# SCALE-SPECIFIC RESPONSES OF SAPROXYLIC BEETLES TO DEAD WOOD ABUNDANCE AND FOREST CHARACTERISTICS

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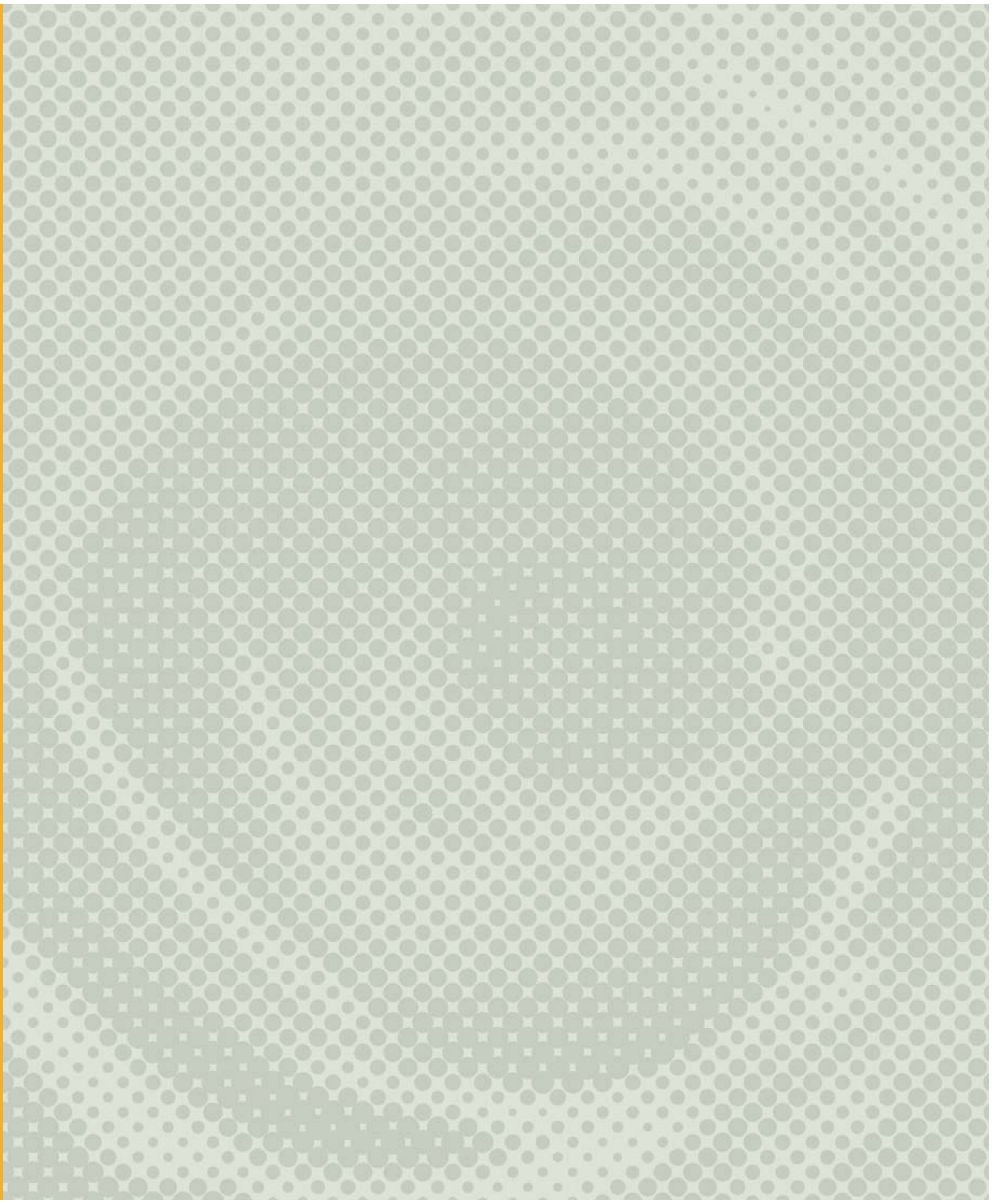

# Preface

First and foremost, I would like to thank my supervisors; Anne Sverdrup-Thygeson and Tone Birkemoe. They have been very helpful, generous with their time and always positive. I could not have had better supervisors. I am also very grateful for their financial support to my fieldwork. But most of all I am grateful for their amiable manner which always made me feel welcome and appreciated.

I would also like to thank the managers of Selvik and Losby Bruk; Erik Juel and Erling Bergsaker. They allowed me to ramble about in their forests, and without the lovely huts that they placed at my disposal at no cost, my fieldwork would have been considerably more strenuous. Their help was vital to my master thesis. I also have to thank my contact at Losby Bruk, Åge Bråten, for being very welcoming and helpful when I first arrived at Losby.

During my fieldwork there was a flood in Selvik Bruk due to the incessant rain that summer. My rental car was stuck for a period in the forests of Selvik Bruk since the road was washed away. I am very grateful for the special consideration Erik Juel showed by restoring the roads up to my rental car as quickly as possible. I am also very grateful that Jon Skaalerud at Rent-A-Wreck Ski was so understanding when I could not return their rental car on time.

I must also thank Adrian Rasmussen, my boyfriend, who kept me company during much of my fieldwork. We also assisted each other as we were both conducting fieldwork for our master thesis that summer. My mother, Vigdis Olafsen, and my good friend Ingebjørg Hagen Agøy also kept me company for periods of my fieldwork. Without the company of these great people it would have been much harder to stay motivated all those weeks.

Several people have been integral in leading me to where I am today, i.e. completing my master degree at the Norwegian University of Life Sciences (UMB, soon to be NMBU). Without lingering, I feel I should mention; my family (Stanley Jacobsen, Vigdis Olafsen, Arild Jacobsen and Knut Stanley Jacobsen), inspirational teachers at UMB (especially Eline Benestad Hågvar, who introduced me to the wonderful world of entomology), all my good friends and Sangkoret Lærken (without which my life at UMB would have been much less eventful).

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Rannveig M. Jacobsen

# Abstract

Insects constitute a major part of global biodiversity. Saproxylic insects seem to be adversely affected by forest management due to the low volume of dead wood in traditionally managed forests. Studies of the relation between species richness of saproxylic insects and dead wood volume have been inconsistent with regard to spatial scale, and multiscale studies have found that this relation can differ depending on scale. Finding the right scale for dead wood surveys will allow for consistent research and management advice.

In this study, dead wood was surveyed at sample sites spread across two relatively large areas in southeast Norway. Mean dead wood volume per ha was calculated for the area surrounding insect sample sites within three different radii; 1 km, 2 km and 3 km. Beetles (*Coleoptera*) were sampled from fresh aspen (*Populus tremula* L.) dead wood. The present study is part of a larger project, "Effect of Forestry Biodiversity Actions", involving several partners. Dead wood volume in general was only significant to saproxylic beetle species richness at the smallest spatial scale, the 1 km radius. However, dead wood of specific categories such as early decay or aspen dead wood had positive correlations for the 2 km radius. No dead wood categories were significant at the largest scale, the 3 km radius.

Variables describing the forest surrounding the insect sample sites were extracted from digital maps for the three different radii. Several of these map-derived forest variables were correlated with saproxylic species richness. The variable describing area of forest with much deciduous wood was the strongest predictor for species richness of aspen associated saproxylic insects. The map-derived variables for abundance of deciduous wood in the surrounding forest were correlated with field data of abundance of aspen dead wood. Furthermore, significantly larger volumes of dead wood were registered in the field at survey sites that were located in forests with higher volume of living trees according to the digital maps.

Forest volume is recorded regularly and nationwide in many countries and made available as digital maps. Dead wood surveys are time-consuming, which tends to limit their scale. Forest volume could be used as a landscape-specific proxy for dead wood volume. This would enable large multiscale studies of the scale-specific response of saproxylic insect species to substrate abundance, which might lead to determination of ecologically relevant spatial scales for dead wood surveys used in studies of saproxylic insects.

**Contents**

# 1. Introduction

Approximately half of the species included in the Norwegian Red List are insect species (Kålås et al. 2010). Most threatened species in Norway are found in the forest. Several of these species seem to be negatively influenced by forest management. In the Norwegian Red List from 2006, 17% of the species depended on dead wood as a substrate (Kålås et al. 2006). The volume of dead wood is much higher in old and unmanaged forests than in managed forests (Gibb et al. 2005; Siitonen 2001). Siitonen (2001) estimated that if an old-growth forest becomes a managed forest, the dead wood volume would decrease with about 90%. Managed forests also tend to display a lower diversity of dead wood since fewer decay classes are well represented (Similä et al. 2003). Dead wood volume is correlated with diversity of saproxylic beetles and fungi, and the correlation is stronger for boreal forests than temperate forests (Lassauce et al. 2011). Saproxylic species are commonly defined as species that during some part of their life-cycle depend on dead or dying wood, or upon other saproxylics (Speight 1989). In Scandinavia, beetles (*Coleoptera*) constitute a major part of all saproxylic species and of all red-listed species (Dahlberg & Stokland 2004; Kålås et al. 2010). Species richness of saproxylic beetles has been found to be significantly higher in old-growth forests relative to managed forests (Martikainen et al. 2000). Clearly, traditional forest management is reducing dead wood volume and its spatiotemporal distribution in a manner that negatively affects species depending on dead wood. Several attempts have been made at determining threshold values for the dead wood volume required by saproxylic species (Müller & Bütler 2010). However, one of the problems with threshold analyses is that they are frequently restricted to a single spatial scale (Lindenmayer & Luck 2005). Studies of the relationship between saproxylic species richness and dead wood abundance can get very different results depending on the scale of the dead wood survey (Økland et al. 1996). In order to provide ecologically sound and consistent management targets for dead wood abundance, researchers need to establish which spatial scales should be used for dead wood surveys both in research and management.

## 1.1 How to find the relevant scale

The relevant scale for a specific study species will depend on its dispersal rate and capacity which in turn determine its population or metapopulation structure (Hanski 1998). For some study organisms the required information might be found in the literature, or it might be inferred from the physiology or ecology of the species (Holland et al. 2005; Wikars 1997). Dispersal rate is poorly known for most insect species, and their dispersal distance is usually defined only by coarse estimates (Ranius 2006). Maximum dispersal distance might be impossible to determine since in the long term those few chance events where a single individual is carried much further than the mean dispersal distance tend to be crucial. Furthermore, when the response variable is species richness of saproxylic insects in general, the different species will depend on substrate availability on different scales. Nilssen (1984) found that some bark beetles could disperse up to 171 km, while other saproxylic species such as *Osmoderma eremita* (Scopoli, 1763) can be very sedentary; only about 15% of the adult population tend to disperse (Hedin et al. 2008; Ranius & Hedin 2001) with estimated mean displacement of 82 meters and only 1% dispersing farther than 1 km (Svensson et al. 2011). For little known species and for species richness or abundance of general categories such as “insects” or “saproxylic insects”, relevant scale can be difficult to infer. Ideally, in such cases one should obtain measures of the studied habitat feature at a range of spatial scales and fit these against the response variable to determine the scale where their correlation is strongest (Holland et al. 2004). However, since dead wood surveys require time-consuming field work, they are rarely conducted at multiple or large scales (Müller & Bütler 2010).

## 1.2 Present knowledge about relevant scales

Dead wood abundance at very small spatial scales such as 100 $m^2$ or 500 $m^2$ has been shown to be a poor predictor for saproxylic species richness and abundance (Gibb et al. 2006; Siitonen 1994). Schiegg (Schiegg 2000a; Schiegg 2000b) likewise found that dead wood volume within 200 m radius did not predict species richness of saproxylic insects, although connectivity of the dead wood objects at this scale was significant. Økland and co-workers (1996) analyzed the importance of different variables connected to dead wood for saproxylic beetle species at three spatial scales; 0.16 ha, 1 $km^2$ and 4 $km^2$. They found only weak relationships at the smallest scale, while variables connected to decaying wood and wood-inhabiting fungi were very important at the medium and large scale with the strongest relationships on the large scale. While Vanderwel and colleagues (2006) found significant correlations between abundance of fungivores and dead wood volume within areas of 20 ha and 79 ha, they did not find significant correlations between the abundance of any other saproxylic guild or saproxylic insects as a whole and dead wood volume at these scales. Ranius and colleagues (2011) found that saproxylic beetle species richness responded most strongly to substrate availability within 93 m radius of their insect sampling sites. However, they conducted a detailed survey of the entire area within 100 m radius of the insect sampling sites, while scales between 100 m and up to their largest scale of 1000 m radius were mapped by stand level data based on sample plots in each stand. The difference in accuracy when describing the habitat at scales up to 100 m radius and the habitat at larger radii might have affected the fit of the response.

In general, dead wood surveys covering spatial scales larger than 1 km in radius seem rare. However, the study of Götmark and colleagues (2011) showed that dead wood abundance at scales over 25 km in diameter can be important to saproxylic species. Relevant scale is a species-specific trait (Bergman et al. 2012; Holland et al. 2004). Thus, it will naturally vary somewhat between studies with different species assemblages. Holland and colleagues (2004) tested the correlation between abundance of saproxylic cerambycid beetle species with no registered tree species preference and forest cover within increasing radii from the sample point up to 2 km. The optimal spatial scale according to the highest correlation coefficient ranged from a radius of 20 m to 1800 m depending on the species. Although there is no single optimal scale, both an upper and lower limit to the range of relevant spatial scales for dead wood surveys can probably be determined. This range might verify the spatial scales used in previous studies, and at least increase the standardization of dead wood surveys and thus the comparability of the research.

## 1.3 Scales in this study

In this study, dead wood was surveyed at sample sites within a maximum radius of 3 km from the sites where saproxylic beetles were sampled. Thus, mean values for dead wood abundance were acquired for areas as large as 28.27 km$^2$ or 2827 ha surrounding the insect sample sites. This 3 km radius was the largest scale used for explanatory variables, while two smaller scales were also used; 2 km radius covering 12.57 km$^2$ and 1 km radius covering 3.14 km$^2$. These are large spatial scales relative to those more commonly used (Gibb et al. 2006; McGeoch et al. 2007; Økland et al. 1996; Ranius et al. 2011; Vanderwel et al. 2006). In addition, variables describing the forests surrounding the insect sample sites were extracted from digital maps. Digital maps can offer relatively detailed information about landscape features for large areas. In Norway, several maps that cover the entire country can be downloaded for free (Skog og Landskap, M.). Explanatory variables can be derived from digital maps with map-analyzing software for multiple and large spatial scales without much effort. Reese and colleagues (2002) analyzed the accuracy of one of the methods used to derive forest variables from satellite images. They concluded that although the error might be large at the pixel level it decreased as scale increased to acceptable levels at scales of 100 ha or more. The present study explored the use of such map-derived forest variables as explanatory variables for saproxylic species richness, and their correlation with dead wood volume surveyed in the same landscape. The use of map-derived variables as a proxy for dead wood volume might enable more detailed and extensive studies into the response of saproxylic insects at different spatial scales (Holland et al. 2004). Insects were sampled from aspen (*Populus tremula* L.) dead wood, a keystone resource in boreal forests for several species of birds, lichen, fungi and insects (Hogstad & Stenberg 1994; Junninen et al. 2007; Kuusinen 1996; Martikainen 2001; Siitonen & Martikainen 1994; Sverdrup-Thygeson & Ims 2002).

The main questions for this study were;

- Is dead wood volume in general or volume of specific categories of dead wood relevant to saproxylic species richness at spatial scales of 3 km$^2$, 12 km$^2$ or 27 km$^2$?
- Can variables derived from digital maps that describe the surrounding forest at these spatial scales explain variation in saproxylic species richness?
- What are the answers to the questions above if only species richness of aspen associated saproxylic insects is considered?
- How are the explanatory variables related to each other in the landscapes? Particularly; is there a correlation between map-derived forest variables and dead wood surveyed in field?

# 2. Methods

## 2.1 Study design

This study used data from insect sampling for a research project by NINA (Norwegian Institute for Nature Research) and NORSKOG (The Norwegian Forestry Association), and thus the location of the insect sampling sites was determined by the study design of the original project. The aim of the research project was to compare nature reserves with woodland key habitats and retention patches, the latter two being protected elements within the managed forest meant to make forestry more sustainable. The "Living Forests" standard (Anon. 2006) dictates that some relatively small biologically valuable areas, most of which are approximately 0.1 ha of forest, are left intact within the managed forest. These areas correspond to the concept of woodland key habitats and are hereby called by that name in this article. The standard also calls for the retention of living trees, either solitary or in patches. The patches can be left along rivers, lakes and mires with a width of 10-15 meters, or as groups of trees retained on clear-cuts.

Three study areas had been chosen for the research project from all forested areas in south-east Norway using the following criteria;

- Existence of one or more nature reserves with coniferous forest in the area.
- Existence of registered woodland key habitats in the area with the substrate dead wood.
- The managed forest in the area was certified by the ISO 14001 and the Norwegian standard for sustainable forestry, "Living Forests" (Anon. 2006) (certified by PEFC, the Programme for the Endorsement of Forest Certification schemes, Norway).

Sites for insect sampling were placed within nature reserves (NR), woodland key habitats (WKH) or retention patches (R). There were 8 sites in each category in each study area. Thus, there were 24 sites for insect sampling in each study area. The forest surrounding each site was assessed by relascope in order to choose sites where the surrounding forest was equally open, since this might affect the ease of access for insects and thus the number of insects caught at each site. More details on the NINA and NORSKOG project can be found in the project report (Sverdrup-Thygeson et al. 2013).

## 2.2 Study areas

Of the three study areas from the research project, two were chosen for the present study (Figure 1).

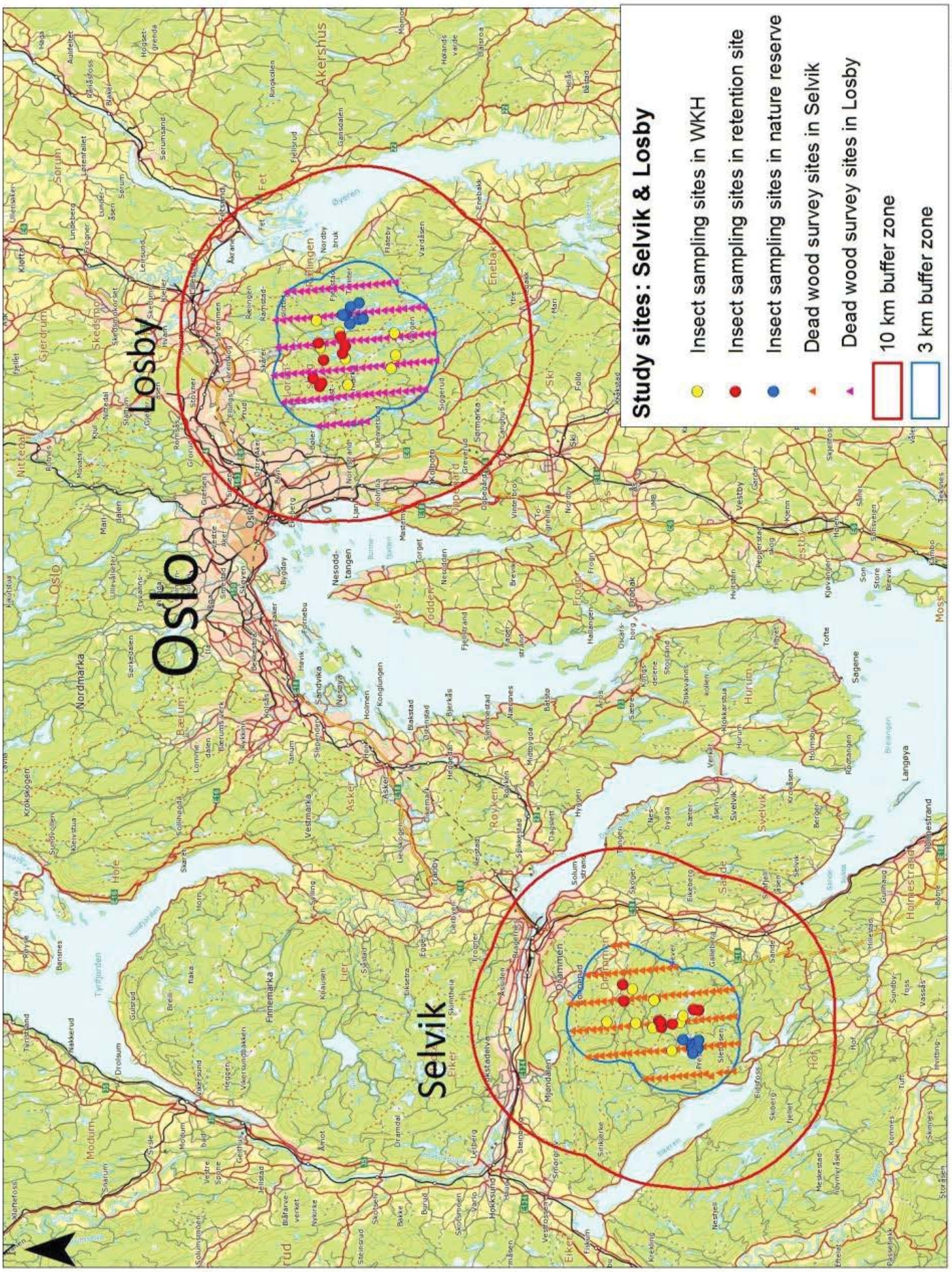

**Figure 1.** The study sites in Selvik and Losby.

### Losby

The area called Losby in this article consisted mainly of forest privately owned by Losby Bruk, but also included the nature reserve Østmarka and some forest owned by Oslo municipality. The bedrock was composed mainly of gneisses. The forest was mostly divided between high or medium productivity classes (Skog og Landskap, K.). Most of the forest was dominated by either pine (*Pinus sylvestris* L.) or spruce (*Picea abies* (L.) H.Karst.). Birch (*Betula pubescens* Ehrh.) was not uncommon, while rowan (*Sorbus aucuparia* L.), alder (*Alnus glutinosa* (L.) Gaertn. and *Alnus incana* (L.) Moench.), aspen and goat willow (*Salix caprea* L.) occurred infrequently. The landscape is in the southern boreal zone. The average annual rainfall was 760 mm and mean temperature in may-august was 13.1$^{o}$C (eKlima 2010). The nature reserve Østmarka was established in 1990 and covered an area of 17.8 km$^2$ (Skog og Landskap, S.). The insect sampling sites in Losby were located about 200 to 300 meters above sea level.

### Selvik

The area called Selvik consisted of forest owned by the forest holding Selvik Bruk and the nature reserve Presteseter. The bedrock was composed of various igneous rocks. Most of the forest was of medium or low productivity class (Skog og Landskap, K.). The area was a mosaic of forest either dominated by spruce or pine, or mixed forest. Birch was not uncommon, while rowan, alder (*A. glutinosa* and *A. incana*), aspen and goat willow occurred infrequently. The landscape is in the southern and mid boreal zone. The average annual rainfall was 975 mm and mean temperature in may-august was 14.7$^{o}$C (eKlima 2010). Presteseter nature reserve was established in 2005 and covered an area of 3.2 km$^2$ located at 400 to 568 meters above sea level (Skog og Landskap, S.). The locations of the insect sampling sites ranged from 100 to 500 meters above sea level.

## 2.3 Insect sampling

Insects were sampled in Selvik and Losby in 2007, 2008 and 2009 for the NINA and NORSKOG research project (Sverdrup-Thygeson et al. 2013). Aspen trees were felled and cut to create 1 m logs with an average diameter of 20 cm. Holes were drilled in the centre of one end of the logs and iron poles were inserted, so that the logs could be positioned as standing dead wood by pressing the protruding part of the iron pole into the ground. The logs were placed in pairs separated by 1.5 m on an east-west line at each of the 24 sites in each study area, thus there were originally 48 logs in Selvik and 48 logs in Losby. Data from two logs at one retention patch site in Selvik is missing as both logs were felled by beavers (*Castor fiber*) in 2007. Window traps were attached to each log. Both logs in the pairs at each site stood exposed the first year after their placement to allow insects to colonize the wood, while during the two following years one of the logs and the attached window trap was covered by a mesh to trap hatching insects. The western logs were covered in 2008 and the eastern logs in 2009. Data from all the years was combined in this study. All beetles (*Coleoptera*) were identified to species level. Species were sorted into the functional groups saproxylics (Sx), aspen associated saproxylics (AA) and aspen specialist saproxylics (AS).

Aspen associated species included all species recorded to utilize aspen, while aspen specialists included species mainly recorded from aspen. This classification relied on the database composed by Dahlberg and Stokland (2004), which was the most complete database for saproxlic insects in Scandinavia. All species were also classified according to the Norwegian Red List (Kålås et al. 2010). Species richness of each insect group was recorded per sample site for statistical analysis.

## 2.4 Dead wood survey

The dead wood survey was conducted during the summer of 2012. In both study areas the survey grid was laid out in a 3 km buffer zone based on the location of the aspen logs used for insect sampling, meaning that all insect sampling sites would have dead wood survey sites within at least 3 km radius. Survey sites were placed with 500 m between them in the north-south direction and 2 km between them in the east-west direction, since the terrain was easier to follow in a north-south direction. The distances were chosen to get the best resolution within the available time for field work. The first north-south transect with survey sites was intentionally placed in the centre of the nature reserves in both areas to ensure that some survey sites represented the dead wood conditions within the nature reserves, since one third of the insect sampling sites in each area had already been placed intentionally in the nature reserves. The reserve in Selvik was small enough to be missed entirely if transects were placed at random. The following north-south transects were laid out from the first with 2 km in between, while the first east-west transect was placed at random and the following with 500 m in between. In Selvik, there were 104 dead wood survey sites spread across a grid that covered 100 km$^2$, while in Losby there were 119 dead wood survey sites on a grid that covered 113 km$^2$.

Each survey site covered 0.04 ha, starting at the GPS coordinate for each site and extending 10 m east, 10 m west and 20 m north. If the GPS coordinate was unreachable, the closest reachable spot was used and a new coordinate was recorded. Four sites were moved due to inaccessibility in Losby and one site in Selvik. At each site, any lying or standing dead wood longer or taller than 1 m and with a diameter of at least 10 cm was recorded. Diameter was measured at breast height (approximately 1.3 m from base) using a calliper. When there was no discernible base to lying logs the diameter was measured at the middle of the log. Length was measured using a measuring tape to the closest half meter, while height was approximated by observation to the closest meter. When logs extended outside the boundaries of the survey site, only the part inside the site was registered. If the base of any such log was outside the site, diameter was measured where the log crossed the site boundary. If the top of a standing dead tree had snapped, but was still attached to the remaining standing trunk, the length of the top was added to the height of the tree. Each log or snag was identified as spruce, pine, aspen or neither of these (the last group effectively consisted of other deciduous trees, mostly birch). These categories will be referred to as tree types, since the last group contains several species. Decay stage was recorded for each dead wood object as one of five decay classes, based on the classification used by Høiland and Bendiksen (1996);

1: Wood hard, bark intact, both larger and smaller branches intact.

2: Wood hard, bark beginning to break up, smaller branches beginning to break off.

3: Wood soft up to 3 cm depth, some bark lost, smaller branches rare.

4: Wood soft for more than 3 cm depth, little bark, larger branches beginning to break off.

5: Wood soft all the way through, little or no bark, few or no branches.

## 2.5 Dead wood variables

Volume of each dead wood (DW) object was calculated using equation (1), which was also used by Fridman and Walheim (2000);

$$V = \frac{\pi d^2}{4} l \qquad \text{[Equation 1]}$$

where V is volume of the dead wood object, d is diameter in meters and l is length or height in meters. Volume of all dead wood objects at each survey site was divided by the area of the site (0.04 ha) to calculate cubic meters of dead wood per hectare. Since there was a varying number of survey sites within 1 km, 2 km or 3 km radius of the different insect sampling sites, the average DW volume per ha was calculated. Each insect sampling site thus had a measure of mean DW volume per ha within 1 km radius (covering 314 ha), within 2 km radius (covering 1257 ha) and within 3 km radius (covering 2827 ha) (Figure 2).

The circular areas of different sites overlapped to varying degree. Of course, the overlap increased as the radius increased. Insect sampling sites sharing the same area within the radii would necessarily have more similar explanatory variables. Some researchers advice to avoid spatial overlapping of explanatory variables in order to avoid spatial autocorrelation (Holland et al. 2004). However, it has also been argued that spatial overlapping does not necessarily lead to spatial autocorrelation, and that interdependent predictors does not necessarily mean interdependent errors which is the critical assumption for statistical modelling (Zuckerberg et al. 2012). In this study, most over the overlapping areas occurred in the nature reserves. It was desirable to both have the same number of insect sampling sites within nature reserves as there were in WKH and retention patches in the same landscape and to have explanatory variables covering relatively large scales. Since there was only one nature reserve in each landscape, while WKH and retention patches were small, scattered and more abundant, the insect sampling sites in the nature reserve were necessarily closer to each other and overlapping of their explanatory variables was unavoidable. The insect sampling sites did have a minimum distance to each other of 300 meters to avoid that logs and the attached window traps had to “compete” to attract or catch the same individual insects.

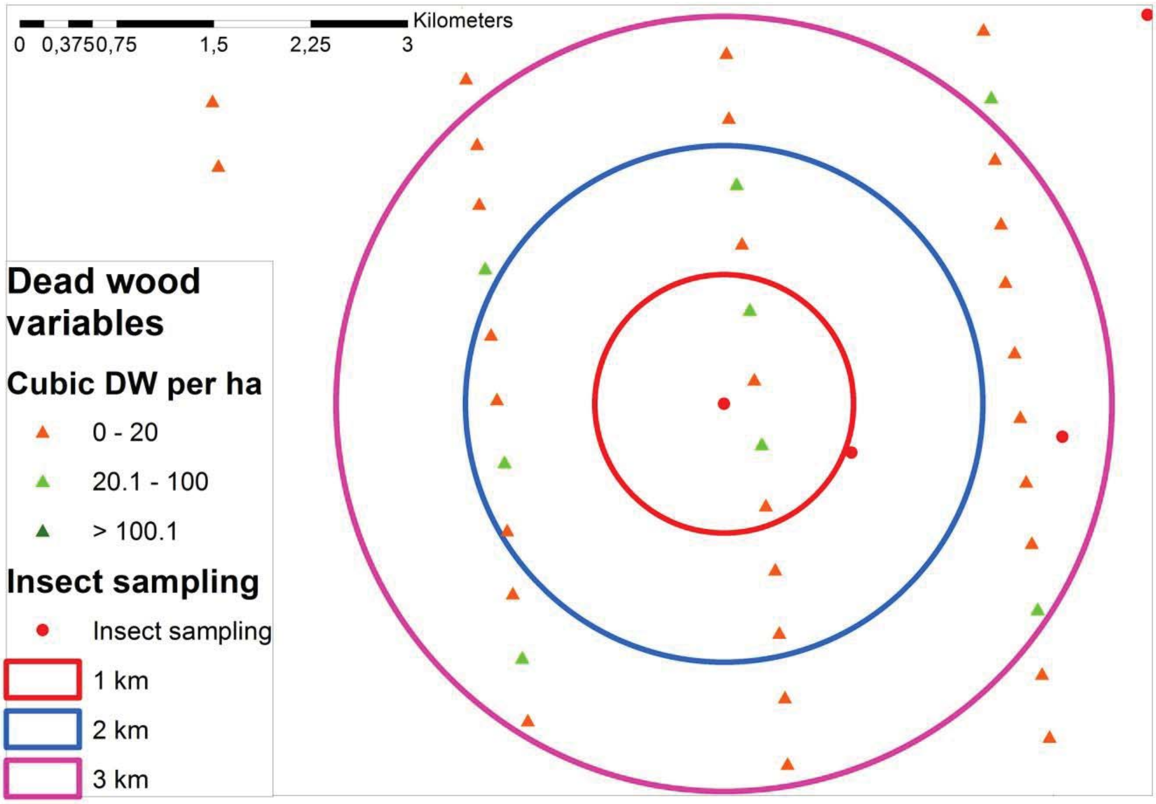

**Figure 2.** Example of the dead wood survey sites (triangles) within the three radii (circles; red = 1 km radius, blue = 2 km radius, pink = 3 km radius) of one insect sampling site (red dot in the centre of the circles). Dead wood abundance within each radius was estimated by calculating the mean dead wood volume per ha for the dead wood survey sites within that radius.

DW volume per ha was partitioned between the different tree types and between the five decay stages, thus providing each insect sampling site with DW volume per ha of each tree type and each decay stage within each radius. Furthermore, DW volume per ha was also divided in three groups depending on the diameter of the dead wood;

- SmallDiam: 10-20 cm

- MidDiam: 21-30 cm

- LargeDiam: >30 cm

DW volume per ha of each diameter group was also calculated for the areas within the radii of each insect sampling site.

## 2.6 Map-derived forest variables

Map layers (“SAT-skog”) describing the forest in the study areas were downloaded from the servers of the Norwegian Forest and Landscape Institute (Skog og Landskap, M.). This data was ultimately derived from satellite images of the landscape, and described attributes such as volume of the forest in $m^3$ per hectare (VUPRHA), volume of deciduous trees in the forest in $m^3$ per hectare (VUPRHAL) and age of the forest in years (ALDER) for forest areas of varying size. Only areas registered as forest were included in the SAT-skog data, although clear-cuts were included. While the data for Losby presumably described the conditions during insect sampling fairly accurately since it came from satellite images taken in 2007, the data for Selvik was derived from satellite images taken in 1999. However, the SAT-skog data from Selvik and Losby showed the same trends as predictor variables for saproxylic insect species richness and 8 years is not a long time in relation to the life-span of trees.

The data was processed in ArcMap version 10.1. Circular areas with radii of 1 km, 2 km and 3 km were constructed for each insect sampling point (Figure 3). These were used to cut the SAT-skog layer into new shape-files, one for each circular area, containing only the data from SAT-skog within the circle and with a new field added to the attribute table in which the new area of the cut forest polygons was calculated. These new polygon areas were summarized in each of these new shape-files by VUPRHA, VUPRHAL and ALDER. This produced dbf-tables with area in m$^2$ for the different values of each of these attributes, three tables (one for each circular area) for each insect sampling point.

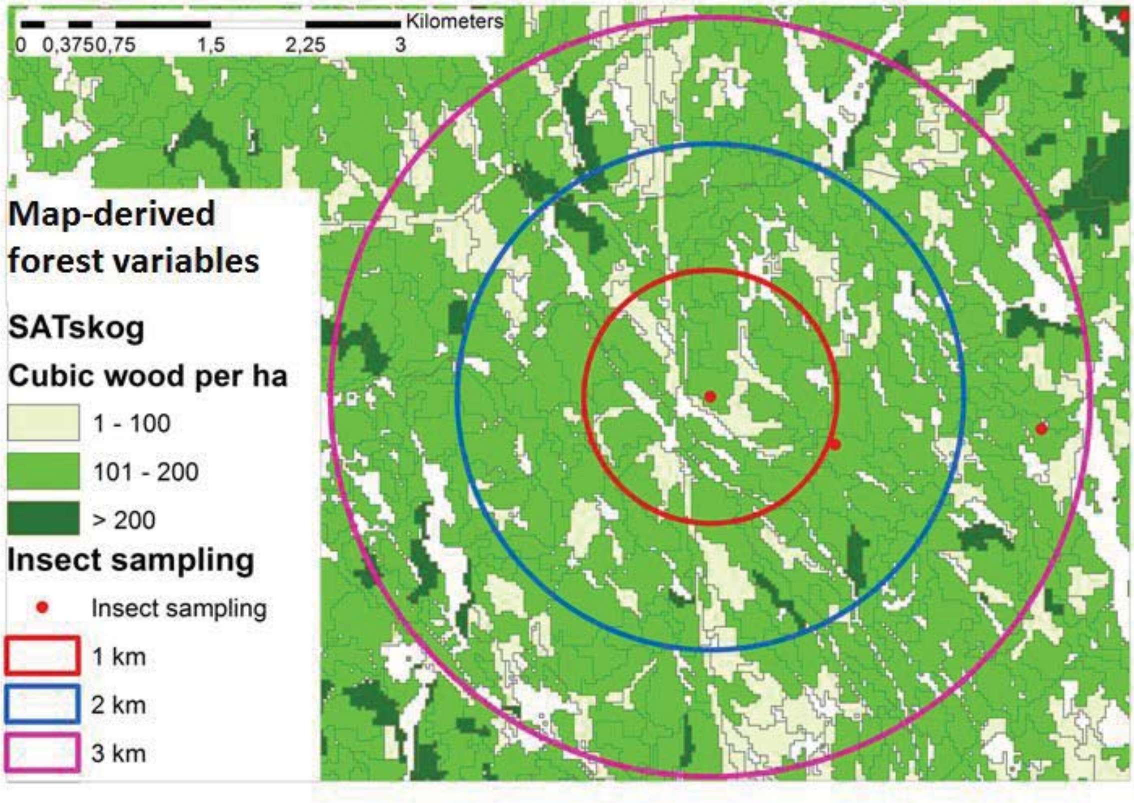

**Figure 3.** Example of the SAT-skog map layer for volume in m$^3$ of forest (VUPRHA) within the three radii (circles; red = 1 km radius, blue = 2 km radius, pink = 3 km radius) of <u>one</u> insect sampling site (red dot in the centre of the circles). The area of all the polygons within each radius was summed up for each category of forest volume.

The data in the dbf-tables was processed further in Mircosoft Office Excel 2007. The values for the attributes VUPRHA, VUPRHAL and ALDER were sorted into groups (Table 1) according to the legend that followed the SAT-skog data (Skog og Landskap, I.).

**Table 1.** Code for the three levels of each of the three SAT-skog categories; VUPRHA,VURPHAL and ALDER.

| Code | Values |
|---|---|
| VUPRHA | |
| LowVolForest | 1-100 $m^3$ forest per ha |
| MidVolForest | 101-200 $m^3$ forest per ha |
| HighVolForest | > 200 $m^3$ forest per ha |
| VUPRHAL | |
| LowDeciForest | 0-35 $m^3$ deciduous wood per ha |
| MidDeciForest | 36-75 $m^3$ deciduous wood per ha |
| HighDeciForest | > 75 $m^3$ deciduous wood per ha |
| ALDER | |
| YoungForest | 1-40 years |
| MidAgeForest | 41-80 years |
| OldForest | > 80 years |

The areas of the polygons within each circular area for each insect sampling site were summed up according to these groups, which resulted in the area of the variables in Table 1 within 1 km, 2 km or 3 km radius of each insect sampling site. Also, the sum of the area of all groups within one category (for instance, YoungForest + MidAgeForest + OldForest) for each circle gave the area of forest within that circle radius; Forest_1km, Forest_2km and Forest_3km, for each insect sampling site. The VUPRHA forest type (LowVolForest, MidVolForest or HighVolForest) of the dead wood survey sites was also registered.

## 2.7 Statistical methods

All data was analyzed in R version 2.15.0.

Unless otherwise stated, the significance level was $\alpha = 0.05$.

As this is a correlation study, cause-effect relationships cannot be derived from significant relationships. The suggestion of cause-effect relationships in the interpretation of the results is based on ecological knowledge and correspondence with prior studies.

The distributions of response variables were investigated using normal QQ plots and frequency histograms, and the Shapiro-Wilk test for normality was used to determine whether to use parametric or non-parametric tests (Teetor 2011). Some variables were log-transformed or square-root transformed to achieve normality.

Normal distributed response variables that were to be tested in groups were first tested for heteroscedacity using the Bartlett test of homogeneity of variances (Dalgaard 2008). If the Bartlett test was significant, the data was analyzed using a one-way analysis of means that does not assume equal variances (Dalgaard 2008). Normal distributed data with homogenous variance was tested for group effects with one-way ANOVA. Data that could not achieve normality was tested for group effects by the Kruskal-Wallis rank sum test. Although the Kruskal-Wallis might also be affected by heteroscedacity, it is more robust than the one-way ANOVA. The chance of making a type I error in a Kruskal-Wallis rank sum test does not seem to increase due to inhomogenous variance, it is rather a very conservative test (Moder 2010). Significance of the grouping effect in an ANOVA, one-way analysis of means or the Kruskal-Wallis test was followed by pairwise tests, either parametric t-tests or non-parametric Wilcoxon rank sum tests. For parametric but heteroscedastic data the pairwise t-tests were performed without pooled standard deviation. All pairwise tests were performed with the sequential Bonferroni adjustment ("holm" in R) of the p-value to correct for multiple testing (Holm 1979). The sequential Bonferroni i.e. the Holm adjustment is the default adjustment for pairwise tests in R, and as such recommended over the original and more conservative Bonferroni adjustment. The p-values from the pairwise Wilcoxon rank sum tests were mostly not exact p-values due to the frequency of tied values within the dataset.

## Model selection process

There were no apparent non-linear trends in the scatter plots for explanatory variables against response variables, therefore linear regression was used with single explanatory variables combined with binary design variables. Explanatory variables that achieved a p-value above 0.10 in the simple linear regression were excluded from the multiple regression analysis. For those variables that had a p-value below 0.10 on several of the spatial scales (the 1 km, 2 km and 3 km radii), the spatial scale at which the variable had the highest adjusted $R^2$ was chosen. Although the standard deviation of the DW variables increased with decreasing scale while the standard deviation of the map-derived forest variables increased with increasing scale, there was no consistent correlation between standard deviation and most significant scale for either category of explanatory variable. The chosen variables were checked for effect of outliers by plotting residuals. The most influential outlier as seen by Cook's distance was temporarily excluded and if the outcome of the regression changed substantially the variable was not included in the initial model. The optimal subset of the variables entered in the multiple regression model was chosen in a stepwise selection in both directions (backward and forward selection) based on the Akaike information criterion (stepAIC-function from the MASS package in R). The Akaike information criterion (AIC) weighs the variation explained by the model against the complexity (i.e. the number of variables) of the model (Akaike 1974). A lower AIC value is preferred. The stepAIC-function in R sometimes keeps insignificant variables in the model. If this occurred, backward selection was used to remove insignificant variables as long as the adjusted $R^2$ of the model remained adequate.

Due to differences between the landscapes and between the forest management categories, two design variables were included in all linear regression models on single explanatory variables; the binary design variable Landscape where 1 signified site in Losby and 0 signified site in Selvik, and the design variable NR where 1 signified nature reserve site and 0 signified woodland key habitat or retention patch site. However, the model selection process (stepAIC) was free to exclude the design variables from the multiple regression model.

Final multiple regression models were assessed by their residual plots for deviation from the assumptions of normally distributed and independent errors with constant variance. In addition, the Durbin-Watson test was used to check for autocorrelation of the residuals (Durbin & Watson 1950; Durbin & Watson 1951). The variables included in the final model were also assessed for interdependency as seen by their Spearman correlation matrix and as judged by their variance inflation factors (the vif-function in the “car” package). The rule of thumb that variance inflation factors above 10 are too high has been commonly used, but in most cases simply as an arbitrary limit without consideration for the effects of multicollinearity within the context of each study (O’brien 2007). O’brien (2007) pointed out that if other measures of the relations within the regression model are sound, such as the p-values of the predictors and the variance explained by the model, then high variance inflation factors simply means that the relations of the model tolerated the increased variance from collinearity. $R^2$ was partitioned among the variables by the calc.relimp-function from the “relaimpo” package (Grömping 2006). Partitioning explained variance among the regressors of a model provides a quantitative measure of the relative importance of each variable. Explained variance can be partitioned quite easily between uncorrelated variables by simply removing or adding the variable to the model and calculating the change in $R^2$. However, the proportion of variance explained by correlated variables depends on the order in which they enter the model. Two methods have been developed for partitioning explained variance between correlated variables; LMG by Lindeman, Merenda and Gold (1980) and PMVD by Feldman (2005). Both calculate relative importance by entering the variables in all possible orders and averaging the proportion explained by each variable over all orders, but PMVD also adds weights to the orders to be able to satisfy the exclusion criterion which states that a variable whose estimator is zero should receive zero explained variance. However, according to Grömping (2007), the exclusion criterion may not be preferable if the intention of the model is causal interpretation of the variables. Grömping (2007) also found in his simulation study that PMVD often has more variable estimates than LMG. Thus, in this study $R^2$ was partitioned with the LMG method. The estimated proportion of $R^2$ explained by each variable was plotted in a bar graph with 95% confidence intervals for the estimated proportion obtained by resampling the data according to the bootstrap procedure.

Principal component analysis (PCA) was used to find the main gradients of variation and correlation in the explanatory variables that had been chosen for model selection. PCA for all explanatory variables at all scales would have required a much greater number of sample sites. The principle components were considered as predictors in the models for species richness instead of the explanatory variables themselves. However, the explanatory variables were preferred as they explained more of the variation in the response variables and allowed the effect of each variable to be recognizable.

# 3. Results

## 3.1 Insect sampling

The insect sampling yielded 512 different beetle species among the 11 159 individual beetles. While 65 species were sampled exclusively in Losby, 188 species were exclusive to Selvik. 345 species (9304 individuals) were considered saproxylic, and among these there were 138 aspen associated species (5594 individuals) while 9 of these species were considered aspen specialists (437 individuals). 21 red-listed species (70 individuals) were sampled, of which only one species represented by one individual was registered in the Norwegian red list as endangered (*Acmaeops septentrionis*, (Thomson 1866)). The remaining 20 red-listed species were registered as either near threatened or vulnerable.

## 3.2 Dead wood survey

The total volume of dead wood registered in the field survey was 96 $m^3$ in Selvik and 119 $m^3$ in Losby, of which 11 $m^3$ and 2 $m^3$ was dead wood of aspen in Selvik and Losby, respectively. Mean volume of dead wood per ha was 23 $m^3$ per ha in Selvik and 25 $m^3$ per ha in Losby.

The areas within the larger radii naturally covered a greater number of dead wood survey sites. To check whether the ratio between the area of the landscape and the number of survey sites was similar for all scales, area within the circles was divided by number of survey sites. Mean area per dead wood survey site was similar in all circular areas (3 km radius: 96.1 ha per site, 2 km radius: 98.9 ha per site, 1 km radius: 93.2 ha per site).

**Table 2.** Proportion the different dead wood types constituted of total dead wood volume in Losby and Selvik. Deciduous = deciduous dead wood excluding aspen dead wood.

| Dead wood type | Proportion in Losby | Proportion in Selvik |
|---|---|---|
| Spruce | 72.7 % | 71.9 % |
| Deciduous | 16.0 % | 14.1 % |
| Aspen | 1.8 % | 4.5 % |
| Pine | 9.5 % | 9.5 % |
| Decay stage 1 | 11.9 % | 8.7 % |
| Decay stage 2 | 44.2 % | 46.7 % |
| Decay stage 3 | 19.5 % | 20.1 % |
| Decay stage 4 | 14.0 % | 12.4 % |
| Decay stage 5 | 10.4 % | 12.1 % |
| Diameter 10-20 cm | 34.9 % | 36.8 % |
| Diameter 21-30 cm | 32.0 % | 34.1 % |
| Diameter > 30 cm | 33.1 % | 29.1 % |

Although each of the three diameter groups constituted roughly one third of the DW volume (Table 2), they differed greatly in their share of the number of DW objects. The smallest diameter group accounted for 81.0% and 77.8% of the total number of DW objects in Selvik and Losby, respectively. Only 4.7% and 5.8% of the DW objects in Selvik and Losby had a diameter of more than 30 cm.

## 3.3 Differences between landscapes and forest management categories

### Landscape

#### Insects

Significantly more species and individuals were sampled in Selvik than in Losby for all categories except aspen specialists, which showed no significant difference (Figure 4 &

Figure 5).

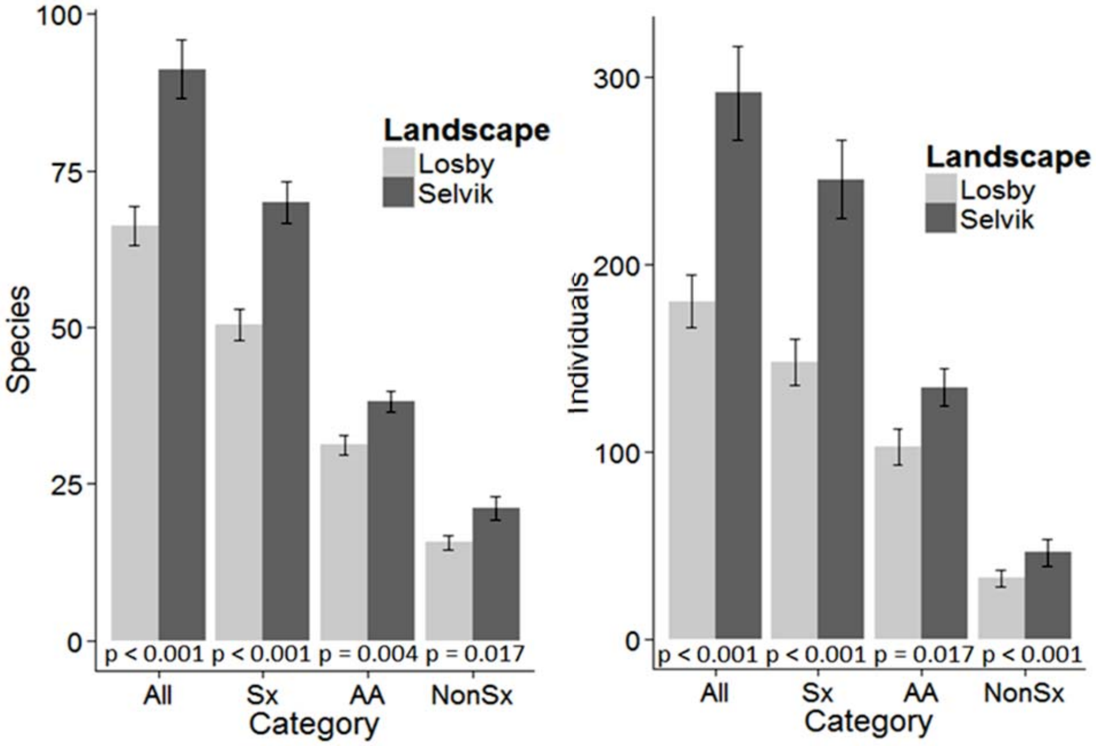

**Figure 4.** Average number with standard error of the mean (SEM) of species and individuals of beetles sampled per sample site in Losby and Selvik in each of the following categories: All – all beetles, Sx – saproxylic beetles, AA – Aspen associated beetles, NonSx – beetles not considered saproxylic (i.e. All minus Sx). P-values from Wilcoxon rank sum tests (NonSx) or Welch two-sample t-tests (All, Sx, AA) for differences between landscapes are shown above the relevant insect categories.

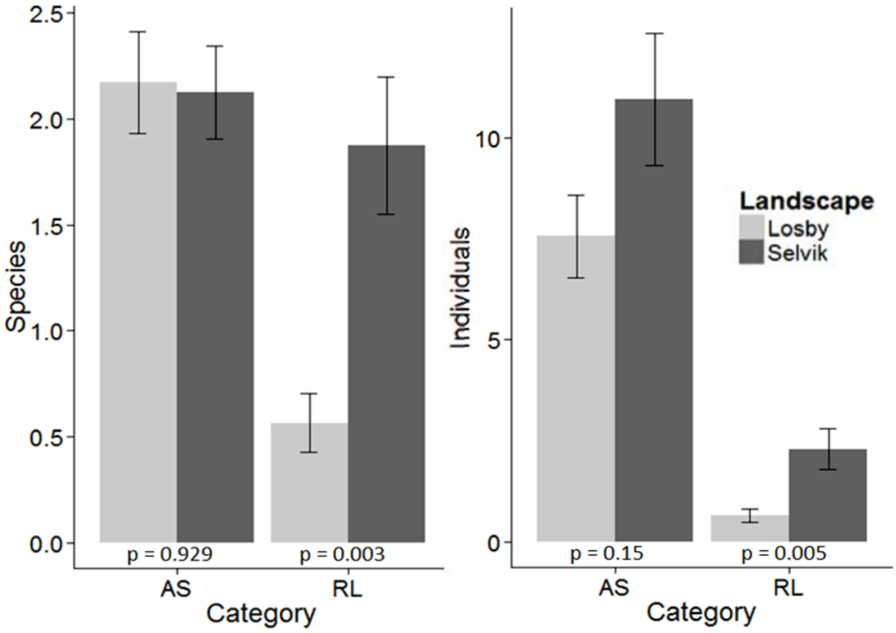

**Figure 5.** Average number with standard error of the mean (SEM) of species and individuals of beetles sampled per sample site in Losby and Selvik in each of the following categories: AS – aspen specialists, RL – red listed. P-values from Wilcoxon rank sum tests for differences between landscapes are shown above the relevant insect categories.

### Dead wood survey

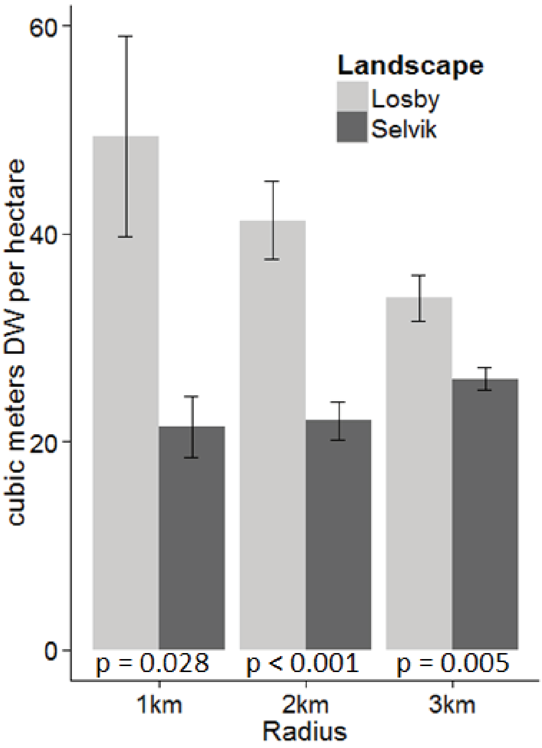

**Figure 6.** Mean m$^3$ dead wood (DW) per ha with standard error of the mean (SEM) within 1 km, 2 km or 3 km radius of the insect sampling sites in Selvik and Losby. P-values from Wilcoxon rank sum tests of the difference in m$^3$ DW per ha between landscapes are shown above the relevant radius.

There was no difference between Selvik and Losby in mean DW volume registered at each survey site (Wilcoxon rank sum test, W = 5434.5, p-value = 0.952). However, the mean DW abundance within the 3 km, 2 km and 1 km radii of the insect sampling sites was significantly higher in Losby (Figure 6). Thus, although similar volumes of DW were found at the survey sites in each landscape, the distribution of the survey sites within the circular areas centred on the insect sampling sites resulted in larger volumes surrounding insect sampling sites in Losby. There was also significantly more dead wood of aspen per ha within the areas covered by the 3 km radii in Losby than in Selvik (appendix table 1 no. 6). Thus, the differences between the landscapes in dead wood abundance were contrary to what one would expect judging from the differences in saproxylic species richness (Figure 4).

### Map-derived forest variables

There were significantly larger areas of forest with medium volume of deciduous wood within the 3 km radius of insect sampling sites in Selvik (appendix table 1 no. 63). There were also significantly larger areas of young forest and forest with low volume of living trees surrounding insect sampling sites in Selvik at all scales (appendix table 1 no. 40-42 & 49-51).

## Forest management categories

Data from both landscapes was combined when testing for differences between forest management categories.

### Insects

Significantly fewer species of all insects and of saproxylic insects were sampled from the sites in nature reserves relative to the sites in woodland key habitat or retention patches (Figure 7). The trend was similar for number of individuals. There were no significant differences for aspen associated saproxylics, aspen specialist saproxylics or red listed insects (Figure 7 & Figure 8).

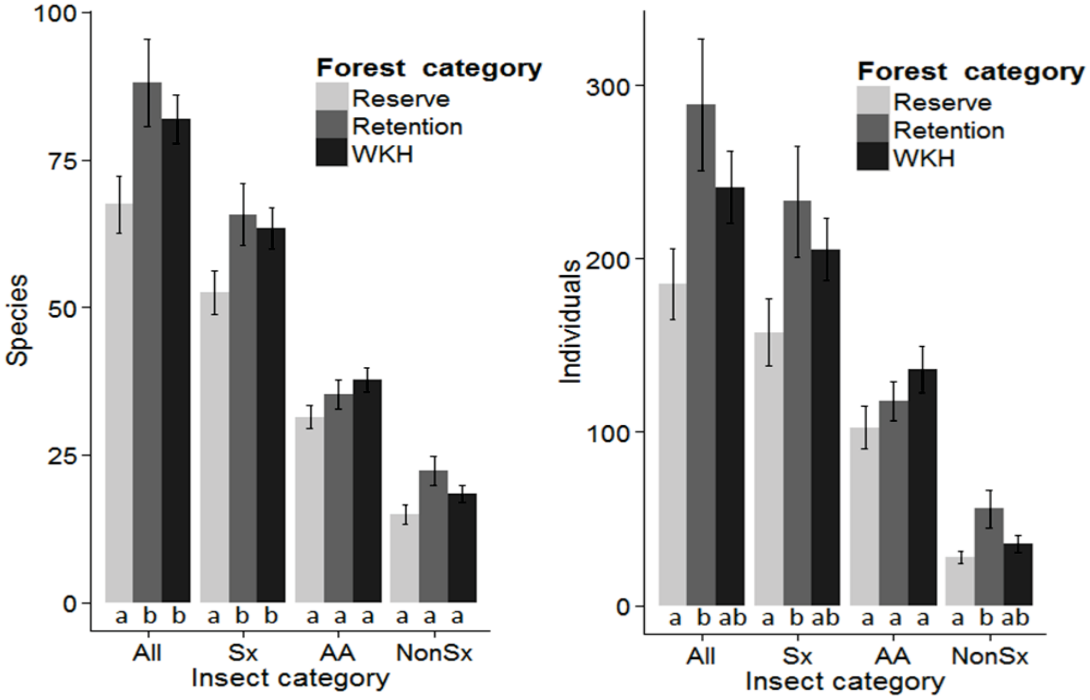

**Figure 7.** Average number with standard error of the mean (SEM) of species and individuals per insect sampling site in the three forest categories nature reserve, retention and woodland key habitat (WKH) in the following insect categories; All – all beetles, Sx – saproxylic beetles, AA – aspen associated beetles, NonSx – beetles not considered saproxylic (i.e. All minus Sx). Different letters below the bars signify statistically significant differences (p-value < 0.05) in pairwise t-tests between the forest categories for that insect category (see appendix table 2 no. 71-82).

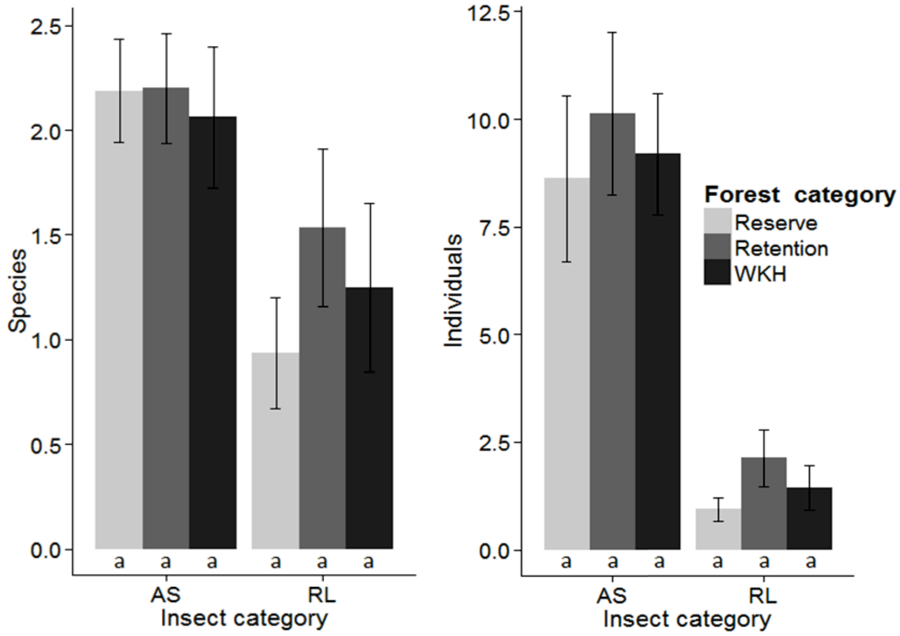

**Figure 8.** Average number with standard error of the mean (SEM) of species and individuals per insect sampling site in the three forest categories nature reserve, retention and woodland key habitat (WKH) in the following insect categories; AS – aspen specialists, RL – red listed. Different letters below the bars signify statistically significant differences (p-value < 0.05) in pairwise t-tests between the forest categories for that insect category (see appendix table 2 no. 71-82).

## Dead wood survey

Significantly larger volumes of dead wood were surveyed around the insect sampling sites in the nature reserves relative to insect sampling sites in WKH and retention sites (Figure 9). There were no significant differences between dead wood volumes of aspen surrounding sites in the different forest management categories (appendix table 2 no. 4-6). The only significant difference between WKH and retention sites was significantly more dead wood of pine within the 1 km radius of the WKH sites (appendix table 2 no. 10).

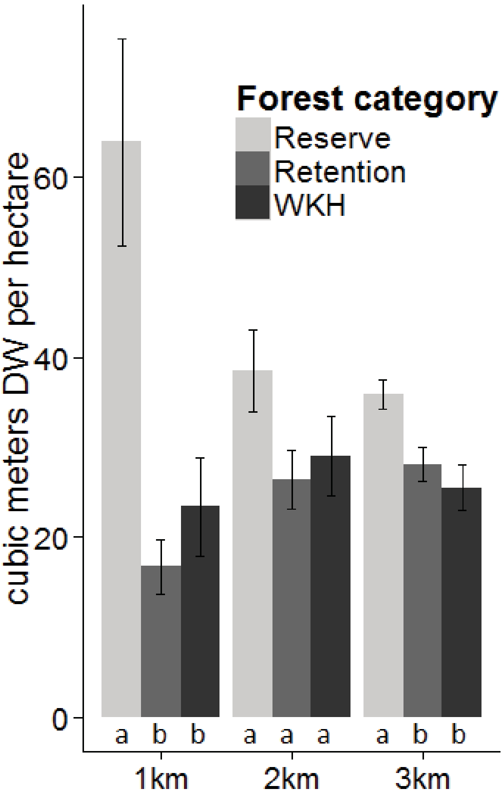

**Figure 9.** Mean $m^3$ dead wood (DW) per ha with standard error of the mean (SEM) within 1 km, 2 km or 3 km radius of the insect sampling sites in either nature reserves, woodland key habitats or retention sites. Different letters below the bars denote statistically significant ($p$-value $< 0.05$) differences from pairwise tests between the forest categories for $m^3$ DW per ha within the specific radius (see appendix table 2 no. 1-3).

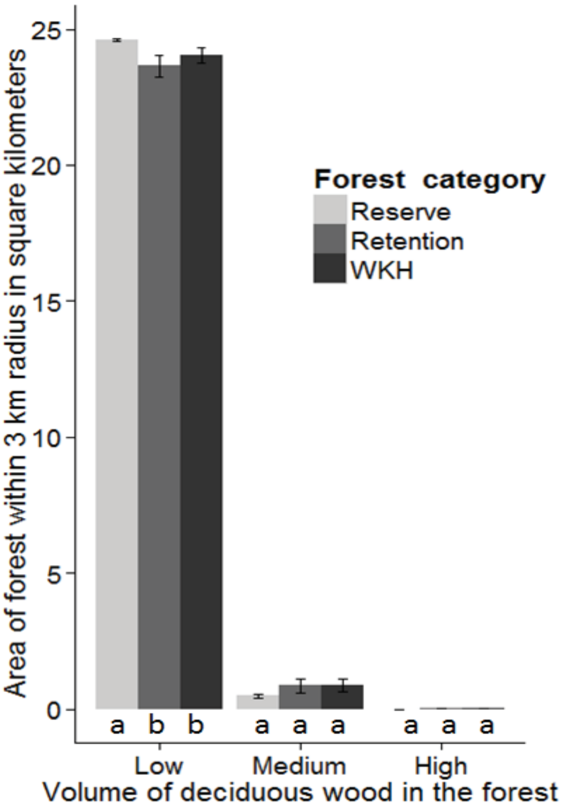

**Figure 10.** Area in $km^2$ with standard error of the mean (SEM) of forest with low, medium or high volume of deciduous wood within 3 km radius of the NR, WKH or retention sites. Different letters below the bars signify statistically significant differences ($p$-value $< 0.05$) between the forest categories for that category of deciduous wood volume (see appendix table 2 no. 51, 54 & 57).

## Map-derived forest variables

There was more forest with little deciduous wood surrounding the NR sites relative to the WKH and retention sites (Figure 10). Sites in woodland key habitats and retention patches were surrounded by significantly larger areas of forest in general and of forest with medium volume of wood within 1 km radius than the sites in nature reserves (appendix table 2 no. 52 & 67). In general, there was more old forest around the nature reserve sites than around the sites in woodland key habitats and retention patches (appendix table 2 no. 46-48).

## 3.4 Explaining variation in insect species richness

Regression models were used to explain the variation in saproxylic species richness or aspen associated saproxylic species richness between the insect sampling sites. Of all the potential explanatory variables, only the variables in Table 3 and Table 4 had relatively robust correlations with p-values under 0.10 in linear regression against saproxylic species richness and aspen associated species richness, respectively. The dead wood variables were only correlated with species richness of saproxylic or aspen associated saproxylic insects at one spatial scale, while the most of the map-derived forest variables were significant at several scales. For these forest variables, only the scale at which they explained the most variance in the response was included in Table 3 and Table 4.

### Species richness of saproxylic insects

Abundance of dead wood within 1 km radius of the insect sampling sites had a positive correlation with saproxylic species richness, while abundance of dead wood in the first decay stage was significant to saproxylic species richness when estimated at the 2 km radius (Table 3). Area of forest with medium (MidDeciForest) or much (HighDeciForest) deciduous wood was positively correlated with saproxylic species richness sampled from the aspen logs, while area of forest with little deciduous wood was negatively correlated (Table 3).

**Table 3.** Explanatory variables and a description of their values, with p-values and slope estimates (β) from simple linear regression together with design variables for landscape and the nature reserve against the log-values for saproxylic species richness. Significant p-values (<0.05) are bold.

| Variable | Values | Estimated β | p-value |
|---|---|---|---|
| DW_1km | $m^3$ dead wood per ha within 1 km radius of the insect sampling sites | 0.002 | **0.042** |
| DWAspen_2km | $m^3$ dead wood of aspen per ha within 2 km radius of the insect sampling sites | 0.085 | 0.058 |
| DWPine_2km | $m^3$ dead wood of pine per ha within 2 km radius of the insect sampling sites | 0.026 | **0.050** |
| DWDecay1st_2km | $m^3$ dead wood in decay stage 1 per ha within 2 km radius of the insect sampling sites | 0.026 | **0.038** |
| DWDecay3rd_1km | $m^3$ dead wood in decay stage 3 per ha within 1 km radius of the insect sampling sites | 0.009 | 0.058 |
| DWMidDiam_1km | $m^3$ per ha of dead wood with diameter 21-30 cm within 1 km radius of the insect sampling sites | 0.005 | 0.064 |
| YoungForest_2km | $m^2$ of forest areas that are 1-40 years old within 2 km radius of the insect sampling sites | $0.109 \times 10^{-6}$ | **0.031** |
| MidAgeForest_1km | $m^2$ of forest areas that are 41-80 years old within 1 km radius of the insect sampling sites | $0.214 \times 10^{-6}$ | **0.004** |
| OldForest_3km | $m^2$ of forest areas that are over 80 years old within 3 km radius of the insect sampling sites | $-0.029 \times 10^{-6}$ | **0.012** |
| MidVolForest_1km | $m^2$ of forest areas with 101-200 $m^3$ forest per ha within 1 km radius of the insect sampling sites | $0.333 \times 10^{-6}$ | **0.005** |
| LowDeciForest_3km | $m^2$ of forest areas with 0-35 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | $-0.069 \times 10^{-6}$ | **0.021** |
| MidDeciForest_2km | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 2 km radius of the insect | $0.227 \times 10^{-6}$ | **0.002** |

| | | | |
|---|---|---|---|
| | sampling sites | | |
| HighDeciForest_2km | $m^2$ of forest areas with over 75 $m^3$ deciduous forest per ha within 2 km radius of the insect sampling sites | $5.850 \times 10^{-6}$ | **0.002** |
| Forest_1km | $m^2$ of forest area within 1 km radius of the insect sampling sites | $0.385 \times 10^{-6}$ | 0.057 |
| Altitude | meters above sea level for each insect sampling site | -0.001 | **0.028** |

All variables in Table 3 together with the design variables were entered in the initial multiple regression model. No interactions were included. The model selection process based on the Akaike information criterion gave the following model;

$$\log(\text{SxSp}) \sim -\ 0.620\ \text{Landscape} - 0.236\ \text{NR} + 0.042\ \text{DWPine\_2km} + 0.008\ \text{DWMidDiam\_1km} + 1.923\text{x}10^{-7}\ \text{MidAgeForest\_1km} + 2.653\text{x}10^{-7}\ \text{MidVolForest\_1km} \quad \text{[Equation 2]}$$

This model had 40 degrees of freedom and an adjusted $R^2$ of 72.24%. All variables were highly significant (p-value < 0.01). Area of middle aged forest within 1 km radius of the insect sampling sites (MidAgeForest_1km) was correlated with both area of forest with medium volume of living trees within 1 km radius (MidVolForest_1km) (Spearman's rank correlation rho = 0.604, p-value < 0.001) and volume per ha of pine dead wood within 2 km radius (DWPine_2km) (Spearman's rank correlation rho = - 0.446, p-value = 0.002). However, variance inflation factors (all < 3) showed no sign of multicollinearity.

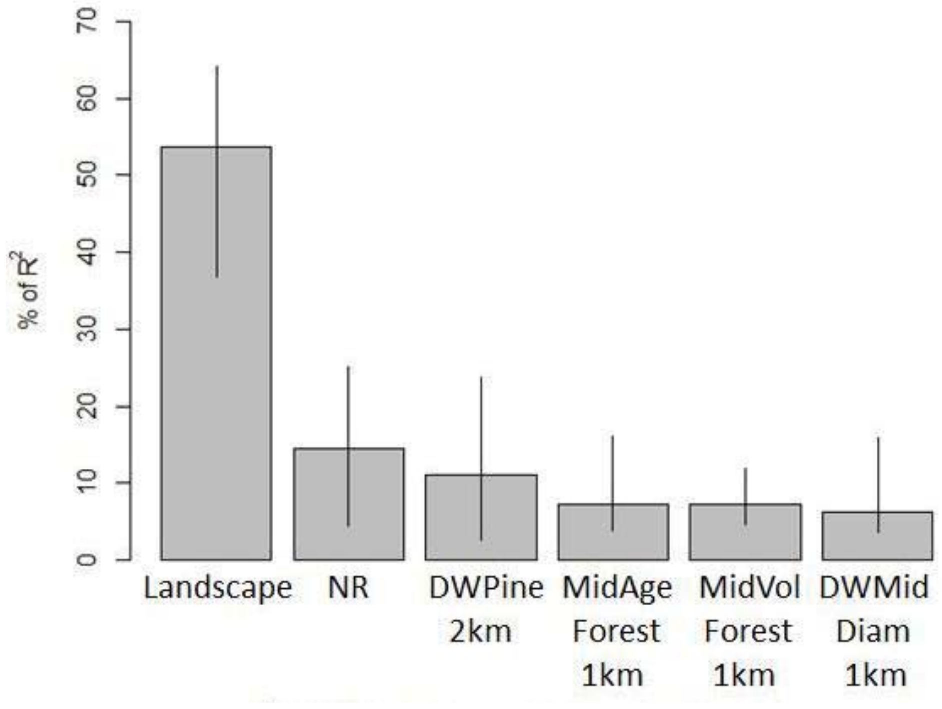

**Figure 11.** Relative importance with 95% bootstrap intervals of the predictor variables included in the final model explaining saproxylic species richness (equation 2) presented as percent of $R^2$. $R^2$ = 75.86%, metrics of the graph were normalized to sum 100%. Variables are explained in Table 3.

Partitioning the $R^2$ among the variables showed that the landscape factor explained the largest portion of the variation in saproxylic species richness (Figure 11), due to the significantly fewer saproxylic species in Losby (Figure 4). The design variable for nature reserve and the variable for dead wood of pine each covered 10 - 20 % of the explained variation, while the remaining variables covered slightly less than 10 % each (Figure 11). Like the landscape factor, the NR factor had a negative effect on saproxylic species richness in the model (equation 2), due to the significantly lower saproxylic species richness at the NR sites (Figure 7). All the other variables in the model had positive effects (equation 2). The significance of pine dead wood both in simple regression (Table 3) and in multiple regression (equation 2) was unexpected.

## Species richness of aspen associated saproxylic insects

Many of the variables that were significant to saproxylic species richness were also significant to the subgroup aspen associated saproxylic species richness (Table 3 & Table 4), but volume of dead wood in decay stage 5 was only correlated with aspen associated species richness. Furthermore, the correlation with volume of aspen dead wood was stronger for aspen associated species richness while the correlation with volume of dead wood in general was weaker.

**Table 4.** Explanatory variables and a description of their values, with p-values and slope estimates (β) from simple linear regression together with design variables for landscape and the nature reserve against aspen associated species richness. Significant p-values (<0.05) are bold.

| Variable | Values | Estimated β | p-value |
|---|---|---|---|
| DW_1km | $m^3$ dead wood per ha within 1 km radius of the insect sampling sites | 0.073 | 0.091 |
| DWAspen_2km | $m^3$ dead wood of aspen per ha within 2 km radius of the insect sampling sites | 4.882 | **0.002** |
| DWPine_2km | $m^3$ dead wood of pine per ha within 2 km radius of the insect sampling sites | 0.926 | 0.053 |
| DWDecay1st_2km | $m^3$ dead wood in decay stage 1 per ha within 2 km radius of the insect sampling sites | 0.924 | **0.037** |
| DWDecay5th_1km | $m^3$ dead wood in decay stage 5 per ha within 1 km radius of the insect sampling sites | 1.643 | **0.031** |
| YoungForest_2km | $m^2$ of forest areas that are 1-40 years old within 2 km radius of the insect sampling sites | $3.645 \times 10^{-6}$ | **0.046** |
| MidAgeForest_1km | $m^2$ of forest areas that are 41-80 years old within 1 km radius of the insect sampling sites | $7.786 \times 10^{-6}$ | **0.004** |
| OldForest_3km | $m^2$ of forest areas that are over 80 years old within 3 km radius of the insect sampling sites | $-0.8729 \times 10^{-6}$ | **0.033** |
| MidVolForest_1km | $m^2$ of forest areas with 101-200 $m^3$ forest per ha within 1 km radius of the insect sampling sites | $14.6 \times 10^{-6}$ | **0.001** |
| LowDeciForest_3km | $m^2$ of forest areas with 0-35 $m^3$ deciduous | $-3.07 \times 10^{-6}$ | **0.004** |

|  |  |  |  |
|---|---|---|---|
|  | forest per ha within 3 km radius of the insect sampling sites |  |  |
| MidDeciForest_3km | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 5.709 x $10^{-6}$ | **< 0.001** |
| HighDeciForest_3km | $m^2$ of forest areas with over 75 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 133.2 x $10^{-6}$ | **< 0.001** |
| Forest_1km | $m^2$ of forest area within 1 km radius of the insect sampling sites | 17.38 x $10^{-6}$ | **0.036** |
| Altitude | meters above sea level for each insect sampling site | -0.039 | **0.006** |

All variables in Table 4 together with the design variables were entered in the initial multiple regression model. No interactions were included. The model selection process based on the Akaike information criterion gave the following model;

AASp ~ – 17.49 Landscape + 0.939 DWPine_2km + 0.974 DWDecay1st_2km + 1.015 DWDecay5th_1km + $1.225 \times 10^{-5}$ MidAgeForest_1km + $1.562 \times 10^{-6}$ OldForest_3km + $1.509 \times 10^{-4}$ HighDeciForest_3km + $1.053 \times 10^{-5}$ Forest_1km [Equation 3]

The final model contained had 38 degrees of freedom and an adjusted $R^2$ of 74.36%. All variables were significant (p-value < 0.05) and all except area of forest (Forest_1km) and volume per ha of dead wood in the fifth decay stage (DWDecay5th_1km) within 1 km radius were highly significant (p-value < 0.01). Several of the variables were significantly correlated (Figure 12). All variance inflation factors were below 5 except for MidAgeForest_1km, for which it was 6.7. Thus, the standard error for MidAgeForest_1km was 2.5 times as high as it would have been without multicollinearity. However, the estimator value for MidAgeForest_1km was still significantly above zero, despite its inflated variance.

While surrounding area of old forest (OldForest_3km) was negatively correlated with aspen associated species richness in simple regression, it had a positive effect in the multiple regression model. Apparently, the original negative correlation might have been a product of the negative correlation between area of old forest and other explanatory variables included in the multiple regression model, namely area of forest (Forest_1km) and area of middle aged forest (MidAgeForest_1km) (Figure 12).

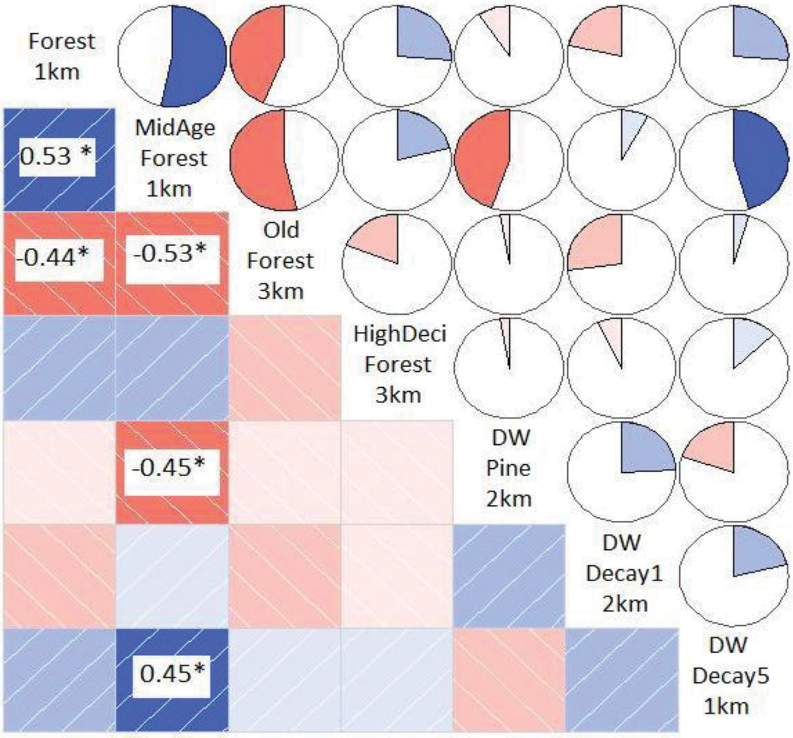

**Figure 12.** Spearman rank correlation rho for all variables included in the final regression model for aspen associated species richness, visualized by colour (red = negative correlation, blue = positive correlation, stronger colours indicate a higher rho value) and the degree to which circles are filled (fuller circles indicate a higher rho value) in a correlation matrix from the corrgram package for R. Asterisks and rho-values indicate significant correlations (p-value < 0.05). Variables are explained in Table 4.

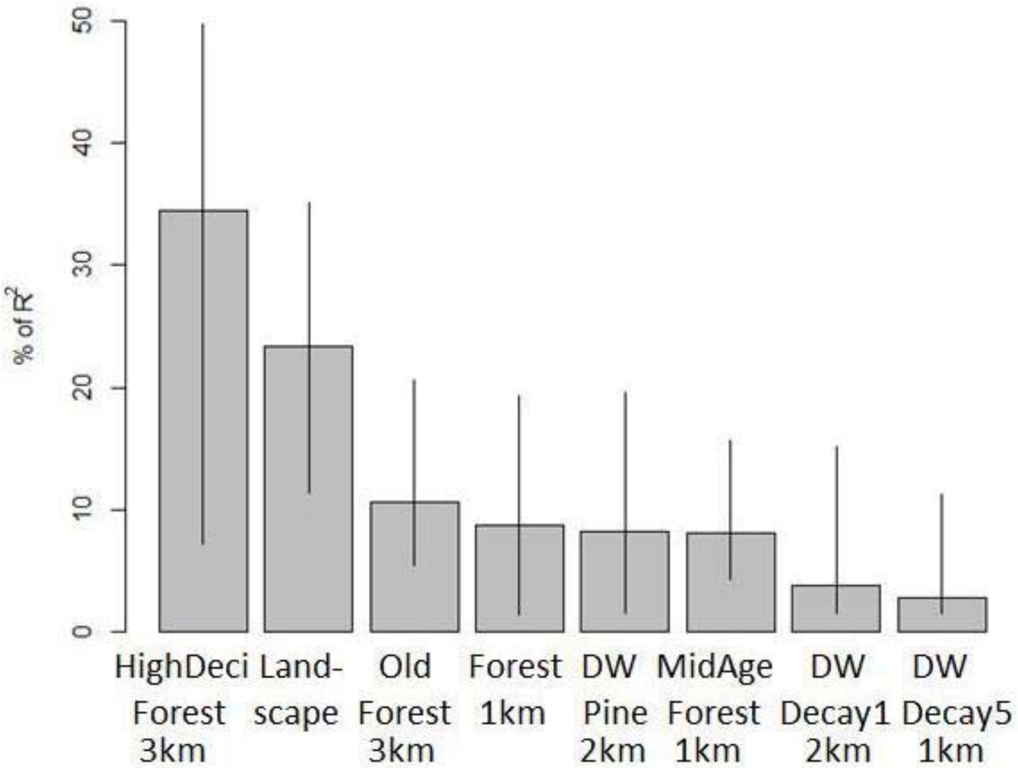

**Figure 13.** Relative importance with 95% bootstrap intervals of the predictor variables included in the final model explaining species richness of aspen associated saproxylic insects (equation 3) presented as percent of $R^2$. $R^2$ = 78.82%, metrics of the graph were normalized to sum 100%. Variables are explained in Table 4.

The largest proportion of the explained variance was partitioned to the surrounding area of forest with over 75 $m^3$ deciduous wood per ha within a 3 km radius from the insect sampling sites (HighDeciForest_3km) (Figure 13). Thus, deciduous forest was much more important to the subgroup aspen associated species than to all of the saproxylic insects sampled in the aspen logs. The second largest proportion of the explained variance was partitioned to the design variable for landscape. The landscape factor again had a negative effect due to the lower species richness in Losby (Figure 4). The NR factor was not included in the multiple regression model for aspen associated species richness, which corresponded with the weaker tendency for aspen associated species to have lower species richness in the NR sites relative to the stronger trend for all saproxylic species (Figure 7). The variables for abundance of dead wood in decay stage 1 (DWDecay1st_2km) and decay stage 5 (DWDecay5th_1km) covered the smallest fractions of the explained variance (Figure 13). All spatial scales were represented in the multiple regression model for aspen associated species richness.

## 3.5 Correlation between the explanatory variables

Many of the explanatory variables were correlated, especially the forest variables that described incompatible attributes of the same geographical area. In order to interpret the correlation of the explanatory variables with insect species richness, the connections between the variables needed to be elucidated.

### Main trends for the explanatory variables

PCA was used to clarify the main relationships between the explanatory variables that were significant to saproxylic species richness or aspen associated saproxylic species richness (Table 3 & Table 4). All of the 18 variables in Table 3 & Table 4 were entered in the PCA, thus 18 components were created. The first component, PC1, explained 78% of the variance between the sites and was almost entirely based upon the map-derived forest variables (appendix table 3). Area of old forest within 3 km radius of the insect sampling sites (OldForest_3km) was very dominant in deciding the PC1 value of each site. Insect sampling sites that were surrounded by large areas of old forest or of forest with low volume of deciduous wood had high PC1 values, while sites surrounded by large areas of young forest or forest with medium volume of deciduous wood had low PC1 values. Thus, the main gradient among the predictor variables went from much old forest to much young forest, and was interlaced with the tendency for young forests and forests with more deciduous wood to occur in the same areas (Figure 14).

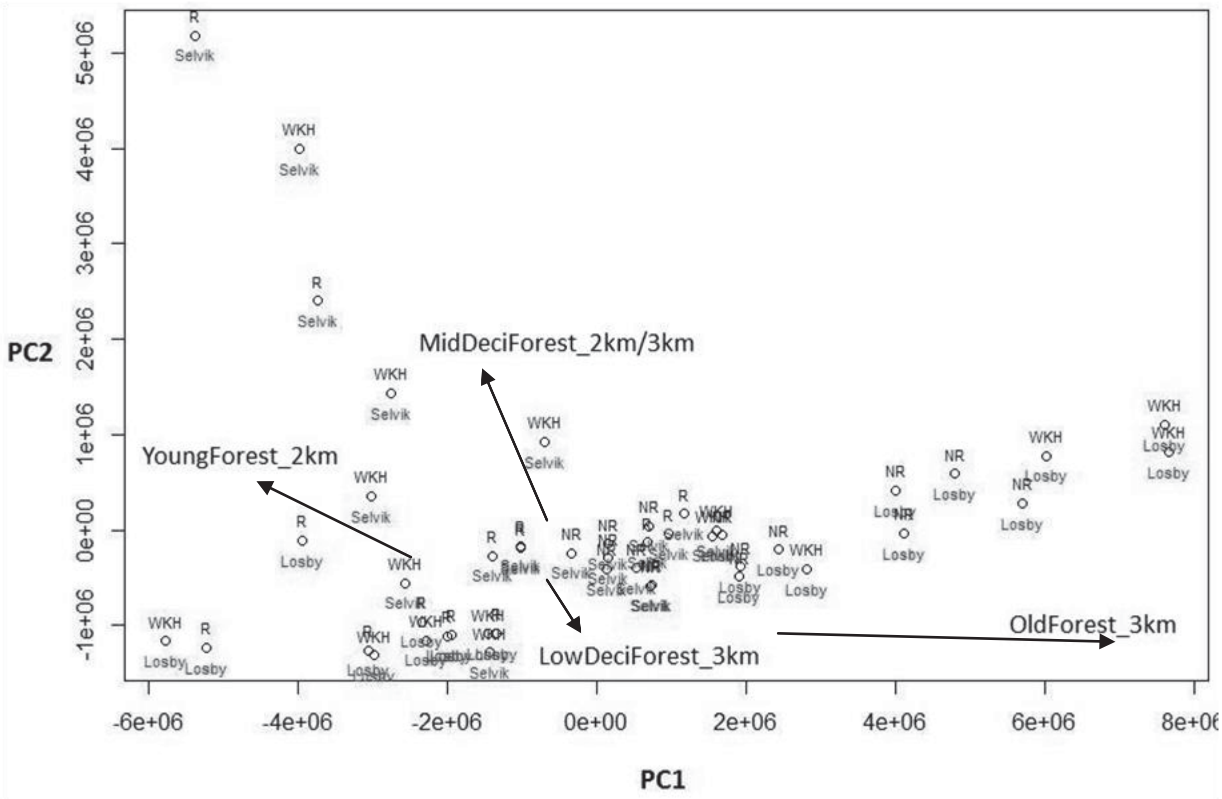

**Figure 14.** Scatterplot of the 48 insect sampling sites according to their values of PC1 and PC2, with each site marked according to its landscape and forest management category. Arrows indicate main gradients of the explanatory variables.

## Dead wood volume at survey sites corresponded with forest volume of the sites registered on the maps

Significantly higher dead wood volumes were surveyed in the field in forest areas registered on the SAT-skog map to have medium or high volumes of living trees (MidVolForest or HighVolForest) than the dead wood volumes surveyed in forest areas that according to the map had low volumes of living trees (LowVolForest) (Table 5, pairwise Wilcoxon rank sum test, p-value = 0.001 for LowVolForest VS MidVolForest, p-value = 0.002 for LowVolForest VS HighVolForest). Although mean dead wood volume surveyed in forests with a high volume of trees was higher than the volume surveyed in forests with a medium volume of trees, the difference was not statistically significant (pairwise Wilcoxon rank sum test, p-value = 0.167).

**Table 5.** Mean m$^3$ dead wood per ha with standard deviation (sd), maximum m$^3$ dead wood per ha and minimum m$^3$ dead wood per ha for n dead wood survey sites in each of the forest volume categories LowVolForest (0-100 m$^3$ forest per ha), MidVolForest (101-200 m$^3$ forest per ha) and HighVolForest (>200 m$^3$ forest per ha).

| Forest volume category | Mean m$^3$ DW per ha (sd) | Min | Max | n |
|---|---|---|---|---|
| **LowVolForest** | 15 (23) | 0.0 | 149 | 109 |
| **MidVolForest** | 25 (37) | 0.0 | 287 | 105 |
| **HighVolForest** | 78 (105) | 0.2 | 363 | 15 |

### Correlation between field-surveyed aspen dead wood and map-derived area of deciduous forest surrounding the insect sampling sites

The relation between volume of living deciduous trees as described by the SAT-skog map layer (VUPRHAL) and volume of aspen dead wood surveyed in field was investigated by testing whether the mean values for the surroundings of the insect sampling sites were correlated. Volume of aspen dead wood was positively correlated with area of forest containing medium (MidDeciForest) or much (HighDeciForest) deciduous wood, and negatively correlated with area of forest containing little deciduous wood (LowDeciForest) (Table 6).

**Table 6.** Spearman's rank correlation rho and p-values from correlation tests between variables describing aspen dead wood and deciduous forest (see Table 3 or Table 4 for descriptions of the variables). Significant p-values (<0.05) are bold.

| Variables | Rho | P-value |
|---|---|---|
| DWAspen_1km VS LowDeciForest_1km | -0.101 | 0.499 |
| DWAspen_1km VS MidDeciForest_1km | 0.508 | **<0.001** |
| DWAspen_1km VS HighDeciForest_1km | -0.010 | 0.506 |
| DWAspen_2km VS LowDeciForest_2km | -0.270 | 0.067 |
| DWAspen_2km VS MidDeciForest_2km | 0.467 | **0.001** |
| DWAspen_2km VS HighDeciForest_2km | 0.226 | 0.127 |
| DWAspen_3km VS LowDeciForest_3km | -0.344 | **0.018** |
| DWAspen_3km VS MidDeciForest_3km | 0.176 | 0.238 |
| DWAspen_3km VS HighDeciForest_3km | 0.500 | **<0.001** |

# 4. Discussion

## 4.1 Dead wood

### Dead wood volume at the right spatial scales

The results of this study show that dead wood volume can be a significant predictor for saproxylic species richness, as has been found in many previous studies (Franc et al. 2007; Götmark et al. 2011; Lassauce et al. 2011; McGeoch et al. 2007; Müller et al. 2008; Müller et al. 2010; Økland et al. 1996; Siitonen 1994). However, several previous studies have failed to find significant correlations between saproxylic species richness and dead wood abundance when dead wood was surveyed at scales between 100 $m^2$ and 1 $km^2$ (Gibb et al. 2006; Økland et al. 1996; Siitonen 1994; Vanderwel et al. 2006). In this study, dead wood volume within circular areas of 3.14 $km^2$ and 12.57 $km^2$ centred on the insect sampling sites was found to be positively correlated with saproxylic and aspen associated beetle species richness in aspen logs. This corresponds with the importance of dead wood at the 4 $km^2$ scale to saproxylic beetles in the study by Økland and colleagues (1996), and with the results from Holland and co-workers (2004) showing that some saproxylic beetle species elicit their strongest response to forest cover within 1 to 2 km radius. Bergman and colleagues (2012) used density of large or hollow oaks within 38 radii of 30 to 5284 meters centred on their insect sampling sites as predictors for species richness of oak specialist saproxylic beetles. They found a clear peak in explanatory power of oak density at 2284 meters in radius. Likewise, volume of aspen dead wood was clearly most significant within 2 km radius to aspen associated species richness in this study.

Dead wood volume within 3 km radius covering an area of 28.27 $km^2$ was not significantly correlated with saproxylic beetle species richness in the aspen logs. This might be an indication that saproxylic insects do not usually disperse 3 km from the dead wood object they emerge from, either due to restricted dispersal ability or due to low dispersal rate. However, Götmark and colleagues (2011) found regional dead wood volume at scales much larger than 28.27 $km^2$ to have a significant positive correlation with saproxylic species richness, and in the present study the 3 km radius was significant for several map-derived forest variables.

## Dead wood decay

Diversity of dead wood might be more important to saproxylic species richness than dead wood volume (Similä et al. 2003). Diversity of dead wood includes diversity in tree species, standing or lying dead wood and diversity in decay stages. Saproxylic species assemblage in dead wood has been found to vary continuously across decay stages (Vanderwel et al. 2006). All the aspen logs in the present study were in decay stage 1 in the first year of insect sampling, while in the third and last year their decay stage ranged from 1 to 3, with an average of 1.6. Accordingly, volume of dead wood in decay stage 1 within 2 km radius from the insect sampling sites had a positive correlation with both saproxylic and aspen associated species richness. Dead wood in the third decay stage within 1 km radius was also important for saproxylic species richness.

### Why not decay stage 2?

It was slightly puzzling that volume of dead wood in decay stage 2 was not significant for species richness in relatively fresh aspen logs, since several of the logs were in decay stage 2 at least during the last year of insect sampling. The second decay stage was the most common decay stage, which it also seems to be in productive forest in Norway in general (Storaunet et al. 2011), so there might have been ample supply around all insect sampling sites. However, Vanderwel and co-workers (2006) found that many saproxylic insect families were abundant in either early or late decay classes. Their definition of the decay classes resembled the definition used in this study, and decay class 2 was rarely favoured by saproxylic insects. Xylophages were most abundant in the first stage of decay, saprophages and parasitoids were relatively abundant in the third decay stage (Vanderwel et al. 2006).

### Decay of pine

The significant positive correlation of dead wood of pine with species richness of saproxylic and aspen associated insects might be connected with the mode of decay of pine trees. Pine trees form intact standing dead trees more often than spruce, birch or aspen (Siitonen et al. 2000). Snags are more prone to desiccation than logs and have a root connection that maintains the chemical defence longer, both of which result in a much slower decay rate for snags than for logs (Jakuš 1998a; Jakuš 1998b). Snags tend to be in early decay classes (Fridman & Walheim 2000) and their saproxylic fauna seems to be arrested without further succession beyond the early colonizers (Boulanger & Sirois 2007). Thus, dead standing pine may remain in the early decay classes for many years, to the benefit of insects specialising in these decay classes (Dahlberg & Stokland 2004; Jonsell et al. 1998). Several of the saproxylic species sampled from the fresh aspen logs in this study might exploit dead pine trees in early decay.

### Why decay stage 5?

It was surprising that dead wood in decay stage 5 had a positive influence on the number of aspen associated species sampled from dead wood in decay stage 1 to 3. Saint-Germain and colleagues (2007b) found that the probability for saproxylic beetles to occur in aspen dead wood increased with age of the dead wood. Age was the strongest predictor for saproxylic beetle occurrence. Age by itself cannot be target of any host-selection mechanism in the insect, and they measured several correlates of age but argued that neither of these was likely to be used as signals for host recognition. The higher probability of insect presence in old dead wood could simply be due to neutral aggregation over time. Thus, in this study, very decayed dead wood within 1 km of the insect sampling sites might have increased species richness at the sites simply by aggregating several saproxylic species over the years. A neutral mechanism like this would be expected to affect saproxylic species richness and aspen associated species richness equally, unless the saproxylic species not associated with aspen did not aggregate over time on dead wood objects indiscriminately of decay stage. Many saproxylic species have been found to prefer dead wood in early decay (Dahlberg & Stokland 2004; Jonsell et al. 1998; Vanderwel et al. 2006). Saint-Germain and colleagues (2007a) found that there were more saproxylic insects in the early decay stages in black spruce (*Picea mariana* (Mill.) B.S.P) and in the later decay stages in aspen (*Populus tremuloides* Michx.). This corresponds with the results of the present study since only aspen associated species richness had a positive correlation with dead wood volume in the fifth decay stage.

## 4.2 Map-derived forest variables

The forest variables derived from digital maps from the Norwegian Institute for Forest and Landscape proved to be relatively strong predictors of saproxylic species richness, and they explained more of the variation in aspen associated species richness than the dead wood variables. Andersson and co-workers (2012) used map layers very similar to the SAT-skog map layers used in this study and extracted similar forest variables for circular areas with radius of 690 m and 977 m centred on insect sampling sites. They found that these map-derived forest variables significantly affected saproxylic insect abundance and species richness of several taxonomic groups. Both this study and that of Andersson and co-workers (2012) show that variables from such maps can be highly relevant for saproxylic species.

## Forest cover

The positive correlation of forest cover with aspen associated species richness might be due to its effect on supply of dead wood (Økland et al. 1996). Landscapes with a higher proportion covered by forest have larger areas where dead wood occasionally appears relative to landscapes with small forest cover. Therefore, less fragmented forests are likely to support larger populations of saproxylic species and thus decrease the chance for local extinctions (Komonen et al. 2000). The forest cover was significantly smaller within the 1 km radius of the nature reserve sites relative to the WKH and retention sites, which might have contributed to the lower species richness at the nature reserve sites.

## Forest volume and dead wood volume

The highest volumes of dead wood were surveyed in forest areas with high or medium volume of living trees on the digital maps. Thus, the positive correlation between saproxylic species richness and area of forest with medium volume of living trees was probably a correlation with amount of dead wood.

This study and previous studies have shown that the relation between saproxylic insects and their substrate is scale-dependent (Bergman et al. 2012; Götmark et al. 2011; Økland et al. 1996). Thus, similar spatial scales should be used in dead wood surveys to produce comparable research results and consistent management advice. This has not been the case so far, and there are too few studies using a range of spatial scales to determine the upper and lower limit of relevant scales for dead wood surveys. Holland and colleagues (2004) presumed that forest cover represented dead wood abundance in order to investigate the response of cerambycid beetles to substrate abundance at a range of spatial scales, but did not test their initial presumption. This study has shown that there is a correlation between forest volume and dead wood volume. Dead wood surveys are labour-intensive, which results in restrictions on the scale that can be covered due to limited time or funding. Variables describing forest volume can easily be obtained from digital maps for a large range of scales. The connection between forest volume and dead wood volume presents the possibility of using forest volume derived from digital maps as a proxy for dead wood volume. This would allow for studies of the scale-specific response of saproxylic insects to substrate abundance at multiple and large spatial scales.

## Deciduous forest and deciduous dead wood volume

There were more deciduous trees in the forests surrounding insect sampling sites in Selvik than in Losby. Selvik also had higher saproxylic species richness. In Sweden, the majority of saproxylic species are associated with deciduous wood (Dahlberg & Stokland 2004). Area of forest with much deciduous wood had a strong positive correlation with saproxylic species richness sampled from the aspen logs, and was the strongest predictor for species richness of aspen associated saproxylic insects. There was also more aspen dead wood in the areas where there was much deciduous wood in the forest, and naturally volume of aspen dead wood was positively correlated with species richness of aspen associated saproxylic insects. Götmark and colleagues (2011) studied saproxylic species associated with oak, and they similarly found that the variables restricted to oak dead wood or oak-dominated forests were the strongest predictors for oak associated species richness.

### Old forests

Area of forest over 80 years within 3 km radius of the insect sampling sites had a positive correlation with aspen associated species richness. Previous studies have also found old forests to have a positive effect on species richness of saproxylic beetles (Olsson et al. 2012; Stenbacka et al. 2010). The old forest category in this study included both managed and unmanaged forest, since rotation periods for spruce in southern Norway are 70 to 90 years. However, while some of those areas might only have been forested for 80 to 90 years, some of the older forests might represent ecological continuity (Nordén & Appelqvist 2001) with stable dead wood dynamics (Rouvinen & Kouki 2002). Some saproxylic species require continuity in substrate supply. Jonsell and Nordlander (2002) found that some insect species living inside polypore fungi were only present at sites where dead wood had been abundant for at least a century. Old forests might also represent important dead wood types such as large diameter dead wood (Hammond et al. 2004) which is favoured by many red-listed saproxylics (Jonsell et al. 1998), and old, large aspen trees that have been left intact in old, unmanaged forests (Lankia et al. 2012).

## 4.3 Ecologically relevant scale

The most relevant scale differed depending on both the explanatory variable and the response.

Aspen is considered to be a pioneer species. Since aspen is a relatively ephemeral habitat, aspen associated species are expected to have greater dispersal capacity than species associated with more stable habitats (Nilsson & Baranowski 1997; Southwood 1977). Aspen rarely forms stable forest stands and is usually found scattered across the landscape (Kouki et al. 2004; Latva-Karjanmaa et al. 2007). Aspen dead wood constituted 1.8% in Losby and 4.5% in Selvik of the dead wood surveyed in the present study. Thus, saproxylic species that prefer or depend upon aspen dead wood were presented with a much more fragmented habitat than saproxylic species that utilize dead wood indiscriminately. Therefore, aspen associated species probably have to disperse further in search of suitable substrate than generalist saproxylics or spruce specialists, and aspen specialists are expected to have relatively high dispersal capacity as an adaptation to the scattered distribution of aspen.

Aspen ecology and the resulting adaptations expected of associated species lead to the following predictions; that aspen dead wood is important to aspen associated species at relatively large scales, and that aspen associated species often respond to other relevant explanatory variables at larger scales than many other saproxylics. These predictions fit well with the results of this study. Abundance of deciduous forest explained most variation in species richness of aspen associated saproxylic insects when measured at the 3 km radius, while the same variable explained most variation in species richness of saproxylic insects when measured at the 2 km radius. Aspen dead wood was only correlated with species richness of aspen associated saproxylics when measured within 2 km radius, while dead wood in general within 1 km radius was correlated with saproxylic species richness. Økland and colleagues (1996) also found that aspen dead wood was the most important predictor for aspen associated species richness at a large scale (4 km$^2$), whereas smaller scales (1 km$^2$) were of less importance.

## 4.4 Forest management

Significantly more saproxylic species were sampled from dead wood in WKH sites or retention patch sites than from dead wood in the nature reserve sites. The managed forests in this study were managed according to the "Living Forests" principles for conservation-oriented forestry in Norway (Anon. 2006). Sustainable forest management can maintain biodiversity values similar to those of forest reserves (Djupström et al. 2008; Hjältén et al. 2012; Müller et al. 2007). Forest management is not the main focus of this article, but the significantly lower species richness sampled in the nature reserve sites bears mention nevertheless. The cause of this was certainly not greater abundance of dead wood around the WKH and retention sites; the nature reserve insect sampling sites were surrounded by significantly more of almost every category of dead wood. However, much larger proportions of the landscapes in Selvik and Losby were managed forest, while the nature reserves covered relatively small areas. The saproxylic fauna connected with the old-growth forests of the nature reserves might already be depauperate in landscapes with so little and fragmented old-growth forest (Siitonen et al. 2001). Alternatively, the conditions within the WKH and retention sites or something about the surrounding area might have increased saproxylic species richness relative to the nature reserve.

### Benefits of managed forests

The insect sampling sites within woodland key habitats and retention patches were probably surrounded by more diverse landscapes than the sites in the nature reserves. The WKHs and retention patches were necessarily within managed forests, and managed forests tend to be a mosaic of forest cut classes. Forests of different age groups might contribute with different habitats and different species, thus increasing species richness (Hammond et al. 2004; Stenbacka et al. 2010). Clear-cuts have also been found to harbour different species assemblages than forested areas (Schroeder et al. 2011; Sverdrup-Thygeson & Ims 2002). Species density on aspen dead wood has been shown to be higher on clear-cuts than in forested sites (Schroeder et al. 2011). This was not due to higher activity levels or higher species richness, but due to a greater number of niches per surface area of aspen dead wood on clear-cuts. Thus, the number of insect species sampled from sites in woodland key habitats and retention patches might have been increased by their presumed greater proximity to clear-cuts relative to the nature reserve sites.

There are several aspects of clear-cuts that might have a positive effect on saproxylic species richness in fresh aspen logs. Sun-exposure is naturally very high at clear-cuts (Sverdrup-Thygeson & Ims 2002) and many red-listed saproxylic beetles prefer sun-exposed sites (Jonsell et al. 1998). Clear-cuts often harbour relatively large volumes of dead wood in early decay (Stenbacka et al. 2010). Furthermore, clear-cuts might provide an opportunity for aspen seedlings to establish. Aspen seems unable to regenerate adequately in the absence of disturbance and used to depend on forest fires for regeneration in the past (Lankia et al. 2012; Linder et al. 1997). Clear-cutting might help atone for the present low frequency of forest fires. Lack of disturbance is a concern for the regeneration of aspen in forest reserves (Latva-Karjanmaa et al. 2007). There was less deciduous forest surrounding the sites in the nature reserves than surrounding the WKHs and retention patches in this study. WKH and retention sites were also surrounded by younger forest than NR sites, and the PCA showed a connection between young forest and deciduous forest. Area of young forest, which included clear-cuts, was positively correlated with saproxylic and aspen associated species richness. Young aspen trees on clear-cuts might be an important source of dead wood for aspen associated insects. Most aspen dead wood registered in this study had less than 20 cm in diameter. Dead wood with small diameter can be important to saproxylics (Brin et al. 2011; Götmark et al. 2011). Furthermore, when aspen trees are retained during thinning and felling operations in sustainable forestry, managed forests might become a valuable source of larger aspen dead wood as well (Latva-Karjanmaa et al. 2007; Myking et al. 2011).

### Drawbacks of managed forests

This study and previous studies show that saproxylic insects are attracted to dead wood in woodland key habitats and retention sites (Djupström et al. 2008; Martikainen 2001; Sverdrup-Thygeson & Ims 2002). However, the role of such small forest patches for population dynamics over time is unknown. Edge effects reduce the core area of woodland key habitats, restricting species that only persist in the core to a much smaller area than the total area (Aune et al. 2005). Furthermore, the connectivity between woodland key habitats might be insufficient for many species to utilize them as a network. At present, there is insufficient knowledge about the long-term effects of sustainable forestry to conclude whether these measures can maintain species richness over time (Davies et al. 2008).

Besides, maximizing species richness is not necessarily the best management target. Single species can be unable to persist even if dead wood abundance meets an estimated threshold value for species richness (Müller & Bütler 2010), due to higher (Bässler & Müller 2010; Siitonen & Saaristo 2000) or more particular demands (Økland et al. 1996). Red-listed species tend to be threatened due to the decline in their particular habitat, such as large diameter dead wood (Hottola et al. 2009; Jonsell et al. 1998) which is usually very scarce in managed forests (Fridman & Walheim 2000). Only saproxylic insects in general were more species rich in the WKH and retention sites in this study, while aspen associated species, aspen specialists and red-listed species showed no significant difference. However, the number of individuals sampled in each of these sub-categories was naturally lower than for saproxylics in general, especially for aspen specialists and red-listed species, which might have been the main reason for the lack of significance. Nevertheless, it has been shown that specialist species can decline in occurrence even while generalist species increase in occurrence in the same area (Nordén et al. in press). Old-growth specialists may not survive even in sustainably managed forest.

## 4.5 Management advice

Managed forests in Fennoscandia offer little deciduous wood, since spruce or pine are the cultivated tree species. The Norwegian National Inventory found that spruce dead wood constituted on average two thirds of the dead wood volume in spruce-dominated forests (Storaunet et al. 2011). About 70% of the dead wood surveyed in this study was spruce. As much as 60% of the Norwegian forest-dwelling red-listed species were associated with deciduous wood (Kålås et al. 2006). The results of this study show that forests with much deciduous wood are important to conserve species richness of aspen associated saproxylic insects. Forest managers should therefore strive to retain deciduous trees in their felling operations. Fresh dead wood and dead wood in advanced decay was also relatively rare in the surveyed landscapes, while also being positively correlated with saproxylic and aspen associated species richness. Clear-cuts conducted in terms with conservation-oriented forestry have been shown to contain more early decay dead wood than old stands managed traditionally (Ekbom et al. 2006). Dead wood in late decay was not more abundant, and might have been destroyed by heavy machinery during the felling. Smaller and lighter machines, or in the best case horses, would probably destroy less of the decayed dead wood. Of course, using horses or small machinery might not be an economically viable option for all managed forests at present, but the machines used in forestry could be developed with this in mind.

While forest management should focus on increasing the abundance of certain types of dead wood that are now rare in managed forests, any measures to increase dead wood volume are also likely to benefit the saproxylic fauna. Larger volumes of dead wood can support larger populations of saproxylic species, decreasing the chance for local extinctions. In addition, increasing dead wood volume will probably to some degree also increase dead wood diversity (Similä et al. 2003). The relatively high number of species sampled from dead wood in woodland key habitats and retention sites in this study indicates that dead wood in managed forests is valuable to saproxylic species richness. Retention of dead wood in managed forests has also been shown to benefit certain red-listed species (Djupström et al. 2012). Increasing the volume of dead wood in managed forests seems to be an ecologically sound strategy for conservation of saproxylic species. Whether the current guidelines for sustainable forestry lead to a satisfactory increase in dead wood volume is difficult to determine. The average abundance of dead wood in Norwegian managed forests has increased over the last decade to the present 12 $m^3$ per ha (Storaunet et al. 2011). This trend should definitely continue. Old-growth forests in Norway still have 3-6 times as much dead wood per ha as managed forests (Storaunet et al. 2011), and a recent review of threshold values for dead wood abundance found that 20-30 $m^3$ per ha seemed to be a critical value for saproxylic species in boreal coniferous forest (Müller & Bütler 2010).

## 4.6 Further research

The results of this study show that forest variables from digital maps can be useful for studies of saproxylic beetles and probably other saproxylic organisms. Especially studies that aim to explore the importance of different scales can benefit greatly from using explanatory variables extracted from digital maps.

Surveys of dead wood volume in forests of varying volume in different landscape types could enable the use of map-derived forest volume as a proxy for dead wood volume in the surveyed landscape types. Using forest volume as a proxy for dead wood volume could enable much more detailed studies into the scale-specific response of saproxylic insects to their substrate, since forest volume on digital maps can be extracted as an explanatory variable for multiple spatial scales covering large areas with high resolution.

Holland and colleagues (2004) and Bergman and colleagues (2012) considered the most relevant scale for the saproxylic insects they studied to be the scale of the predictor that gave the best model fit against insect abundance, occurrence or species richness. However, if multiscale studies were repeated in several similar landscapes, each landscape could serve as a repetition of the estimate of the model fit parameter for each spatial scale and the effect of scale could be statistically tested. Thus, it could be possible to determine the range of spatial scales that are significantly better at explaining variation in saproxylic insect communities, at least within a landscape type.

## 4.7 Conclusions

This study has confirmed that saproxylic insects have a scale-specific relation to the surrounding environment. Dead wood volume within 1 km radius was positively correlated with species richness of saproxylic beetles. Specific categories of dead wood were correlated with species richness of saproxylic or aspen associated saproxylic beetles at scales up to 2 km radius. No category of dead wood was significantly correlated with species richness at the largest scale which covered 3 km radius. This indicates an upper limit to the relevant scales for dead wood surveys. However, some map-derived forest variables explained most variation in species richness when measured within 3 km radius.

Dead wood in the first stage of decay was correlated with both saproxylic and aspen associated species richness. The positive correlation of very decayed dead wood with aspen associated species richness in fresh aspen logs was unexpected. The largest proportion of surveyed dead wood was in the second decay stage, which was not correlated with species richness of saproxylic beetles. Even though they constituted a low proportion of total dead wood volume, dead wood of pine and aspen were correlated with saproxylic species richness.

Several of the map-derived variables describing forest characteristics were correlated with species richness of saproxylic or aspen associated saproxylic insects. Area of surrounding forest with much deciduous wood was the strongest predictor for species richness of aspen associated saproxylic insects. This variable explained most variation in aspen associated species richness when measured within 3 km radius, while it explained most variation in saproxylic species richness when measured within 2 km radius. The map-derived variables describing abundance of deciduous wood in the surrounding forests were also correlated with estimates of aspen dead wood abundance from the dead wood survey. In general, forest volume registered on the digital maps reflected dead wood abundance surveyed in the forests.

This study has underlined the need to use ecologically relevant scales in research and management, and suggested the use of digital maps in research as an effective method to narrow down the range of relevant scales. The use of ecologically relevant spatial scales in research and forest management can lead to better and more successful conservation of forest biodiversity.

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# Appendix

Table 1) Mean and standard deviation of the different dead wood and landscape variable categories for Selvik and Losby, tested by parametric or non-parametric t-tests for significant differences between the landscapes. P-values under 0.10 are marked in bold.

| **Variable** | **Values** | **Mean ± sd for Selvik** | **Mean ± sd for Losby** | **Test** | **p-value** | **No.** |
|---|---|---|---|---|---|---|
| DW_1km | $m^3$ dead wood per ha within 1 km radius of the insect sampling sites | 21.370 ± 14.377 | 49.352 ± 46.370 | Wilcoxon rank sum test | W = 380, **p-value = 0.028** | 1 |
| DW_2km | $m^3$ dead wood per ha within 2 km radius of the insect sampling sites | 21.995 ± 8.904 | 41.278 ± 17.872 | Wilcoxon rank sum test | W = 452, **p-value < 0.001** | 2 |
| DW_3km | $m^3$ dead wood per ha within 3 km radius of the insect sampling sites | 26.041 ± 5.422 | 33.860 ± 10.668 | Wilcoxon rank sum test | W = 410, **p-value = 0.005** | 3 |
| DWAspen_1km | $m^3$ dead wood of aspen per ha within 1 km radius of the insect sampling sites | 0.020 ± 0.102 | 0.560 ± 1.208 | Wilcoxon rank sum test | W = 327, **p-value = 0.064** | 4 |
| DWAspen_2km | $m^3$ dead wood of aspen per ha within 2 km radius of the insect sampling sites | 0.375 ± 0.901 | 0.434 ± 0.484 | Wilcoxon rank sum test | W = 330, p-value = 0.229 | 5 |
| DWAspen_3km | $m^3$ dead wood of aspen per ha within 3 km radius of the insect sampling sites | 0.441 ± 0.648 | 0.621 ± 0.416 | Wilcoxon rank sum test | W = 390.5, **p-value = 0.014** | 6 |
| DWDeciduous_1km | $m^3$ dead wood of deciduous wood other than aspen per ha within 1 km radius of the insect sampling sites | 3.304 ± 2.196 | 4.695 ± 3.469 | Wilcoxon rank sum test | W = 336.5, p-value = 0.201 | 7 |
| DWDeciduous_2km | $m^3$ dead wood of deciduous wood other than aspen per ha within 2 km radius of the insect sampling sites | 3.037 ± 0.993 | 5.004 ± 1.963 | Wilcoxon rank sum test | W = 399, **p-value = 0.009** | 8 |
| DWDeciduous_3km | $m^3$ dead wood of deciduous wood other than aspen per ha within 3 km radius of the insect sampling sites | 3.358 ± 1.054 | 5.126 ± 1.139 | Wilcoxon rank sum test | W = 479.5, **p-value < 0.001** | 9 |
| DWPine_1km | $m^3$ dead wood of pine per ha within 1 km radius of the insect sampling sites | 5.804 ± 7.521 | 1.269 ± 4.098 | Wilcoxon rank sum test | W = 158, **p-value = 0.006** | 10 |
| DWPine_2km | $m^3$ dead wood of pine per ha within 2 km radius | 3.158 ± | 1.734 ± | | W = 168.5, **p-value** | 11 |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
|  | of the insect sampling sites | 2.649 | 2.286 |  | **= 0.022** |
| DWPine_3km | $m^3$ dead wood of pine per ha within 3 km radius of the insect sampling sites | 2.575 ± 0.796 | 2.082 ± 1.394 | Wilcoxon rank sum test | W = 180.5, **p-value = 0.043** |
| DWSpruce_1km | $m^3$ dead wood of spruce per ha within 1 km radius of the insect sampling sites | 12.245 ± 10.670 | 42.830 ± 47.371 | Wilcoxon rank sum test | W = 362.5, **p-value = 0.067** |
| DWSpruce_2km | $m^3$ dead wood of spruce per ha within 2 km radius of the insect sampling sites | 15.437 ± 8.783 | 34.095 ± 18.901 | Wilcoxon rank sum test | W = 430.5, **p-value = 0.001** |
| DWSpruce_3km | $m^3$ dead wood of spruce per ha within 3 km radius of the insect sampling sites | 19.687 ± 5.008 | 26.043 ± 10.747 | Welch two-sample t-test | t = 2.580, df = 30.832, **p-value = 0.015** |
| DWDecay1st_1km | $m^3$ dead wood in decay stage 1 per ha within 1 km radius of the insect sampling sites | 6.658 ± 6.692 | 4.421 ± 4.981 | Wilcoxon rank sum test | W = 234.5, p-value = 0.382 |
| DWDecay1st_2km | $m^3$ dead wood in decay stage 1 per ha within 2 km radius of the insect sampling sites | 3.479 ± 2.497 | 4.400 ± 2.752 | Wilcoxon rank sum test | W = 332, p-value = 0.237 |
| DWDecay1st_3km | $m^3$ dead wood in decay stage 1 per ha within 3 km radius of the insect sampling sites | 2.670 ± 0.925 | 4.208 ± 1.720 | Wilcoxon rank sum test | W = 418, **p-value = 0.003** |
| DWDecay2nd_1km | $m^3$ dead wood in decay stage 2 per ha within 1 km radius of the insect sampling sites | 6.308 ± 9.284 | 24.213 ± 27.970 | Wilcoxon rank sum test | W = 367.5, **p-value = 0.053** |
| DWDecay2nd_2km | $m^3$ dead wood in decay stage 2 per ha within 2 km radius of the insect sampling sites | 9.587 ± 5.526 | 18.547 ± 11.962 | Wilcoxon rank sum test | W = 378, **p-value = 0.031** |
| DWDecay2nd_3km | $m^3$ dead wood in decay stage 2 per ha within 3 km radius of the insect sampling sites | 11.516 ± 1.772 | 14.886 ± 5.990 | Wilcoxon rank sum test | W = 380.5, **p-value = 0.027** |
| DWDecay3rd_1km | $m^3$ dead wood in decay stage 3 per ha within 1 km radius of the insect sampling sites | 6.137 ± 5.861 | 10.108 ± 11.219 | Wilcoxon rank sum test | W = 334.5, p-value = 0.217 |
| DWDecay3rd_2km | $m^3$ dead wood in decay stage 3 per ha within 2 km radius of the insect sampling sites | 4.987 ± 2.568 | 8.717 ± 3.557 | Wilcoxon rank sum test | W = 427.5, **p-value = 0.001** |
| DWDecay3rd_3km | $m^3$ dead wood in decay stage 3 per ha within 3 km radius of the insect sampling sites | 5.804 ± 1.752 | 6.900 ± 1.735 | Wilcoxon rank sum test | W = 378.5, **p-value = 0.030** |
| DWDecay4th_1km | $m^3$ dead wood in decay stage 4 per ha within 1 km radius of the insect sampling sites | 1.575 ± 1.218 | 7.313 ± 8.793 | Wilcoxon rank sum test | W = 389, **p-value = 0.016** |
| DWDecay4th_2km | $m^3$ dead wood in decay stage 4 per ha within 2 km radius of the insect sampling sites | 1.875 ± 1.510 | 6.439 ± 2.531 | Wilcoxon rank sum test | W = 524, **p-value < 0.001** |
| DWDecay4th_3km | $m^3$ dead wood in decay stage 4 per ha within 3 km radius of the insect sampling sites | 2.679 ± 0.835 | 5.008 ± 1.575 | Wilcoxon rank sum test | W = 495.5, **p-value < 0.001** |

| | | | | | | |
|---|---|---|---|---|---|---|
| DWDecay5th_1km | $m^3$ dead wood in decay stage 5 per ha within 1 km radius of the insect sampling sites | 0.691 ± 0.738 | 3.282 ± 2.000 | Wilcoxon rank sum test | W = 477.5, **p-value < 0.001** | 28 |
| DWDecay5th_2km | $m^3$ dead wood in decay stage 5 per ha within 2 km radius of the insect sampling sites | 2.100 ± 2.810 | 3.186 ± 1.244 | Wilcoxon rank sum test | W = 453.5, **p-value < 0.001** | 29 |
| DWDecay5th_3km | $m^3$ dead wood in decay stage 5 per ha within 3 km radius of the insect sampling sites | 3.375 ± 1.716 | 2.839 ± 0.912 | Wilcoxon rank sum test | W = 215.5, p-value = 0.201 | 30 |
| DWSmallDiam_1km | $m^3$ dead wood with diameter 10-20 cm per ha within 1 km radius of the insect sampling sites | 7.254 ± 3.855 | 10.708 ± 4.888 | Wilcoxon rank sum test | W = 398.5, **p-value = 0.009** | 31 |
| DWSmallDiam_2km | $m^3$ dead wood with diameter 10-20 cm per ha within 2 km radius of the insect sampling sites | 7.858 ± 2.724 | 10.765 ± 2.700 | Welch two-sample t-test | t = 3.673, df = 44.945, **p-value = 0.001** | 32 |
| DWSmallDiam_3km | $m^3$ dead wood with diameter 10-20 cm per ha within 3 km radius of the insect sampling sites | 8.787 ± 1.044 | 10.434 ± 2.013 | Welch two-sample t-test | t = 3.498, df = 32.736, **p-value = 0.001** | 33 |
| DWMidDiam_1km | $m^3$ dead wood with diameter 21-30 cm per ha within 1 km radius of the insect sampling sites | 9.183 ± 9.025 | 18.130 ± 19.230 | Wilcoxon rank sum test | W = 335, p-value = 0.211 | 34 |
| DWMidDiam_2km | $m^3$ dead wood with diameter 21-30 cm per ha within 2 km radius of the insect sampling sites | 8.466 ± 4.344 | 14.495 ± 7.847 | Wilcoxon rank sum test | W = 390.5, **p-value = 0.015** | 35 |
| DWMidDiam_3km | $m^3$ dead wood with diameter 21-30 cm per ha within 3 km radius of the insect sampling sites | 9.054 ± 1.210 | 11.517 ± 4.458 | Wilcoxon rank sum test | W = 358, **p-value = 0.083** | 36 |
| DWLargeDiam_1km | $m^3$ dead wood with diameter >30 cm per ha within 1 km radius of the insect sampling sites | 4.641 ± 6.544 | 20.365 ± 25.759 | Wilcoxon rank sum test | W = 357.5, **p-value = 0.068** | 37 |
| DWLargeDiam_2km | $m^3$ dead wood with diameter >30 cm per ha within 2 km radius of the insect sampling sites | 5.583 ± 5.672 | 15.934 ± 9.370 | Wilcoxon rank sum test | W = 452.5, **p-value < 0.001** | 38 |
| DWLargeDiam_3km | $m^3$ dead wood with diameter >30 cm per ha within 3 km radius of the insect sampling sites | 7.929 ± 4.459 | 11.843 ± 5.105 | Wilcoxon rank sum test | W = 407.5, **p-value = 0.005** | 39 |
| YoungForest_1km | $m^2$ of forest areas that are 1-40 years old within 1 km radius of the insect sampling sites | 588377 ± 263250.5 | 281499.8 ± 209648 | Wilcoxon rank sum test | W = 95, **p-value < 0.001** | 40 |
| YoungForest_2km | $m^2$ of forest areas that are 1-40 years old within 2 km radius of the insect sampling sites | 3080471 ± 538114.7 | 1259719 ± 775039 | Wilcoxon rank sum test | W = 11, **p-value < 0.001** | 41 |
| YoungForest_3km | $m^2$ of forest areas that are 1-40 years old within 3 km radius of the insect sampling sites | 7532200 ± 719910.1 | 2873328 ± 1037611 | Wilcoxon rank sum test | W = 0, **p-value < 0.001** | 42 |
| MidAgeForest_1km | $m^2$ of forest areas that are 41-80 years old within 1 km radius of the insect sampling sites | 904481.6 ± 357800.4 | 1591567 ± 583360.3 | Wilcoxon rank sum test | W = 459, **p-value < 0.001** | 43 |

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| MidAgeForest_2km | m$^2$ of forest areas that are 41-80 years old within 2 km radius of the insect sampling sites | 3954497 ± 943585.7 | 6074427 ± 1821319 | Wilcoxon rank sum test | W = 457, **p-value < 0.001** |
| MidAgeForest_3km | m$^2$ of forest areas that are 41-80 years old within 3 km radius of the insect sampling sites | 9514882 ± 1216600 | 12961491 ± 3029997 | Wilcoxon rank sum test | W = 460, **p-value < 0.001** |
| OldForest_1km | m$^2$ of forest areas that are over 80 years old within 1 km radius of the insect sampling sites | 1203037 ± 448358.5 | 866691.3 ± 685579.2 | Wilcoxon rank sum test | W = 193, **p-value = 0.079** |
| OldForest_2km | m$^2$ of forest areas that are over 80 years old within 2 km radius of the insect sampling sites | 3913533 ± 991892.9 | 3773750 ± 2477828 | Wilcoxon rank sum test | W = 260, p-value = 0.742 |
| OldForest_3km | m$^2$ of forest areas that are over 80 years old within 3 km radius of the insect sampling sites | 7862990 ± 1561697 | 8958802 ± 4051900 | Welch two-sample t-test | t = 1.214, df = 28.164, p-value = 0.235 |
| LowVolForest_1km | m$^2$ of forest areas with 1-100 m$^3$ forest per ha within 1 km radius of the insect sampling sites | 1314586 ± 347501.5 | 392174.1 ± 348179.3 | Wilcoxon rank sum test | W = 21, **p-value < 0.001** |
| LowVolForest_2km | m$^2$ of forest areas with 1-100 m$^3$ forest per ha within 2 km radius of the insect sampling sites | 6042995 ± 1149434 | 1756161 ± 1232575 | Wilcoxon rank sum test | W = 6, **p-value < 0.001** |
| LowVolForest_3km | m$^2$ of forest areas with 1-100 m$^3$ forest per ha within 3 km radius of the insect sampling sites | 13902716 ± 2198662 | 4120741 ± 1460442 | Wilcoxon rank sum test | W = 0, **p-value < 0.001** |
| MidVolForest_1km | m$^2$ of forest areas with 101-200 m$^3$ forest per ha within 1 km radius of the insect sampling sites | 1225308 ± 250270.2 | 1778953 ± 374496.8 | Welch two-sample t-test | t = 5.933, df = 38.173, **p-value < 0.001** |
| MidVolForest_2km | m$^2$ of forest areas with 101-200 m$^3$ forest per ha within 2 km radius of the insect sampling sites | 4382616 ± 718303.7 | 7298866 ± 839159.8 | Wilcoxon rank sum test | W = 552, **p-value < 0.001** |
| MidVolForest_3km | m$^2$ of forest areas with 101-200 m$^3$ forest per ha within 3 km radius of the insect sampling sites | 9672984 ± 1120169 | 16748676 ± 1106828 | Wilcoxon rank sum test | W = 552, **p-value < 0.001** |
| HighVolForest_1km | m$^2$ of forest areas with >200 m$^3$ forest per ha within 1 km radius of the insect sampling sites | 158166.3 ± 247148.6 | 581013.3 ± 506778.1 | Wilcoxon rank sum test | W = 444.5, **p-value < 0.001** |
| HighVolForest_2km | m$^2$ of forest areas with >200 m$^3$ forest per ha within 2 km radius of the insect sampling sites | 592130.1 ± 736147.6 | 2052883 ± 1606235 | Wilcoxon rank sum test | W = 454, **p-value < 0.001** |
| HighVolForest_3km | m$^2$ of forest areas with >200 m$^3$ forest per ha within 3 km radius of the insect sampling sites | 1342821 ± 1384515 | 3913572 ± 2396035 | Wilcoxon rank sum test | W = 465, **p-value < 0.001** |
| LowDeciForest_1km | m$^2$ of forest areas with 0-35 m$^3$ deciduous forest per ha within 1 km radius of the insect sampling sites | 2607256 ± 245582.9 | 2695768 ± 113243.3 | Wilcoxon rank sum test | W = 339, p-value = 0.184 |
| LowDeciForest_2km | m$^2$ of forest areas with 0-35 m$^3$ deciduous forest per ha within 2 km radius of the insect sampling | 10590947 ± 729084.6 | 10939779 ± 274082.9 | Wilcoxon rank sum test | W = 342, p-value = 0.163 |

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|  | sites |  |  |  |  |
| LowDeciForest_3km | $m^2$ of forest areas with 0-35 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 23864609 ± 1505486 | 24353514 ± 432813.5 | Wilcoxon rank sum test | W = 326, p-value = 0.292 |
| MidDeciForest_1km | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 1 km radius of the insect sampling sites | 88366 ± 188260.9 | 43911.28 ± 63102.91 | Wilcoxon rank sum test | W = 326.5, p-value = 0.243 |
| MidDeciForest_2km | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 2 km radius of the insect sampling sites | 352852 ± 610465.1 | 166683.6 ± 147651.7 | Wilcoxon rank sum test | W = 321, p-value = 0.342 |
| MidDeciForest_3km | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 1034380 ± 1045902 | 433858.9 ± 169638.2 | Wilcoxon rank sum test | W = 178, **p-value = 0.038** |
| HighDeciForest_1km | $m^2$ of forest areas with >75 $m^3$ deciduous forest per ha within 1 km radius of the insect sampling sites | 2438.406 ± 9533.532 | 78.25913 ± 375.3176 | Wilcoxon rank sum test | W = 264, p-value = 0.564 |
| HighDeciForest_2km | $m^2$ of forest areas with >75 $m^3$ deciduous forest per ha within 2 km radius of the insect sampling sites | 8269.688 ± 22615.49 | 1447.825 ± 3587.092 | Wilcoxon rank sum test | W = 327, p-value = 0.173 |
| HighDeciForest_3km | $m^2$ of forest areas with >75 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 19532.65 ± 43523.28 | 4136.047 ± 5718.463 | Wilcoxon rank sum test | W = 328, p-value = 0.256 |
| Forest_1km | $m^2$ of forest area within 1 km radius of the insect sampling sites | 2695895 ± 212277.4 | 2739758 ± 112244.9 | Welch two-sample t-test | t = 0.891, df = 35.242, p-value = 0.379 |
| Forest_2km | $m^2$ of forest area within 2 km radius of the insect sampling sites | 10948502 ± 545948.5 | 11107896 ± 229219.4 | Wilcoxon rank sum test | W = 311, p-value = 0.463 |
| Forest_3km | $m^2$ of forest area within 3 km radius of the insect sampling sites | 24910072 ± 803855.3 | 24793622 ± 383860.1 | Wilcoxon rank sum test | W = 202, p-value = 0.118 |
| Altitude | meters above sea level at the insect sampling sites | 434.200 ± 114.154 | 267.900 ± 28.216 | Wilcoxon rank sum test | W = 55, **p-value < 0.001** |

Table 2) Mean and standard deviation of the different dead wood and landscape variable categories plus saproxylic and aspen associated species richness for the forest management categories with combined data from Selvik and Losby, tested by parametric or non-parametric tests for significant differences between the forest management categories. All pairwise tests followed an analysis of variance or an equivalent test suitable for the data, and were conducted with the sequential Bonferroni correction (the "holm" correction in R). P-values under 0.10 are marked in bold.

| **Variable** | **Values** | **Mean ± sd for NR** | **Mean ± sd for R** | **Mean ± sd for WKH** | **Test** | **Test statistics from tests for any difference, or if this was significant, for the following pairwise tests;** | | | **No.** |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | **p-value NR vs R** | **p-value NR vs WKH** | **p-value R vs WKH** | |
| **DW_1km** | $m^3$ dead wood per ha within 1 km radius of the insect sampling sites | 63.940 ± 45.953 | 16.700 ± 11.786 | 23.400 ± 21.685 | Pairwise Wilcoxon rank sum test | **< 0.001** | **0.007** | 0.593 | 1 |
| **DW_2km** | $m^3$ dead wood per ha within 2 km radius of the insect sampling sites | 38.537 ± 18.211 | 26.400 ± 12.852 | 29.043 ± 17.608 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 3.393, df = 2, p-value = 0.183 | | | 2 |
| **DW_3km** | $m^3$ dead wood per ha within 3 km radius of the insect sampling sites | 35.906 ± 6.662 | 28.120 ± 7.477 | 25.468 ± 10.035 | Pairwise t-test with pooled sd | **0.023** | **0.002** | 0.373 | 3 |
| **DWAspen_1km** | $m^3$ dead wood of aspen per ha within 1 km radius of the insect sampling sites | 0 ± 0 | 0.613 ± 1.338 | 0.262 ± 0.720 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 3.511, df = 2, p-value = 0.173 | | | 4 |
| **DWAspen_2km** | $m^3$ dead wood of aspen per ha within 2 km radius of the insect sampling sites | 0.200 ± 0.287 | 0.580 ± 0.871 | 0.443 ± 0.851 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.003, df = 2, p-value = 0.999 | | | 5 |
| **DWAspen_3km** | $m^3$ dead wood of aspen per ha within 3 km radius of the insect sampling sites | 0.506 ± 0.563 | 0.580 ± 0.623 | 0.506 ± 0.489 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.413, df = 2, p-value = 0.814 | | | 6 |
| **DWDeciduous_1km** | $m^3$ dead wood of deciduous wood other than aspen per ha within 1 km radius of the insect sampling sites | 3.718 ± 1.479 | 3.720 ± 2.365 | 4.500 ± 4.327 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.005, df = 2, p-value = 0.997 | | | 7 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **DWDeciduous_2km** | $m^3$ dead wood of deciduous wood other than aspen per ha within 2 km radius of the insect sampling sites | 3.793 ± 1.581 | 3.680 ± 2.066 | 4.506 ± 1.814 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.391, df = 2, p-value = 0.499 | | | 8 |
| **DWDeciduous_3km** | $m^3$ dead wood of deciduous wood other than aspen per ha within 3 km radius of the insect sampling sites | 5.068 ± 0.819 | 3.726 ± 1.510 | 3.843 ± 1.446 | Pairwise Wilcoxon rank sum test | **0.047** | **0.047** | 0.828 | 9 |
| **DWPine_1km** | $m^3$ dead wood of pine per ha within 1 km radius of the insect sampling sites | 7.625 ± 8.425 | 0.113 ± 0.269 | 2.800 ± 5.128 | Pairwise Wilcoxon rank sum test | **0.054** | 0.621 | **0.043** | 10 |
| **DWPine_2km** | $m^3$ dead wood of pine per ha within 2 km radius of the insect sampling sites | 3.331 ± 3.225 | 2.086 ± 1.976 | 1.943 ± 2.174 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.995, df = 2, p-value = 0.608 | | | 11 |
| **DWPine_3km** | $m^3$ dead wood of pine per ha within 3 km radius of the insect sampling sites | 2.106 ± 1.155 | 2.400 ± 0.607 | 2.500 ± 1.498 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.074, df = 2, p-value = 0.584 | | | 12 |
| **DWSpruce_1km** | $m^3$ dead wood of spruce per ha within 1 km radius of the insect sampling sites | 52.612 ± 51.350 | 12.253 ± 11.798 | 15.837 ± 19.530 | Pairwise Wilcoxon rank sum test | **0.009** | **0.009** | 0.953 | 13 |
| **DWSpruce_2km** | $m^3$ dead wood of spruce per ha within 2 km radius of the insect sampling sites | 31.225 ± 20.494 | 20.060 ± 11.894 | 22.137 ± 16.996 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.067, df = 2, p-value = 0.356 | | | 14 |
| **DWSpruce_3km** | $m^3$ dead wood of spruce per ha within 3 km radius of the insect sampling sites | 28.200 ± 6.777 | 21.460 ± 6.716 | 18.650 ± 10.009 | Pairwise Wilcoxon rank sum test | **0.020** | **0.010** | 0.358 | 15 |
| **DWDecay1st_1km** | $m^3$ dead wood in decay stage 1 per ha within 1 km radius of the insect sampling sites | 8.606 ± 7.288 | 4.046 ± 4.315 | 3.943 ± 4.848 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 3.006, df = 2, p-value = 0.223 | | | 16 |
| **DWDecay1st_2km** | $m^3$ dead wood in decay stage 1 per ha within 2 km radius of the insect sampling sites | 4.681 ± 2.434 | 3.313 ± 2.321 | 3.756 ± 3.061 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 3.054, df = 2, p-value = 0.217 | | | 17 |
| **DWDecay1st_3km** | $m^3$ dead wood in decay | 3.662 ± | 3.640 ± | 2.981 ± | Kruskal-Wallis | Kruskal-Wallis chi-squared = 2.568, | | | 18 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | stage 1 per ha within 3 km radius of the insect sampling sites | 1.242 | 1.441 | 1.926 | rank sum test | df = 2, p-value = 0.277 | | | |
| **DWDecay2nd_1km** | $m^3$ dead wood in decay stage 2 per ha within 1 km radius of the insect sampling sites | 28.100 ± 32.142 | 6.526 ± 8.353 | 10.050 ± 12.304 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.871, df = 2, p-value = 0.238 | | | 19 |
| **DWDecay2nd_2km** | $m^3$ dead wood in decay stage 2 per ha within 2 km radius of the insect sampling sites | 18.587 ± 13.010 | 11.113 ± 6.318 | 12.037 ± 8.840 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.843, df = 2, p-value = 0.241 | | | 20 |
| **DWDecay2nd_3km** | $m^3$ dead wood in decay stage 2 per ha within 3 km radius of the insect sampling sites | 16.468 ± 4.265 | 12.426 ± 2.859 | 10.556 ± 4.589 | Pairwise Wilcoxon rank sum test | **0.013** | **0.002** | 0.128 | 21 |
| **DWDecay3rd_1km** | $m^3$ dead wood in decay stage 3 per ha within 1 km radius of the insect sampling sites | 16.118 ± 9.585 | 2.346 ± 1.215 | 5.418 ± 6.856 | Pairwise Wilcoxon rank sum test | **0.001** | **0.006** | **0.093** | 22 |
| **DWDecay3rd_2km** | $m^3$ dead wood in decay stage 3 per ha within 2 km radius of the insect sampling sites | 8.187 ± 2.756 | 6.100 ± 3.825 | 6.106 ± 3.906 | Pairwise Wilcoxon rank sum test | **0.072** | **0.072** | 0.906 | 23 |
| **DWDecay3rd_3km** | $m^3$ dead wood in decay stage 3 per ha within 3 km radius of the insect sampling sites | 7.375 ± 1.124 | 5.973 ± 1.769 | 5.650 ± 2.023 | Pairwise Wilcoxon rank sum test | **0.065** | **0.058** | 0.678 | 24 |
| **DWDecay4th_1km** | $m^3$ dead wood in decay stage 4 per ha within 1 km radius of the insect sampling sites | 9.037 ± 9.679 | 1.960 ± 2.925 | 2.000 ± 2.175 | Pairwise Wilcoxon rank sum test | **0.006** | **0.012** | 0.513 | 25 |
| **DWDecay4th_2km** | $m^3$ dead wood in decay stage 4 per ha within 2 km radius of the insect sampling sites | 4.681 ± 3.528 | 3.313 ± 2.394 | 3.756 ± 3.204 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.114, df = 2, p-value = 0.573 | | | 26 |

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|---|---|---|---|---|---|---|---|---|---|
| **DWDecay4th_3km** | $m^3$ dead wood in decay stage 4 per ha within 3 km radius of the insect sampling sites | 4.281 ± 1.303 | 3.540 ± 1.949 | 3.618 ± 1.834 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 3.855, df = 2, p-value = 0.146 |  |  | 27 |
| **DWDecay5th_1km** | $m^3$ dead wood in decay stage 5 per ha within 1 km radius of the insect sampling sites | 2.087 ± 1.554 | 1.826 ± 2.419 | 1.956 ± 2.012 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.149, df = 2, p-value = 0.563 |  |  | 28 |
| **DWDecay5th_2km** | $m^3$ dead wood in decay stage 5 per ha within 2 km radius of the insect sampling sites | 2.256 ± 1.280 | 2.580 ± 1.903 | 3.056 ± 3.152 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.050, df = 2, p-value = 0.975 |  |  | 29 |
| **DWDecay5th_3km** | $m^3$ dead wood in decay stage 5 per ha within 3 km radius of the insect sampling sites | 4.075 ± 1.164 | 2.553 ± 0.944 | 2.675 ± 1.507 | Pairwise Wilcoxon rank sum test | **0.004** | **0.028** | 1.000 | 30 |
| **DWSmallDiam_1km** | $m^3$ dead wood with diameter 10-20 cm per ha within 1 km radius of the insect sampling sites | 9.418 ± 4.690 | 8.620 ± 4.756 | 8.775 ± 4.869 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.029, df = 2, p-value = 0.986 |  |  | 31 |
| **DWSmallDiam_2km** | $m^3$ dead wood with diameter 10-20 cm per ha within 2 km radius of the insect sampling sites | 8.537 ± 2.895 | 9.146 ± 3.066 | 10.150 ± 3.182 | One-way analysis of variance | Df SSq MSq F Pr(>F)<br>Cat 2 21.20 10.59 1.14 0.329<br>Error 44 409.23 9.30 |  |  | 32 |
| **DWSmallDiam_3km** | $m^3$ dead wood with diameter 10-20 cm per ha within 3 km radius of the insect sampling sites | 10.681 ± 1.700 | 8.973 ± 1.273 | 9.087 ± 1.848 | Pairwise t-test | **0.017** | **0.017** | 0.847 | 33 |
| **DWMidDiam_1km** | $m^3$ dead wood with diameter 21-30 cm per ha within 1 km radius of the insect sampling sites | 27.137 ± 17.009 | 5.693 ± 8.221 | 7.362 ± 8.835 | Pairwise Wilcoxon rank sum test | **< 0.001** | **0.001** | 0.674 | 34 |
| **DWMidDiam_2km** | $m^3$ dead wood with diameter 21-30 cm per ha within 2 km radius of the | 15.293 ± 7.360 | 8.473 ± 5.538 | 10.300 ± 6.236 | Pairwise Wilcoxon rank sum test | **0.100** | **0.100** | 0.450 | 35 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | insect sampling sites | | | | | | | | |
| **DWMidDiam_3km** | $m^3$ dead wood with diameter 21-30 cm per ha within 3 km radius of the insect sampling sites | 12.187 ± 3.446 | 9.726 ± 3.103 | 8.831 ± 2.976 | Pairwise Wilcoxon rank sum test | 0.110 | **0.026** | 0.452 | 36 |
| **DWLargeDiam_1km** | $m^3$ dead wood with diameter >30 cm per ha within 1 km radius of the insect sampling sites | 26.768 ± 25.852 | 2.393 ± 6.339 | 7.225 ± 13.329 | Pairwise Wilcoxon rank sum test | **< 0.001** | **0.004** | 0.160 | 37 |
| **DWLargeDiam_2km** | $m^3$ dead wood with diameter >30 cm per ha within 2 km radius of the insect sampling sites | 14.475 ± 8.786 | 8.806 ± 7.518 | 8.550 ± 10.408 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 5.481, df = 2, **p-value = 0.065** | | | 38 |
| **DWLargeDiam_3km** | $m^3$ dead wood with diameter >30 cm per ha within 3 km radius of the insect sampling sites | 12.918 ± 2.516 | 9.160 ± 4.597 | 7.412 ± 6.148 | Pairwise Wilcoxon rank sum test | **0.030** | **0.028** | 0.384 | 39 |

| **Variable** | **Values** | **Mean ± sd for NR** | **Mean ± sd for R** | **Mean ± sd for WKH** | **Test** | **p-value for NR VS R** | **p-value for NR VS WKH** | **p-value for R VS WKH** | **No.** |
|---|---|---|---|---|---|---|---|---|---|
| **YoungForest_1km** | $m^2$ of forest areas that are 1-40 years old within 1 km radius of the insect sampling sites | 234522.4 ± 186618.9 | 552103.1 ± 115803.9 | 535102.5 ± 360384.8 | Pairwise Wilcoxon rank sum test | **< 0.001** | **0.015** | 0.540 | 40 |
| **YoungForest_2km** | $m^2$ of forest areas that are 1-40 years old within 2 km radius of the insect sampling sites | 1867600 ± 1294080 | 2557370 ± 538293.6 | 2166419 ± 1314984 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.272, df = 2, p-value = 0.529 | | | 41 |
| **YoungForest_3km** | $m^2$ of forest areas that are 1-40 years old within 3 km radius of the insect sampling sites | 4850912 ± 2857107 | 5740111 ± 1803388 | 5196444 ± 2785100 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.840, df = 2, p-value = 0.657 | | | 42 |
| **MidAgeForest_1km** | $m^2$ of forest areas that are 41-80 years old within 1 km radius of the insect | 920674.8 ± 506612.9 | 1437903 ± 589792.7 | 1375891 ± 562230.5 | Pairwise Wilcoxon rank sum test | **0.029** | **0.029** | 0.797 | 43 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | sampling sites | | | | | | | | |
| **MidAgeForest_2km** | $m^2$ of forest areas that are 41-80 years old within 2 km radius of the insect sampling sites | 3977885 ± 1238863 | 5767850 ± 1823252 | 5278491 ± 1823550 | Pairwise Wilcoxon rank sum test | **0.009** | **0.052** | 0.6781 | 44 |
| **MidAgeForest_3km** | $m^2$ of forest areas that are 41-80 years old within 3 km radius of the insect sampling sites | 10143011 ± 1533237 | 12263059 ± 3179836 | 11264838 ± 3304774 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.908, df = 2, p-value = 0.234 | | | 45 |
| **OldForest_1km** | $m^2$ of forest areas that are over 80 years old within 1 km radius of the insect sampling sites | 1471540 ± 466278.8 | 747401.5 ± 486858.3 | 878194.7 ± 579100.5 | Pairwise Wilcoxon rank sum test | **0.002** | **0.012** | 0.594 | 46 |
| **OldForest_2km** | $m^2$ of forest areas that are over 80 years old within 2 km radius of the insect sampling sites | 5175833 ± 934152.6 | 2575372 ± 1286628 | 3704821 ± 2142164 | Pairwise Wilcoxon rank sum test | **< 0.001** | **0.100** | 0.140 | 47 |
| **OldForest_3km** | $m^2$ of forest areas that are over 80 years old within 3 km radius of the insect sampling sites | 10091082 ± 1727198 | 6521536 ± 1902040 | 8467741 ± 3976897 | Pairwise t-test without pooled sd | **< 0.001** | 0.190 | 0.190 | 48 |
| **LowVolForest_1km** | $m^2$ of forest areas with 1-100 $m^3$ forest per ha within 1 km radius of the insect sampling sites | 746545.1 ± 724295.1 | 876030.1 ± 411660.7 | 967806.6 ± 565715.6 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.426, df = 2, p-value = 0.490 | | | 49 |
| **LowVolForest_2km** | $m^2$ of forest areas with 1-100 $m^3$ forest per ha within 2 km radius of the insect sampling sites | 3882101 ± 3496042 | 4115483 ± 1596373 | 3848607 ± 1999699 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.036, df = 2, p-value = 0.982 | | | 50 |
| **LowVolForest_3km** | $m^2$ of forest areas with 1-100 $m^3$ forest per ha within 3 km radius of the insect sampling sites | 9082601 ± 6896167 | 9191148 ± 4217181 | 9078337 ± 4614870 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.134, df = 2, p-value = 0.935 | | | 51 |
| **MidVolForest_1km** | $m^2$ of forest areas with 101-200 $m^3$ forest per ha within | 1257663 ± | 1589830 ± | 1647078 ± | Pairwise t-test without pooled sd | **0.024** | **0.024** | 0.723 | 52 |

|  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|
|  | 1 km radius of the insect sampling sites | 239604.7 | 378327.5 | 506948.9 |  |  |  |  |  |
| **MidVolForest_2km** | m$^2$ of forest areas with 101-200 m$^3$ forest per ha within 2 km radius of the insect sampling sites | 5155628 ± 1515609 | 5838499 ± 1522709 | 6436824 ± 1773415 | Pairwise Wilcoxon rank sum test | 0.171 | **0.078** | 0.281 | 53 |
| **MidVolForest_3km** | m$^2$ of forest areas with 101-200 m$^3$ forest per ha within 3 km radius of the insect sampling sites | 12366522 ± 3490683 | 13175925 ± 3825480 | 13866744 ± 3984297 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 4.789, df = 2, **p-value = 0.091** |  |  | 54 |
| **HighVolForest_1km** | m$^2$ of forest areas with >200 m$^3$ forest per ha within 1 km radius of the insect sampling sites | 622528.8 ± 635646.7 | 275012.3 ± 273762.5 | 192103.2 ± 160026.5 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.646, df = 2, p-value = 0.724 |  |  | 55 |
| **HighVolForest_2km** | m$^2$ of forest areas with >200 m$^3$ forest per ha within 2 km radius of the insect sampling sites | 2089469 ± 2013309 | 952315.4 ± 921116.2 | 856949.8 ± 667390.7 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.011, df = 2, p-value = 0.995 |  |  | 56 |
| **HighVolForest_3km** | m$^2$ of forest areas with >200 m$^3$ forest per ha within 3 km radius of the insect sampling sites | 3636170 ± 3215857 | 2171151 ± 1789295 | 1968367 ± 1203861 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.005, df = 2, p-value = 0.998 |  |  | 57 |
| **LowDeciForest_1km** | m$^2$ of forest areas with 0-35 m$^3$ deciduous forest per ha within 1 km radius of the insect sampling sites | 2621787 ± 68728.32 | 2629922 ± 289169.2 | 2698712 ± 175697.4 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.908, df = 2, p-value = 0.234 |  |  | 58 |
| **LowDeciForest_2km** | m$^2$ of forest areas with 0-35 m$^3$ deciduous forest per ha within 2 km radius of the insect sampling sites | 10947651 ± 131462.1 | 10537437 ± 818269.7 | 10785853 ± 538990.1 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.366, df = 2, p-value = 0.306 |  |  | 59 |
| **LowDeciForest_3km** | m$^2$ of forest areas with 0-35 m$^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 24599905 ± 203850.6 | 23653672 ± 1536082 | 24029867 ± 1105627 | Pairwise Wilcoxon rank sum test | **< 0.001** | **0.022** | 0.353 | 60 |
| **MidDeciForest_1km** | m$^2$ of forest areas with 36- | 4950 ± | 107048.9 | 90363.17 | Pairwise | 0.448 | **0.013** | 0.448 | 61 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 75 $m^3$ deciduous forest per ha within 1 km radius of the insect sampling sites | 8854.829 | ± 211623.8 | ± 116457.4 | Wilcoxon rank sum test | | | | |
| **MidDeciForest_2km** | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 2 km radius of the insect sampling sites | 73216.83 ± 79379.21 | 359375.4 ± 600566.7 | 358754.4 ± 479705.4 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.160, df = 2, p-value = 0.340 | | | 62 |
| **MidDeciForest_3km** | $m^2$ of forest areas with 36-75 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 481640.6 ± 228670.1 | 868911.2 ± 1004050 | 878996.9 ± 948827.9 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.885, df = 2, p-value = 0.642 | | | 63 |
| **HighDeciForest_1km** | $m^2$ of forest areas with >75 $m^3$ deciduous forest per ha within 1 km radius of the insect sampling sites | 0 ± 0 | 3901.449 ± 11966.65 | 112.4975 ± 449.99 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 2.355, df = 2, p-value = 0.308 | | | 64 |
| **HighDeciForest_2km** | $m^2$ of forest areas with >75 $m^3$ deciduous forest per ha within 2 km radius of the insect sampling sites | 449.995 ± 929.5031 | 9485.021 ± 24488 | 5143.577 ± 15388.16 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.330, df = 2, p-value = 0.848 | | | 65 |
| **HighDeciForest_3km** | $m^2$ of forest areas with >75 $m^3$ deciduous forest per ha within 3 km radius of the insect sampling sites | 3458.928 ± 5606.162 | 19841.46 ± 48264.16 | 13184.25 ± 28138.35 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.730, df = 2, p-value = 0.694 | | | 66 |
| **Forest_1km** | $m^2$ of forest area within 1 km radius of the insect sampling sites | 2626737 ± 70536.25 | 2737408 ± 156689.4 | 2789188 ± 215694.4 | Pairwise t-test without pooled sd | **0.043** | **0.031** | 0.449 | 67 |
| **Forest_2km** | $m^2$ of forest area within 2 km radius of the insect sampling sites | 11021318 ± 182804 | 10900592 ± 453750.3 | 11149731 ± 544350.9 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 3.263, df = 2, p-value = 0.196 | | | 68 |
| **Forest_3km** | $m^2$ of forest area within 3 km radius of the insect sampling sites | 25085005 ± 287602 | 24524706 ± 739189.6 | 24929023 ± 673422.7 | Pairwise Wilcoxon rank sum test | **0.026** | 0.564 | 0.321 | 69 |
| **Altitude** | meters above sea level at the insect sampling sites | 392.5 ± 136.611 | 335.7 ± 100.880 | 328.9 ± 110.549 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.235, df = 2, p-value = 0.539 | | | 70 |

| Variable | Values | Mean ± sd for NR | Mean ± sd for R | Mean ± sd for WKH | Test | p-value for NR VS R | p-value for NR VS WKH | p-value for R VS WKH | No. |
|---|---|---|---|---|---|---|---|---|---|
| **AllSp** | number of insect species trapped at the insect sampling sites | 67.437 ± 19.342 | 81.875 ± 16.476 | 88.066 ± 28.758 | Pairwise t-test with pooled sd | **0.026** | **0.060** | 0.586 | 71 |
| **SxSp** | number of saproxylic insect species trapped at the insect sampling sites | 52.500 ± 14.953 | 65.733 ± 20.394 | 63.500 ± 13.995 | Pairwise t-test with pooled sd | **0.072** | **0.073** | 0.832 | 72 |
| **AASp** | number of aspen associated insect species trapped at the insect sampling sites | 31.437 ± 8.074 | 35.266 ± 9.199 | 37.750 ± 8.053 | One-way analysis of variance | Df SSq MSq F Pr(>F)<br>Cat 2 323.41 161.70 2.27 0.115<br>Error 44 3135.87 71.27 | | | 73 |
| **NonSxSp** | number of non-saproxylic insect species trapped at the insect sampling sites | 14.938 ± 6.245 | 18.375 ± 5.608 | 22.333 ± 9.648 | Pairwise Wilcoxon rank sum test | 0.052 | 0.191 | 0.812 | 74 |
| **ASSp** | number of aspen specialist saproxylic insect species trapped at the insect sampling sites | 2.188 ± 0.981 | 2.063 ± 1.34 | 2.2 ± 1.014 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.804, df = 2, p-value =0.669 | | | 75 |
| **RLSp** | number of red-listed insect species trapped at the insect sampling sites | 0.938 ± 1.062 | 1.25 ± 1.612 | 1.533 ± 1.457 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 1.548, df = 2, p-value = 0.461 | | | 76 |
| **AllInd** | number of insect individuals trapped at the insect sampling sites | 185.313 ± 81.326 | 241.25 ± 83.167 | 288.8 ± 147.703 | Pairwise t-test with pooled sd | **0.015** | 0.101 | 0.339 | 77 |
| **SxInd** | number of saproxylic insect individuals trapped at the insect sampling sites | 157.5 ± 77.758 | 205.375 ± 72.444 | 233.066 ± 123.457 | Pairwise t-test with pooled sd | **0.048** | 0.107 | 0.585 | 78 |
| **AAInd** | number of aspen associated saproxylic insect individuals trapped at the insect sampling sites | 102.75 ± 48.730 | 136.25 ± 53.993 | 117.866 ± 44.496 | One-way analysis of variance | Df SSq MSq F Pr(>F)<br>Cat 2 0.810 0.405 2.049 0.141<br>Error 44 8.701 0.198 | | | 79 |
| **NonSxInd** | number of non-saproxylic insect individuals trapped at the insect sampling sites | 27.813 ± 13.273 | 35.875 ± 20.002 | 55.733 ± 43.201 | Pairwise t-test with pooled sd | **0.018** | 0.263 | 0.163 | 80 |
| **ASInd** | number of aspen specialist saproxylic insect individuals trapped at the insect sampling sites | 8.625 ± 7.702 | 9.1875 ± 5.671 | 10.133 ± 7.308 | Kruskal-Wallis rank sum test | Kruskal-Wallis chi-squared = 0.812, df = 2, p-value =0.666 | | | 81 |
| **RLInd** | number of red-listed insect | 0.938 ± | 1.4375 ± | 2.133 ± | Kruskal-Wallis | Kruskal-Wallis chi-squared = 2.458, | | | 82 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | individuals trapped at the insect sampling sites | 1.062 | 2.032 | 2.559 | rank sum test | df = 2, p-value = 0.293 |

Table 3) Loadings from the 18 variables to the principal components PC1 and PC2. Highest loading in each component is bold. Last cell shows proportion of variance in the dataset explained by each principal component.

| **Variables** | **PC1** | **PC2** |
|---|---|---|
| YoungForest_2km | -0.230 | 0.125 |
| MidAgeForest_1km | -0.092 | -0.120 |
| OldForest_3km | **0.943** | 0.240 |
| MidVolForest_1km | -0.009 | -0.010 |
| LowDeciForest_3km | 0.158 | **-0.767** |
| MidDeciForest_2km | -0.074 | 0.266 |
| MidDeciForest_3km | -0.134 | 0.502 |
| HighDeciForest_2km | -0.002 | 0.011 |
| HighDeciForest_3km | -0.004 | 0.022 |
| Forest_1km | -0.019 | 0.007 |
| Altitude | <0.001 | <0.001 |
| DW_1km | <0.001 | <0.001 |
| DWAspen_2km | <0.001 | <0.001 |
| DWPine_2km | <0.001 | <0.001 |
| DWMidDiam_1km | <0.001 | <0.001 |
| DWDecay3rd_1km | <0.001 | <0.001 |
| DWDecay5th_1km | <0.001 | <0.001 |
| DWDecay1st_2km | <0.001 | <0.001 |
| Proportion of variance explained by component | 0.780 | 0.117 |