 (2): 145-161.

Jonsell, M., Nordlander, G. & Ehnström, B. (2001). Substrate associations of insects breeding in fruiting bodies of wood-decaying fungi. *Ecological Bulletins*: 173-194.

Jonsell, M., Schroeder, M. & Larsson, T. (2003). The saproxylic beetle Bolitophagus reticulatus: its frequency in managed forests, attraction to volatiles and flight period. *Ecography*, 26 (4): 421-428.

Jonsell, M. & Nordlander, G. (2004). Host selection patterns in insects breeding in bracket fungi. *Ecological Entomology*, 29 (6): 697-705.

Jonsson, B. G. & Jonsell, M. (1999). Exploring potential biodiversity indicators in boreal forests. *Biodiversity & Conservation*, 8 (10): 1417-1433.

Jonsson, B. G. (2012). Population dynamics and evolutionary strategies. In *Biodiversity in Dead Wood*, pp. 338-355. Cambridge: Cambridge University Press.

Jonsson, M., Jonsell, M. & Nordlander, G. (2001). Priorities in conservation biology: a comparison between two polypore-inhabiting beetles. *Ecological Bulletins*: 195-204.

Jonsson, M., Kindvall, O., Jonsell, M. & Nordlander, G. (2003). Modelling mating success of saproxylic beetles in relation to search behaviour, population density and substrate abundance. *Animal Behaviour*, 65 (6): 1069-1076.

Junninen, K. & Kouki, J. (2006). Are woodland key habitats in Finland hotspots for polypores (Basidiomycota)? *Scandinavian Journal of Forest Research*, 21 (1): 32-40.

Junninen, K. & Komonen, A. (2011). Conservation ecology of boreal polypores: a review. *Biological Conservation*, 144 (1): 11-20.

Kahlos, K., Kiviranta, J. L. & Hiltunen, R. V. (1994). Volatile constituents of wild and in vitro cultivated Gloeophyllum odoratum. *Phytochemistry*, 36 (4): 917-922.

Kaila, L. (1993). A new method for collecting quantitative samples of insects associated with decaying wood or wood fungi. *Entomologica Fennica*, 4: 21-23.

Kauserud, H., Colman, J. E. & Ryvarden, L. (2008). Relationship between basidiospore size, shape and life history characteristics: a comparison of polypores. *Fungal Ecology*, 1 (1): 19-23.

Kindvall, O. & Petersson, A. (2000). Consequences of modelling interpatch migration as a function of patch geometry when predicting metapopulation extinction risk. *Ecological Modelling*, 129 (1): 101-109.

Komonen, A., Penttilä, R., Lindgren, M. & Hanski, I. (2000). Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos*: 119-126.

Komonen, A. (2001). Structure of insect communities inhabiting old-growth forest specialist bracket fungi. *Ecological Entomology*, 26 (1): 63-75.

Komonen, A. (2003). Hotspots of insect diversity in boreal forests. *Conservation biology*, 17 (4): 976-981.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. (2001). Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research*, 16 (S3): 27-37.

Kruess, A. & Tscharntke, T. (2000). Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on Vicia sepium. *Oecologia*, 122 (1): 129-137.

Köhler, F. (2000). Saproxylic beetles in nature forests of the northern Rhineland. Comparative studies on the saproxylic beetles of Germany and contributions to German nature forest research. *Schrr. LÖBF/LAfAO NRW (Recklinghausen)*, 18: 1-351.

Kålås, J., Viken, Å., Henriksen, S. & Skjelseth, S. (2010). The 2010 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Norway*.

MacArthur, R. H. & Wilson, E. O. (1967). *The theory of island biogeography*, vol. 1: Princeton University Press.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological conservation*, 94 (2): 199-209.

Martin, M. M. (1979). Biochemical implications of insect mycophagy. *Biological reviews*, 54 (1): 1-21.

Moen, A., Odland, A. & Lillethun, A. (1998). *Vegetasjon*. Atlas : vegetasjon. Hønefoss: Norges geografiske oppmåling.

Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in ecology & evolution*, 10 (2): 58-62.

Nojes, J. S. (2015). Universal Chalcidoidea Database. In *Natural History Museum, London* (accessed: 30.09.2015).

Nordén, J. (2012, 2012-09-05 - 2012-09-06). *Habitat fragmentation and pathways to extinction in dead-wood dependent fungi*. MILJØ2015 seminar for PhD students and post docs, Holmenkollen, Oslo.

Nordén, J. (2015). *PATHEXT*. Email to Marianne Hansen (27.9.2015).

Norwegian Environment Agency. (2010). Faktaark over Mørkvassjuvet. Available at: http://faktaark.naturbase.no/Vern?id=VV00002193 (accessed: 29.04.2015).

Norwegian Environmental Agency. (1999). Faktaark over Sandalslia Ø. Available at: http://faktaark.naturbase.no/naturtype?id=BN00039341 (accessed: 29.04.2015).

Norwegian Environmental Agency. (2011). Faktaark over Rudskampen. Available at: http://faktaark.naturbase.no/naturtype?id=BN00047091 (accessed: 29.04.2015).

Norwegian Environmental Agency. (2013). Faktaark over Tjøstøl. Available at: http://faktaark.naturbase.no/Vern?id=VV00001019 (accessed: 29.04.2015).

Norwegian Environmental Agency. (2014). Faktaark over Spålen-Katnosa. Available at: http://faktaark.naturbase.no/Vern?id=VV00001808 (accessed: 29.04.20015).

Norwegian Environmental Agency. (2015). Naturbase (accessed: 12.10.2015).

Noss, R. F. & Cooperrider, A. (1994). *Saving nature's legacy: protecting and restoring biodiversity*: Island Press.

Ohlson, M., Söderström, L., Hörnberg, G., Zackrisson, O. & Hermansson, J. (1997). Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological conservation*, 81 (3): 221-231.

Peltonen, M. & Heliövaara, K. (1999). Attack density and breeding success of bark beetles (Coleoptera, Scolytidae) at different distances from forest-clearcut edge. *Agricultural and Forest Entomology*, 1 (4): 237-242.

Penttilä, R., Siitonen, J. & Kuusinen, M. (2004). Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. *Biological Conservation*, 117 (3): 271-283.

Penttilä, R., Lindgren, M., Miettinen, O., Rita, H. & Hanski, I. (2006). Consequences of forest fragmentation for polyporous fungi at two spatial scales. *Oikos*, 114 (2): 225-240.

Pimm, S. L. (1991). *The balance of nature?: ecological issues in the conservation of species and communities*: University of Chicago Press.

Primack, R. B. (2010). *Essentials of conservation biology*. 5th ed. ed. Sunderland, Mass: Sinauer Associates.

Prop. 1 S. (2015-2016). *For budsjettåret 2016*.

Reid, W. V. (1998). Biodiversity hotspots. *Trends in Ecology & Evolution*, 13 (7): 275-280.

Roland, J. & Taylor, P. D. (1997). Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, 386 (6626): 710-713.

Rosenzweig, M. L. (1995). *Species diversity in space and time*: Cambridge University Press.

Rukke, B. A. & Midtgaard, F. (1998). The importance of scale and spatial variables for the fungivorous beetle Bolitophagus reticulatus (Coleoptera, Tenebrionidae) in a fragmented forest landscape. *Ecography*: 561-572.

Rukke, B. A. (2000). Effects of habitat fragmentation: increased isolation and reduced habitat size reduces the incidence of dead wood fungi beetles in a fragmented forest landscape. *Ecography*, 23 (4): 492-502.

SAS Institute Inc. (2012). *JMP Pro 10.0*. Cary, NC: SAS Institute Inc. .

Schigel, D. S. (2009). Polypore assemblages in boreal old-growth forests, and associated Coleoptera.

Schigel, D. S. (2012). Fungivory and host associations of Coleoptera: a bibliography and review of research approaches. *Mycology*, 3 (4): 258-272.

Schwartz, M. W. & van Mantgem, P. J. (1997). The value of small preserves in chronically fragmented landscapes. In *Conservation in highly fragmented landscapes*, pp. 379-394: Springer.

Schwartz, M. W. (1999). Choosing the appropriate scale of reserves for conservation. *Annual review of ecology and systematics*: 83-108.

Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S. & Müller, J. (2014). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*.

Shaw, M. R. & Hochberg, M. E. (2001). The neglect of parasitic Hymenoptera in insect conservation strategies: the British fauna as a prime example. *Journal of Insect Conservation*, 5 (4): 253-263.

Shmida, A. & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of biogeography*: 1-20.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological bulletins*: 11-41.

Siitonen, J., Penttilä, R. & Kotiranta, H. (2001). Coarse woody debris, polyporous fungi and saproxylic insects in an old-growth spruce forest in Vodlozero National Park, Russian Karelia. *Ecological Bulletins*: 231-242.

Siitonen, J. (2012a). Microhabitats. In *Biodiversity in Dead Wood*, pp. 150-183. Cambridge: Cambridge University Press.

Siitonen, J. (2012b). Threatened saproxylic species. In *Biodiversity in Dead wood*, pp. 356-379. Cambridge Cambridge University Press.

Similä, M., Kouki, J., Mönkkönen, M., Sippola, A.-L. & Huhta, E. (2006). Co-variation and indicators of species diversity: Can richness of forest-dwelling species be predicted in northern boreal forests? *Ecological Indicators*, 6 (4): 686-700.

Sippola, A.-L., Lehesvirta, T. & Renvall, P. (2001). Effects of selective logging on coarse woody debris and diversity of wood-decaying polypores in eastern Finland. *Ecological Bulletins*: 243-254.

Sippola, A.-l., Similä, M., Mönkkönen, M. & Jokimäki, J. (2004). Diversity of polyporous fungi (Polyporaceae) in northern boreal forests: effects of forest site type and logging intensity. *Scandinavian Journal of Forest Research*, 19 (2): 152-163.

Soule, M. E. & Simberloff, D. (1986). What do genetics and ecology tell us about the design of nature reserves? *Biological conservation*, 35 (1): 19-40.

Stokland, J. N. (2012a). The saproxylic food web. In *Biodiversity in Dead Wood*, pp. 29-57. Cambridge: Cambridge University Press.

Stokland, J. N. (2012b). Wood decomposition. In *Biodiversity in Dead Wood*, pp. 10-28. Cambridge: Cambridge University Press.

Stokland, J. N. & Siitonen, J. (2012). Mortality factors and decay succession. In *Biodiversity in Dead Wood*, pp. 110-149. Cambridge: Cambridge University Press.

Stokland, J. N., Siitonen, J. & Jonsson, B. G. (2012). Biodiversity in Dead Wood. In, p. 509. Cambridge: Cambridge University Press.

Stokland, J. N., Eriksen, R. & Granhus, A. (2014). Tilstand og utvikling i norsk skog 1994-2012 for noen utvalgte miljøegenskaper: Oppdragsrapport fra Skog og landskap 03/14:. V, 41 pp.

Sullivan, B. T. & Berisford, C. W. (2004). Semiochemicals from fungal associates of bark beetles may mediate host location behavior of parasitoids. *Journal of chemical ecology*, 30 (4): 703-717.

Svantesson, S. (2012). *Ecological requirements of corticioid fungi - a study on species richness and community composition in south-eastern Norway*: Göteborgs universitet, Institutionen för biologi och miljövetenskap. 39 pp.

Sverdrup-Thygeson, A. (1994). *Wood-fungus insects in the boreal forest: spatial distribution and habitat preferences of the darkling beetle Bolitophagus reticulatus*. Oslo. 54 pp.

Sverdrup-Thygeson, A. & Lindenmayer, D. (2003). Ecological continuity and assumed indicator fungi in boreal forest: the importance of the landscape matrix. *Forest Ecology and Management*, 174 (1): 353-363.

Sverdrup-Thygeson, A., Bendiksen, E., Birkemoe, T. & Larsson, K. H. (2014). Do conservation measures in forest work? A comparison of three area-based conservation tools for wood-living species in boreal forests. *Forest Ecology and Management*, 330: 8-16.

Swedish Forest Agency. (2004). Information om vald nyckelbiotop. Available at: http://www.skogsstyrelsen.se/skogens-parlor/Nyckelbiotop/?objektid=2955477 (accessed: 15.11.2015).

Tamm, C. O. (1991). *Nitrogen in terrestrial ecosystems: questions of productivity, vegetational changes, and ecosystem stability*. Ecological Studies, vol. Vol. 81. Berlin: Springer

Thunes, K. H., Midtgaard, F. & Gjerde, I. (2000). Diversity of coleoptera of the bracket fungus Fomitopsis pinicola in a Norwegian spruce forest. *Biodiversity & Conservation*, 9 (6): 833-852.

Timonen, J., Siitonen, J., Gustafsson, L., Kotiaho, J. S., Stokland, J. N., Sverdrup-Thygeson, A. & Mönkkönen, M. (2010). Woodland key habitats in northern Europe: concepts, inventory and protection. *Scandinavian Journal of Forest Research*, 25 (4): 309-324.

Webb, N. & Hopkins, P. (1984). Invertebrate diversity on fragmented Calluna heathland. *Journal of Applied Ecology*: 921-933.

White, P. R. & Birch, M. C. (1987). Female sex pheromone of the common furniture beetleAnobium punctatum (Coleoptera: Anobiidae): Extraction, identification, and bioassays. *Journal of chemical ecology*, 13 (7): 1695-1706.

Økland, B., Bakke, A., Hågvar, S. & Kvamme, T. (1996). What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodiversity & Conservation*, 5 (1): 75-100.

Ås, S. (1993). Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography*: 219-228.

Ås, S. (1999). Invasion of matrix species in small habitat patches. *Conservation Ecology*, 3 (1): 1.

Appendix 1

The values of the environmental variables use in the analysis. The values are given for each forest area with a standard deviation (S.D.) is given per variable.

Environmental variables	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Mean	S.D.
Forest level								
Forest size (ha)	431.7	5.1	2431.8	13.1	1844.0	11.4	789.5	996.6
Study plot level								
Polypore diversity (Sjannon's H)*	1.917	2.004	2.360	1.946	2.177	2.020	2.071	0.156
Hymenophore area of polypores (cm^2/ha)	17 802	58 352	19 605	10 915	8 000	12 380	21 176	17 381
Hymenophore area of F. pinicola (cm^2/ha)	1 617	1 813	771	284	1 293	2 263	1 352	659
Volume of dead wood (m^3/ha)	18	166	242	78	83	64	108	75
Sporocarp level								
Total volume of sporocarps (cm^3)	1 633	1 359	2 018	3 760	3 703	927	118	122
Proportion of decomposition classes (%)	27/66/7	60/27/13	27/46/27	0/60/40	47/47/6	33/40/27	32/48/20	19/13/12
Total number of beetle species (#species)	9	7	6	8	10	8	8	1.3
Total number of beetles (#individuals)	279	622	109	1366	125	91	432	455.8

*The abundance and number of polypore species used to calculate the polypore diversity is presented in Appendix 7

Appendix 2

Correlations between environmental variables in the window trap study (Table 1) and sporocarp study (Table 2).

Table 3: Pearson's Product-Moment correlations between the different environmental variables in the window trap study. Significant correlations are marked in bold.

	Polypore diversity	Dead Wood	Forest size
Dead wood	**0.766**		
Forest size	**0.921**	**0.549**	
Hymenophore area of polypores	- 0.133	**0.428**	- 0.295

Table 4: Pearson's Product-Moment correlations between the different environmental variables in the sporocarps study. Significant correlations are marked in bold.

	Dead Wood	Forest size	Hymenophore area of *F. pinicola*	Volume of sporocarps	Number of beetle species
Forest size	**0.556**				
Hymenophore area of *F. pinicola*	- 0.293	**- 0.373**			
Volume of sporocarps	0.026	0.215	- 0.226		
Number of beetle species	- 0.178	- 0.161	- 0.053	0.148	
Amount of beetles	- 0.050	- 0.228	- 0.250	0.286	0.271

Appendix 3

Difference in number of beetles reared from sporocarps of F. pinicola, between the different decomposition class I, II and III respectively (material and methods). The values of the Y-axis is Log-transformed. Significant differences ($p < 0.05$) is marked with the letters a and b.
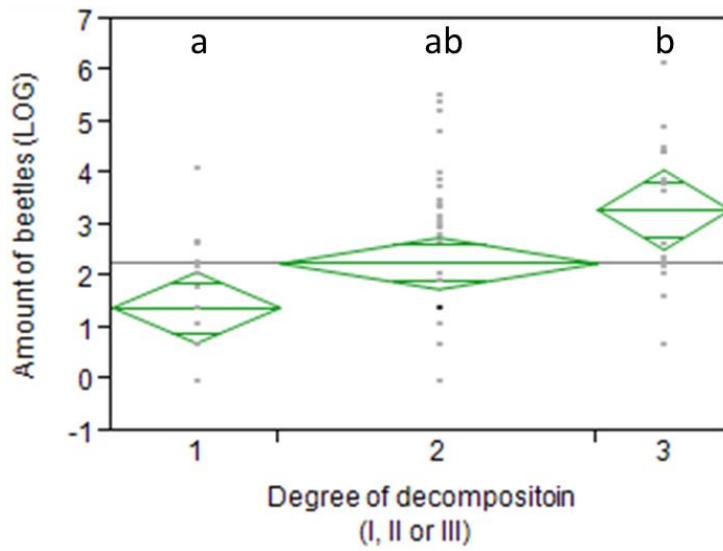
Appendix 4

The occurrence and total abundance of all saproxylic beetle species collected using window traps. The subset of fungivorous beetles is marked in bold. Red listed species are marked with threatened category (Kålås et al. 2010). .

Family/species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Anobiidae:							
Cacotemnus thomsoni (NT)		X	X		X		7
Dorcatoma dresdensis				X			1
Dryophilus pusillus		X					1
Ernobius abietis		X		X			4
Ernobius mollis		X					1
Hadrobregmus pertinax		X	X	X			3
Ptinus subpillosus	X	X	X	X			9
Anthribidae:							
Anthribus nebulosus		X					1
Cantharidae:							
Malthodes brevicollis	X	X	X	X			20
Malthodes crassicornis		X		X			2
Malthodes fibulatus			X				1
Malthodes fuscus	X	X	X	X	X	X	13
Malthodes guttifer		X		X			3
Malthodes mysticus		X					1
Podistra schoenherri	X		X	X	X	X	12
Cerambycidae:							
Alosterna tabacicolor	X						1
Anastrangalia sanguinolenta				X			1
Judolia sexmaculata				X			1
Molorchus minor		X	X	X			4
Oxymirus cursor	X	X	X	X			6
Pachyta lamed		X					1
Pogonocherus fasciculatus	X			X			2
Rhagium inquisitor		X					1
Rhagium mordax		X		X			2
Stenurella melanura				X			1
Stictoleptura maculicornis		X		X			2
Tetropium castaneum		X			X		2
Cerylonidae:							
Cerylon fagi		X					2
Ciidae:							
Cis castaneus		X	X				2
Cis dentatus				X			1
Cis festivus		X	X	X			11

Appendix 4 (*Continued*)

Family/species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Ciidae (continued):							
Cis jacquemartii	X			X			5
Cis micans			X	X			2
Cis punctulatus	X	X	X				4
Ennearthron cornutum		X					1
Hadreule elongatula (NT)		X					1
Octotemnus glabriculus		X					1
Orthocis alni		X					1
Cleridae:							
Thanasimus femoralis			X				1
Corylophidae:							
Orthoperus atomus		X					1
Cryptophagidae:							
Atomaria alpine			X				1
Atomaria ornata	X		X	X			11
Atomaria subangulata (NT)				X			1
Atomaria turgida	X	X	X	X	X	X	53
Cryptophagus dorsalis		X					1
Cryptophagus micaceus	X		X	X			4
Cryptophagus scanicus	X		X		X		11
Micrambe abietis	X	X	X	X	X	X	26
Pteryngium crenatum	X						1
Curculionidae:							
Cryphalus asperatus				X			2
Crypturgus cinereus	X	X	X	X			10
Crypturgus hispidulus	X	X	X				17
Dryocoetes autographus	X	X	X	X	X	X	95
Hylastes brunneus		X		X			9
Hylastes cunicularius	X	X	X	X	X	X	289
Hylobius abietis		X	X				2
Hylobius piceus			X		X		3
Hylobius pinastri		X		X			2
Hylurgops palliatus			X	X			2
Ips typographus		X	X	X			8
Phloeotribus spinulosus		X	X	X			6
Pityogenes bidentatus			X				1
Pityogenes chalcographus	X	X	X	X		X	12
Pityophthorus micrographus		X					2
Polygraphus poligraphus		X	X	X	X	X	18
Rhyncolus ater		X		X			2
Rhyncolus sculpturatus		X					3
Scolytus intricatus		X					1

Appendix 4 (*Continued*)

Family/species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Curculionidae (continued):							
Strophosoma capitatum	X	X	X	X			82
Trypodendron domesticum	X						1
Trypodendron lineatum	X		X	X			5
Xyleborinus saxesenii		X					1
Dermestidae:							
Megatoma undata		X					1
Elateridae:							
Ampedus balteatus		X		X			2
Ampedus nigrinus	X	X	X	X			25
Ampedus tristis		X					1
Athous subfuscus	X	X	X	X	X	X	333
Denticollis linearis		X	X	X			3
Melanotus castanipes	X	X	X	X	X		82
Sericus brunneus	X	X		X			4
Endomychidae:							
Endomychus coccineus			X				4
Erotylidae:							
Triplax aenea		X					1
Triplax rufipes		X					1
Triplax russica		X		X			6
Eucnemidae:							
Hylis cariniceps (NT)		X					5
Microrhagus pygmaeus		X					3
Xylophilus corticalis	X	X	X				7
Hydrophilidae:							
Megasternum concinnum			X				1
Latridiidae:							
Cartodere nodifer	X						1
Corticaria rubripes			X	X			4
Enicmus rugosus	X	X	X	X			19
Enicmus testaceus	X	X	X	X			20
Latridius minutus		X	X				3
Stephostethus rugicollis		X	X				2
Leiodidae:							
Agathidium badium		X					1
Agathidium seminulum	X	X		X			12
Anisotoma castanea	X	X		X	X	X	15
Anisotoma humeralis		X	X	X			6
Anisotoma orbicularis			X				1

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Appendix 4 (*Continued*)

Family/species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Lycidae:							
Dictyoptera aurora	X	X	X	X	X	X	19
Platycis minutus	X						1
Pyropterus nigroruber		X					1
Melandryidae:							
Hallomenus axillaris (NT)				X			2
Hallomenus binotatus	X						1
Orchesia undulata			X				1
Xylita laevigata		X		X			4
Zilora ferruginea				X			1
Melyridae:							
Aplocnemus nigricornis		X					1
Dasytes caeruleus			X				2
Dasytes plumbeus		X	X	X			9
Monotomidae:							
Rhizophagus cribratus				X			1
Rhizophagus dispar		X			X		3
Rhizophagus ferrugineus		X	X	X	X	X	20
Rhizophagus nitidulus		X	X				3
Mordellidae:							
Mordellochroa abdominalis				X			1
Mycetophagidae:							
Mycetophagus fulvicollis (NT)				X			1
Nitidulidae:							
Cychramus luteus	X	X	X	X			33
Cychramus variegatus	X	X	X				7
Epuraea laeviuscula			X				1
Epuraea marseuli		X		X	X		5
Epuraea pallescens		X					2
Epuraea pygmaea	X	X	X	X		X	29
Glischrochilus hortensis	X	X	X	X			73
Glischrochilus quadripunctatus						X	1
Pityophagus ferrugineus		X		X	X	X	8
Oedemeridae:							
Chrysanthia geniculata		X		X			2
Salpingidae:							
Rabocerus foveolatus			X				1
Salpingus ruficollis					X		1
Scarabaeidae:							
Trichius fasciatus				X			2

Appendix 4 (*Continued*)

Family/species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Scraptiidae:							
Anaspis marginicollis		X	X	X		X	12
Anaspis rufilabris	X	X	X	X	X	X	25
Scydmaenidae:							
Stenichnus bicolor	X						1
Silvanidae:							
Dendrophagus crenatus				X			1
Silvanoprus fagi	X	X					7
Sphindidae:							
Aspidiphorus orbiculatus	X	X		X			9
Staphylinidae:							
Atheta myrmecobia				X			1
Atheta picipes	X						1
Atheta pilicornis			X				1
Atrecus pilicornis			X	X			3
Bibloporus bicolor	X	X	X	X			25
Dadobia immersa				X			1
Euplectus decipiens		X		X			2
Euplectus karstenii			X				1
Euplectus punctatus		X					1
Gabrius splendidulus	X	X					2
Leptusa pulchella	X	X	X				5
Nudobius lentus		X					1
Phloeopora testacea		X					1
Phyllodrepa linearis		X					1
Placusa depressa		X					1
Placusa tachyporoides			X				1
Quedius maurus					X		1
Quedius plagiatus					X	X	7
Quedius xanthopus	X	X	X	X	X		87
Tachinus laticollis		X	X		X	X	7
Tachinus rufipes	X	X					3
Tyrus mucronatus				X			1
Trogossitidae:							
Nemozoma elongatum		X					1

References

Kålås, J., Viken, Å., Henriksen, S. & Skjelseth, S. (2010). The 2010 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Norway.*

Appendix 5

The occurrence and total abundance of all beetle species reared from sporocarps of F. pinicola. Red listed species are marked with threatened category (Kålås et al. 2010).

Family/species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Carabidae:							
Notiophilus biguttatus					X		1
Cerylonidae:							
Cerylon fagi	X						1
Cerylon ferrugineum		X					1
Ciidae:							
Cis bidentatus					X	X	5
Cis castaneus	X			X			4
Cis dentatus	X	X	X	X		X	13
Cis festivus						X	1
Cis glabratus	X	X	X	X	X	X	2124
Cis jacquemartii				X	X		2
Cis lineatocribratus				X			3
Cis quadridens (NT)	X	X	X	X	X	X	406
Ropalodontus perforatus		X					1
Curculionidae:							
Hylurgops palliatus			X				1
Monotomidae:							
Rhizophagus dispar	X				X		4
Nitidulidae:							
Epuraea variegata					X		1
Ptinidae:							
Dorcatoma punctulata		X		X		X	6
Scraptiidae:							
Anaspis rufilabris				X			1
Staphylinidae:							
Acrulia inflata	X				X	X	3
Gyrophaena boleti		X					4
Leptusa fumida	X						4
Leptusa pulchella			X		X		2
Lordithon trinotatus	X						1
Quedius plagiatus					X		1
Stenichnus bicolor						X	1
Trogossitidae:							
Thymalus limbatus			X				1

References

Kålås, J., Viken, Å., Henriksen, S. & Skjelseth, S. (2010). The 2010 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Norway.*

Appendix 6

The occurrence and total abundance of all parasitoid wasp species reared from sporocarps of F. pinicola. The known hosts are listed for each of the species and species groups (Artsdatabanken 2015; Nojes 2015).

Species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	Total	Host species
Ceraphronidae:							
Aphanogmus sp.					X	1	
Eulophidae:							
Astichus arithmeticus	X			X		3	Ciidae
Astichus polyporicola	X	X	X			13	Ciidae
Mymaridae:							
Cleruchus polypori	X	X		X	X	83	Ciidae
Pteromalidae:							
Cyclogastrella simplex				X		1	Coleoptera, Lepidoptera and Bethylidae
Spalangia erythromera					X	2	Diptera
Bethylidae:							
Cephalonomia formiciformis		X				1	Ciidae
Figitidae:							
Kleidotoma sp.	X				X	26	Diptera
Trybliographa sp.		X			X	3	
Ichneumonidae:							
Ichneumonidae sp.	X				X	2	

References

Artsdatabanken (2015). Available at: http://www.artsdatabanken.no/ (accessed: 16.09.2015).

Nojes, J. S. (2015). Universal Chalcidoidea Database. In Natural History Museum, London (accessed: 30.09.2015).

Appendix 7

The occurrence, abundance and total abundance of all polypore species registered in the 4 ha study plot. Red listed species are marked with threatened category (Kålås et al. 2010).

Species	EastLarge	EastSmall	WestLarge	WestSmall	NorthLarge	NorthSmall	Total
Amylocystis lapponica (EN)					8		8
Antrodia heteromorpha			1		1		2
Antrodia serialis	27	23	36	48	42	35	211
Antrodia sinuosa	2	9	2	5	4	3	25
Antrodiella citrinella (VU)			6	2	6	8	22
Cinereomyces lindbladii		1		3			4
Fomitopsis pinicola	42	57	35	17	42	47	240
Fomitopsis rosea (NT)			39	37		5	81
Ischnoderma benzoinum	6	1	4		3		14
Junghuhnia luteoalba (NT)			2	7	1		10
Leptoporus mollis						2	2
Phanerochaete sanguinea	3		2	1	1	1	8
Phlebia centrifuga (NT)			9	1	20	2	32
Phlebiella vaga						1	1
Physisporinus vitreus	2	2	4		7	6	21
Postia caesia	18	23	14	27	20	27	129
Postia fragilis	1	1		1			3
Postia leucomallella			4	2			6
Postia stiptica		1					1
Postia tephroleuca	6	4					10
Skeletocutis amorpha	2		2			2	6
Skeletocutis brevispora				1	1		2
Skeletocutis carneogrisea (VU)	10	17	2	1		3	33
Skeletocutis kuehneri		3					3
Trichaptum abietinum	46	45	28	8	24	27	178

References

Kålås, J., Viken, Å., Henriksen, S. & Skjelseth, S. (2010). The 2010 Norwegian red list for species. *Norwegian Biodiversity Information Centre, Norway.*