



Norwegian University  
of Life Sciences

Master's Thesis 2017 60 ECTS

Faculty of Environmental Sciences and Natural Resource Management

# **Five-year numerical response of saproxylic beetles following a dead wood pulse left by moth outbreaks in northern Scandinavia**

Petter Bernhard Carlsen  
Master in biology



## Acknowledgments:

This is the final thesis of my master's degree in biology, with a specialization within animal ecology and entomology at the Norwegian University of Life Sciences (NMBU). This thesis is also a part of the Birchmoth project at the University of Tromsø (UIT), and consequently a collaboration between NMBU and the UIT.

First, I would like to express my gratitude towards my supervisors Anne Sverdrup-Thygeson, Tone Birkemoe, Ole Petter Laksforsmo Vindstad and Jane Uhd Jepsen for their assistance, encouragement and excellent feedback. This thesis would not be possible without your support and knowledge. Ole Petter also gave invaluable help with fieldwork and analyses. I also want to give a thanks to Sindre Ligaard who identified all the beetle species. Then I wish to thank everybody at the Northern Populations and Ecosystems group and the at UIT for valuable discussions, helpful tips and motivation during my time there, in addition to some fun months in Tromsø (which at the time was a new and unknown habitat for me). Thanks to my fellow master students at NMBU for helpful tips and motivation, and for suffering along during the final months of the master thesis-writing process. Special thanks goes to whoever put the coffee machine at the master students' office at NMBU. You're a lifesaver!

Finally, I want to give a big thanks to my family for always giving me good support, motivation and for believing in what I do.

Petter Bernhard Carlsen



*Salpingus ruficollis* (Linnaeus 1761)

(Chalupa 1995)

## **Summary:**

Saproxylic insects are important for the decomposition of dead wood, and therefore crucial for maintaining healthy forest ecosystems. There is, however, little knowledge about their ability to respond to massive resource pulses of dead wood caused by outbreaks of defoliating insects. This study investigates the numerical response of saproxylic beetles to increased availability of dead wood caused by outbreaks of geometrid moths in the mountain birch forest of Finnmark, Northern Norway. Beetles were sampled with window (flight interception) traps in 2011, 2012, 2015 and 2016 along two 20 km long transects with differences in habitats and defoliation histories. Both transects started in forest that was damaged by outbreaks during the period 2001-2009 (high dead wood abundance) and ran towards healthy, undamaged forest (normal dead wood abundance). Galleries and exit-holes made by saproxylic beetles on dead stems were also counted along the same transects in 2016. This were done to assess differences in utilization rates of dead trees by the beetles between damaged and undamaged forest and transects. The abundance of saproxylic beetles in the study system increased from 2011 to 2015. However, this response was seemingly driven by a few dominant species related to early successional stages of wood decay. Habitat variations between transects did in addition appear to heavily affect most of the beetle community, including the dominant species. The beetles appeared to favor areas with more variation and productivity, which corresponds with the utilization rates of dead trees by saproxylic beetles. The rates of galleries and exit-holes were highest in such areas as well as on stems with high diameters. However, the saproxylic beetle community has yet to utilize all the dead wood resources of the area as of 2016, and the wood remains in an early stage of decomposition. Less preferable dead wood resources and the cold climate of the region may partially explain why the beetle community have been unable to mount a sufficient numerical response to handle all the dead wood resources. The dead wood created by the moth outbreak may therefore spend longer time to decompose past the earliest successional stages than anticipated.

## **Sammendrag:**

Saproxyle innsekter er viktige for nedbrytningen av død ved, og essensielle for å opprettholde sunne økosystemer i skog. Det er imidlertid lite kunnskap om deres evne til å respondere på omfattende resurspulser av død ved forårsaket gjennom utbrudd av defolierende innsekter. Denne studien undersøker den numeriske responsen til saproxyle biller etter økt tilgang på død ved forårsaket gjennom utbrudd av herbivore målere i de nordlige fjellbjørkeskogene i Finnmark, Norge. Biller ble samlet ved bruk av vindusfeller i 2011, 2012, 2015 og 2016 langs to transekter med ulike habitater og defolieringsbakgrunner. Begge transektene startet i bjørkeskog som var hardt påvirket av målerutbrudd i perioden 2001-2009 (høy tilgang på død ved), og løp mot sunn skog tilsynelatende upåvirket av målerutbruddene (normal tilgang på død ved). Gallerier og utgangshull laget av saproxyle biller på døde stammer ble også telt langs de samme transektene i 2016. Dette ble gjort for å undersøke forskjeller i andelen av brukt og ubrukt død ved av saproxyle biller mellom skadet og uskadet skog og mellom transektene. Antallet saproxyle biller i studiesystemet økte fra 2011 til 2015, men denne responsen var tilsynelatende styrt av noen få dominante arter relatert til tidlige stadier av nedbrytningsprosessen til død ved. Variasjoner i habitatene mellom transektene så ut til å påvirke mesteparten av billesamfunnet betydelig. Dette gjelder også de mest dominerende artene. Billene favoriserte tilsynelatende områder med høyere variasjon og produktivitet, noe som sammenfaller med områder hvor andelen gallerier og utgangshull fra saproxyle biller var høyest i død ved. Andelen trær med gallerier og utgangshull var høyest i områder med høy produktivitet og blant trær med større diameter. Det saproxyle billesamfunnet har likevel ikke klart å iverksette en tilstrekkelig numerisk respons for å anvende all død ved i området innen 2016, hvor veden ser fortsatt ut til å befinne seg i et tidlig stadium av nedbrytningsprosessen. Årsaker til dette kan være det kalde klimaet til regionen, og at den døde veden forekommer i en mindre foretrukket variant. Den døde veden forårsaket av målerutbruddene vil antageligvis bruke lengre tid på å brytes ned forbi de første stadiene av nedbrytningsprosessen.

# Table of contents

Acknowledgments: .....	I
Summary:.....	II
Sammendrag:.....	III
Table of contents.....	IV
<b>1. Introduction:</b> .....	1
<i>1.1 Hypotheses:</i> .....	6
<b>2. Materials and methods:</b> .....	6
<i>2.1 Study system:</i> .....	6
<i>2.2 Study design &amp; data collection:</i> .....	7
<i>2.3 Statistical analyses:</i> .....	11
<b>3. Results:</b> .....	12
<i>3.1 Overall beetle community structure:</i> .....	12
<i>3.2 Single species:</i> .....	16
<i>3.3 Insect galleries and exit-holes:</i> .....	22
<b>4. Discussion:</b> .....	23
<b>5. Conclusions:</b> .....	27
<b>References:</b> .....	27
<b>Appendices:</b> .....	32
<b>Appendix 1. List of beetle species:</b> .....	32
<b>Appendix 2. Biological information for selected single species:</b> .....	42
<b>Appendix 3. Terrain variables:</b> .....	44

## **1. Introduction:**

Sudden inputs of resources made available to organisms in abnormal quantities can drastically alter the stability of any given ecosystem. Massive pulsed increases in resource availability, termed resource pulses, are a widespread phenomenon found in nature, even though they tend to occur infrequently within any given ecosystem. The definition of such resource pulses, given by Yang et al. (2008), are that of infrequent events which lead to increased availability of certain resources over short periods of time. These pulses are usually caused by natural or unnatural disturbance factors that significantly alters the stability of a given ecosystem, such as forest fires, El Niño rainfalls, mass migration and mass mortality of certain organisms (Carlton & Goldman 1984; Davis et al. 2012; Letnic et al. 2005; Polis et al. 1997; Yanai & Kochi 2005; Yang 2006; Yang et al. 2008; Yang et al. 2010).

Resource pulses occur in a wide variety of habitats, ranging across most climates in both aquatic and terrestrial ecosystems, and differ greatly in frequency, duration, magnitude and nature of the pulsed resource. Therefore, it may be difficult to predict their general effects on ecosystems and groups of organisms (Yang et al. 2008; Yang et al. 2010). Still, some general patterns can be outlined. Consumers who rely on reproductive responses, which reacts by producing more or less offspring, are usually slower and weaker in their responses compared to the more aggregative responders, which reacts through migration. On the other hand, a reproductive response tends to be more persistent within the local community than an aggregative response. In addition, a pulsed resource from a low trophic level, especially those among primary producers, has a tendency to generate the largest responses among consumers. However, consumers of such resources often belong to low trophic levels themselves, and may be susceptible to top-down effects from consumers of higher trophic levels (Yang et al. 2010).

Dead wood is a common example of a resource that occasionally and periodically is made available in pulses through a wide variety of natural disturbance factors. Some important factors include forest fires, windfalls, landslides, flooding and outbreaks of tree killing bark beetles and other insects. Several of these disturbance factors tend to occur with intervals of varying regularity (Collins et al. 2012; Elia et al. 2012; Perera et al. 2015). Such factors generate resource pulses of dead wood in cycles of differing length, which may create repeated possibilities for observation and studying, and then contribute to a better understanding of their consequences on the affected ecosystems. Besides, dead wood is an

important resource in forest ecosystems for a wide variety of organisms, including many groups and species of invertebrates, fungi and other microorganisms. Therefore, these pulses may give valuable insight to how dead wood utilizing organisms respond to the dead wood pulses (Elia et al. 2012; Stokland et al. 2012; Ulyshen 2014; Yang 2012).

Saproxyllic insects are one group of organisms that may benefit from increased availability of dead wood resources. They are recognized as one of the most important groups of wood decomposing organisms, and are defined by Speight (1989) as those species that are:

*“dependent, during some part of their life cycle, upon dead or dying wood from moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxyllic species”* (Speight 1989).

About 20-30% of all insect species living in forests depend on dead or dying wood, and some of the major functional groups among them are phloem and wood feeders, fungus feeders, detritus feeders and predators of other saproxyllic species (Speight 1989; Stokland et al. 2012).

In addition to a wide variety of functional groups, saproxyllic insect species also differ greatly in their preferences and requirements for different dead wood qualities. These include differences in moisture content, stem diameter, temperature, species of the host tree and decomposition stage to mention a few (Stokland et al. 2012; Ulyshen 2014). The cause of tree mortality may also play an important role for some species. For example, some insect species prefer burned wood and are specially adapted to detect forest fires from a long distance (Elia et al. 2012; Gullan et al. 2010; New 2014). Climate is another factor which may be limiting for many insect species as they are not adapted to too cold or too warm temperatures (Gullan et al. 2010; Speight 1989; Stokland et al. 2012). When considering all these factors, a specific disturbance factor may only provide a resource pulse of dead wood for a small fraction of saproxyllic species shortly after it occurs. For many other saproxyllic species, the increased resources may only become accessible a long time after it occurred, which could be up to several years, or not at all due to adaptations that require a specific mortality cause (Ehnström & Axelsson 2002; Stokland et al. 2012; Wermelinger et al. 2002).

Not only is dead wood an important resource for wood decaying organisms, wood decomposition is also an important process for maintaining healthy forest ecosystems. The decomposition process is typically divided into four stages, from the beginning of tree death to a tree is fully decomposed (Ehnström & Axelsson 2002). The first stage of decomposition usually lasts from one to five years, where the bark is still intact even though early



successional species feed heavily upon the cambium. Later stages usually lasts longer and act as a habitat for an increasingly diverse array of species (Ehnström & Axelsson 2002; Stokland et al. 2012; Ulyshen 2014; Ulyshen et al. 2016). If this process goes slowly, forest ecosystems may accumulate large amounts of dead woody material, which contain a lot of nutrients. These nutrients becomes slowly and gradually available to the environment through decomposition (Franklin et al. 1987; Ulyshen 2014). High tree mortality may then significantly affect an ecosystem.

Several factors such as climate, temperature, moisture and oxygen availability play important roles in determining the availability of dead wood to many saproxylic species, and thereby help determine the decay rates of dead wood. (Hicks et al. 2003; Stokland et al. 2012). As a general rule, the rate of decomposition increases with warmer climate on a global scale. Low temperatures, especially beneath freezing point, tends to arrest activity of saproxylic organisms, and as a result halts wood decomposition. In areas with colder climates, the productive season for saproxylic species are therefore often shorter, which leads to slower decomposition rates (Chen 1999; Hicks et al. 2003; Stokland et al. 2012; Yatskov et al. 2003). Low temperatures may also reduce moisture by binding water in ice. Decomposition requires a minimum amount of moisture for wood degrading enzymes to function and for metabolism of saproxylic organisms to occur. Too much moisture can however prevent their oxygen intake, thereby reducing their respiration and decay rates (Stokland et al. 2012). Fragmentation also help increase moisture content and respiration in wood, and creates easier accessibility for many saproxylic organisms that are unable to create passages into the wood by themselves. Just as the surrounding environment often influence these factors, they are also significantly affected by the mortality factor, especially in the early stages of decomposition (Chen 1999; Franklin et al. 1987; Stokland et al. 2012).

Outbreaks of defoliating insects is a disturbance factor that periodically creates vast amounts of dead wood (Jepsen et al. 2013; Kamata 2002; Weed et al. 2013). As with most other mortality factors, insect outbreaks generates dead wood with certain traits. Trees killed by insect attacks are left standing, and usually die slowly over the course of several years, draining the nutrients within. While some outbreaking insects like bark beetles may promote colonization of wood decaying fungi and other microorganisms, defoliating insects mostly weakens trees by reducing their ability for photosynthesis and respiration (Persson et al. 2009; Persson et al. 2011; Yang 2012). The potential effects of these outbreaks on their respective ecosystems have lately gotten more and more attention, as they often result in high tree

mortality with important changes to ecosystems over longer periods of time (Yang 2012). In the last decades, insect outbreaks have become an increasing disturbance factor in many forest ecosystems worldwide. The need for understanding the ecological impacts of these outbreaks is therefore increasing (Jepsen et al. 2013; Kamata 2002; Weed et al. 2013).

Beetles are a highly species rich and diverse order of insects, which includes a great diversity of saproxylic species (Stokland & Meyke 2008). Their response to large-scale forest disturbance factors are therefore highly relevant and has been given much attention in the latest decades. Several species among saproxylic beetles are known to be dependent on early successional stages of wood decay, and are important for initiating colonization by other saproxylic organisms (Ehnström & Axelsson 2002; Hansen 1954; Persson et al. 2011; Stokland et al. 2012). It has been documented that populations of saproxylic beetles have increased after disturbance factors that provide resource pulses of dead wood, such as wind, logging and forest fires. However, most of these studies have focused on saproxylic species without much consideration for how non-saproxylic beetles respond to such events, and if they differ from saproxylic beetles (New 2014; Thibault & Moreau 2016; Wermelinger et al. 2002). In addition, mortality factor is considered to be one of the most important factors that determines community development in dead wood, at least in the early stages of decay (Stokland et al. 2012). Dead wood left by insect outbreaks may therefore not necessarily lead to the same amount of numerical responses in saproxylic insects, and the species compositions may be different. Some studies does however give evidence for positive numerical responses among saproxylic beetles to dead wood left by insect outbreaks. However, this subject is still relatively poorly understood, and their response compared to non-saproxylic beetles even more (Müller et al. 2010; Schultze 2012; Vindstad et al. 2014).

Two geometrid moth species, the autumnal moth (*Epirrita autumnata*) and the winter moth (*Operophtera brumata*) each had a major outbreak in their populations in the period 2000 – 2008. The outbreak of both species occurred mainly in the northern Fennoscandia, where they caused severe defoliation in birch forests over a large area. The most heavily affected area was in the Varanger region in northeast Norway (Jepsen, J. U. et al. 2009; Jepsen et al. 2013). These outbreaks have left large amounts of dead birch as a resource pulse for saproxylic insects in the area. Outbreaks by geometrid moths have occurred in these areas before, but not in the same magnitude and severity as this last one. It is implied that warmer climate caused by climate change may have had an effect on the ability of these moths to generate such a huge outbreak. Both *E. autumnata* and *O. brumata* have extended their distribution ranges,

possibly due to warmer climate (Bylund 1999; Jepsen et al. 2008; Jepsen, Jane U. et al. 2009; Jepsen et al. 2013). In addition, the outbreaks of the two moth species occurred with a time lag of a few years, and the spread of the two species were slightly different, resulting in a mosaic of local differences in outbreak histories (Jepsen, J. U. et al. 2009; Jepsen, Jane U. et al. 2009).

Previous studies in this area suggests that local variations in factors that affect dead wood quality lead to different responses among saproxylic beetles and other organism between habitats (Jepsen et al. 2013; Vindstad et al. 2014; Vindstad et al. 2015). Some saproxylic beetles had already shown a weak numerical response in 2011 – 2012. This was however, limited to a few early successional species that were highly abundant compared to the rest, and other factors seemed to affect the beetles just as much or even more than the dead wood abundance (Vindstad et al. 2014). Because the magnitude of dead wood left by the moth outbreaks are so unusual and new to this area, it is unknown how the local populations of saproxylic beetles will respond over time following new successional stages of wood decomposition (Vindstad et al. 2014).

## ***1.1 Hypotheses:***

In this study, I will compare beetle counts from four sampling seasons (namely 2011, 2012, 2015 and 2016), from damaged and undamaged forest, between two sampling areas with different defoliation backgrounds and habitat qualities. Vindstad et al. (2014) have already described the main patterns of the first two sampling seasons (2011 and 2012), while the patterns of the two latest sampling seasons are first described in this study. The goal is to investigate the following hypotheses:

- 1) The numerical response of the saproxylic beetle community to the dead wood left by the moth outbreaks has increased in 2015 and 2016 compared to the response found in the two first sampling seasons, described by Vindstad et al. (2014).
- 2) Differences in habitats and defoliation history between the two sampling areas lead to different responses in the saproxylic beetles living in the two areas, with a greater positive numerical response of saproxylic beetles in the Kirkenes transects compared to the Tana transect, on both community level and species level.
- 3) In the two latest trapping seasons, early successional species are less abundant, than in earlier observations done by Vindstad et al. (2014), while species related to later stages of decomposition are more abundant.

## **2. Materials and methods:**

### ***2.1 Study system:***

The study area is located in Varanger, a region in the eastern part of Finnmark County in northern Norway (figure 2). This region is located at roughly 70°N and 29°E. The climate in this region is characterized by cold temperatures at winter, but has relatively warm summer temperatures for Northern Norway. The woody vegetation in this area is mainly dominated by mountain birch (*Betula pubescens*) with some occurrence of patches with aspen (*Populus tremula*) and Scots pine (*Pinus sylvestris*) (Jepsen, J. U. et al. 2009; Vindstad et al. 2014). The birch forests generally grow on quite nutrient poor soil, and the birch trees are as a result characterized by multiple stems with small diameters (personal observations).

About every 10 years, the mountain birch ecosystem in northern Fennoscandia experiences outbreaks of the two geometrid moth species *E. autumnata* (autumnal moth) and *O. brumata* (winter moth) (Bylund 1999). Although these outbreaks vary in intensity, they can cause severe defoliation in a large amount of mountain birch trees. During the period 2000 – 2008, a particularly severe outbreak caused defoliation in up to 10-15% of the total birch forest area in Fennoscandia, with 30-40 000 km<sup>2</sup> of severely defoliated birch forest in total. About one third (just above 10 000 km<sup>2</sup>) of the affected areas were located on the Varanger region, which was the most severely affected region of this outbreak (Jepsen, Jane U. et al. 2009; Vindstad et al. 2014).

Two transects of 20 km each, with different defoliation backgrounds, were established in 2011, and are henceforth referred to as Tana (70°03' N, 27°45' E) and Kirkenes (69°46' N, 29°20' E). The average temperature in January is at approximately -10.3°C at the weather station Kirkenes Lufthavn (2000-2016), which is the closest weather station to the Kirkenes transect, and -10°C at the weather station Rustefelbma (2000-2013), which is the closest weather station to the Tana transect. The average temperature in July is at approximately 12.7°C at the weather station Kirkenes Lufthavn (2000-2016), and 13°C at the weather station Rustefelbma (2000-2012) [monthly normal temperature 2000-2016 by Norwegian Meteorological institute (<http://eklima.met.no>)].

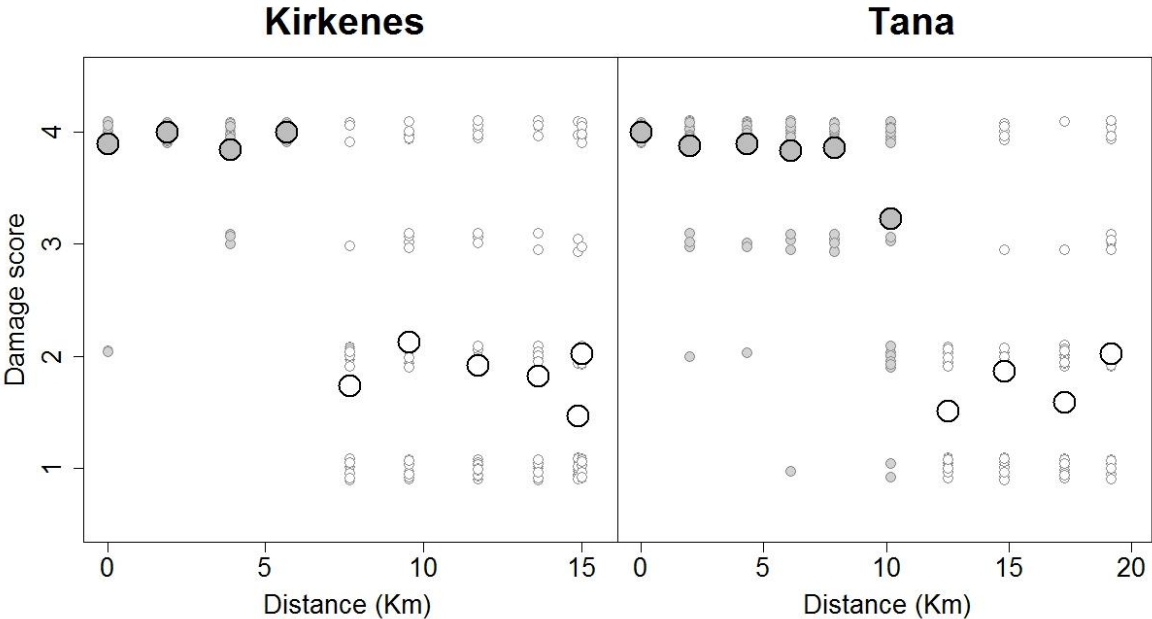
The moth outbreak has produced a large amount of dead wood in Varanger, but the transition between affected and unaffected forest does not appear to be gradual. Instead, there is an abrupt shift between undamaged and heavily damaged forest areas (Vindstad et al. 2014).

## ***2.2 Study design & data collection:***

For data collection in this study, we utilized the methods developed by Vindstad et al. (2014) described below. This procedure was first performed in 2011 and in 2012 for the study done by Vindstad et al. (2014), and then repeated in 2015 and 2016 for this study. The current study utilized data from all four sampling years.

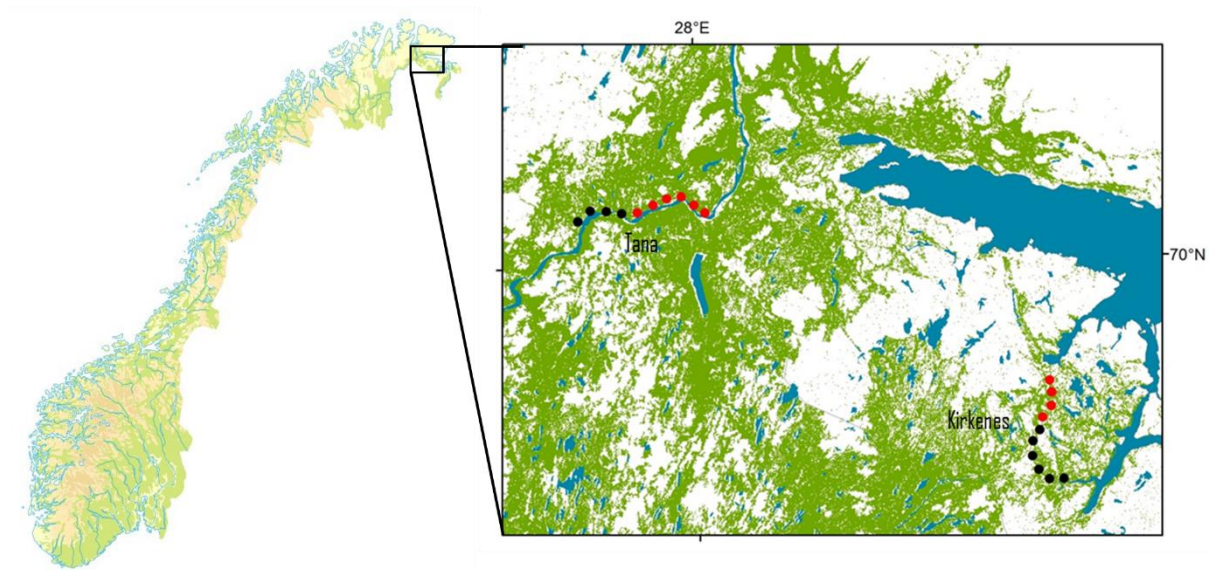
The two transects include 10 sampling stations each. The sampling stations are located every other km along the transects. There are both healthy, undamaged birch forest, and forest that has been heavily damaged by the last moth outbreak in each of the areas where the transects are set up. Vindstad et al. (2014) established the measures of forest damage which this study

utilizes. Originally, four wood vitality scores were established to grade the damage of the forest at each sampling station, with vitality score 1 categorized as live undamaged forest, and vitality score 4 as dead forest. However, since there was no gradual change in mean wood vitality detected between sampling stations with forest damaged by the moth outbreaks and stations with unaffected forest, but rather an abrupt shift between heavily damaged forest and undamaged forest, the forest are categorized as either damaged or undamaged forest (Vindstad et al. 2014, figure 1, figure 2).



**Figure 1: Damage scores for each sampling station in the two transects Kirkenes and Tana.** Large circles represent the average score per station. Filled circles represent stations in heavily damaged forest, while empty circles represent stations in normal healthy forest. Small circles represent original data points. Numbers on the x-axis represents the distance (in Km) from the first sampling station within each transect. From Vindstad et al. (2014).

Each of the two transects cover both damaged and undamaged forest, with sampling stations 1-4 in Kirkenes and sampling stations 1-6 in Tana located in damaged forest. The remaining sampling stations in both transects are located in healthy undamaged forests (Figure 2). The reason why the number of stations in damaged and undamaged forest is not equal for each transect is because they were originally based on satellite images of the defoliation in these areas, with the goal to include a gradual transition of damaged and undamaged forest that was later revealed to not exist.



**Figure 2: The Varanger region in Finnmark, Norway showing the location of the two transects named Tana and Kirkenes.** The red and black dots each indicates the locations of a sampling station in outbreak-damaged and undamaged forests, respectively.

To sample beetles, three large window traps (flight interception traps) with two crossed 40x60 cm window panels were put up in each sampling station. This totals 60 traps, with 30 traps in each transect. The traps were mounted between two birch stems so that the upper edge of the window panels hang roughly 1.5-2 m above the forest floor (Figure 3), with one trap mounted as close to the center of the station as possible and the other two mounted approximately 50 m to the north and south of this center trap. The traps were first put up in late May, and emptied in early July and again in early August. This results in two trapping periods of about 4 weeks each. The contents of the traps were filled in plastic containers that contained glycol and then kept as cool as possible in outdoor shadow until the individual beetles could be separated from non-beetles in a lab and transferred into ethanol (Vindstad et al. 2014).



**Figure 3:** One of the window traps used in this study shortly after it was assembled (Photo: Petter Carlsen).

All individual beetles from the window traps were sent to an expert for identification to species level. The beetle species were then classified as either saproxylic or non-saproxylic if their dead wood association were known. If their dead wood association were unknown, the species were simply classified as “unknown dead wood relation”. Beetle species were also classified according to their larval trophic guild, which includes predators, fungivores, herbivores, wood-feeding (separate from herbivores), multiple guilds (species belonging to more than one guild), other (guilds that were rare in this study such as scavengers, coprophages and detritus-feeders) and unknown trophic guild. All classifications were done with the use of information gathered by Vindstad et al. (2014), Köhler (2000), and the online saproxylic database by Stokland & Meyke (2008).

To observe the amount of trees used by saproxylic beetles as of 2016, in both damaged and undamaged forest and the two transects, 20 dead birch trees were randomly selected at each sampling station for observations of insect galleries and exit-holes identified as made by saproxylic beetles. However, in two stations in the Tana transect, namely station 8 and 9, there was a lack of sufficient amounts of dead trees. 15 dead birch stems were found and observed in station 8, and only five dead stems were observed in station 9. If a selected tree had several stems, the thickest stem above 150 cm was selected. The diameter of each selected stem were measured at 130 cm above the ground, then the bark was removed with a



large knife along the length of each tree from 70 cm above ground to 150 cm above ground, regardless of the diameter of the selected stem. Each gallery and exit-hole found along this area of the selected stems, that were identified as made by a saproxylic beetle, were then counted as an observation.

### ***2.3 Statistical analyses:***

The main goals of this study was to investigate how the numerical responses of saproxylic beetles, as a community and as single species, have developed since the beginning of the study period. The development of the non-saproxylic beetle community since the outbreak, which were not expected to respond to the increase of dead wood resources, were investigated as well. This were done to help detect any unpredictable effects of years, locations and other effects that may influence the entire beetle community, and are not related to the numerical responses of saproxylic beetles to the dead wood abundances. Beetle counts were therefore used as the response variable, with separate analyses on the saproxylic and non-saproxylic beetle communities. Beetle samples were pooled across traps and sampling periods, to have one data point for each sampling station per year.

Because the living-dead wood contrasts were not gradual, it was assumed that the responses of saproxylic beetles would follow the same non-gradual changes. Forest damage was therefore modelled as a categorical (dead or living) predictor variable, and used as the focal (most important) predictor variable in all statistical analyses. To account for variations in the beetle communities between transects and study years, location (Tana and Kirkenes) and year (2011, 2012, 2015 and 2016) were used as additional predictor variables in all models.

The beetle abundance data were analyzed by using generalized linear mixed models (GLMMs) with negative binomial distributions and random intercepts for each sampling station to account for random variations between the stations. Negative binomial models were used to avoid problems with overdispersion due to high variations in beetle counts between stations. The Akaike Information Criterion (AIC) was used to adjust for small sample size and to select the best models by testing and excluding all predictor variables and all interactions to find the best balance between the fit of the models to the data and the number of predictor variables. However, forest damage was the focal predictor variable and therefore included in all models.

These models were fitted to assess the effects of forest damage, year and location on saproxylic beetles as a community, and non-saproxylic beetles as a separate community. Models were also fitted for selected species, which were common enough for separate analyses. These species were restricted to 10 saproxylic beetle species which were sampled in numbers above a certain set threshold at 100 individuals in total, along with the two most abundant non-saproxylic beetle species for comparison.

To assess how the amount of dead stems used by saproxylic beetles, and to which extent they were used, differ depending on forest damage and habitat quality, the data on insect galleries and exit-holes were analyzed using generalized linear mixed models with log-linear distributions. First, the data were used to investigate which factors that influence the probability of a stem to be used. The probability of whether a stem had insect galleries and/or exit-holes or not were used as the response variable, with damage (living or dead), location (Tana and Kirkenes) and tree diameter as predictor variables. Then, insect galleries and exit-holes were analyzed separately to investigate how these factors influence the extent of use by saproxylic beetles. The number of galleries and exit-holes were separately used as response variables, with forest damage, location and tree diameter still used as predictor variables.

All analyses were done using R 3.3.2 (R development core team 2016).

### **3. Results:**

#### ***3.1 Overall beetle community structure:***

A total of 13'257 individual beetles from 288 species were sampled with the window traps during all four sampling years of this study. Saproxylic species accounted for 43.4% of all individuals and 45% of all species. Non-saproxylic species accounted for 55.5% of individuals and 46.2% of species, while species with “unknown” relation to dead wood accounted for the rest (table 1). Predators and fungivores were the most abundant and species rich trophic guilds in total, and among both saproxylic beetles as well. Among the non-saproxylic beetles, predators and herbivores were the most abundant trophic guilds, but many observed species were classified under “Other” and “Unknown guild” (table 1).

**Table 1:** Total numbers of individuals (species) caught during the sampling periods for each DWA group and larval trophic guild.

<b>Trophic guild</b>	<b>Saproxylic</b>	<b>Non-saproxylic.</b>	<b>Unknown dead wood relation</b>	<b>Sum</b>
Predator	1776 (50)	4106 (48)	62 (9)	5944 (107)
Fungivore	2573 (43)	95 (16)	69 (6)	2737 (65)
Herbivore	1 (1)	2463 (18)	1 (1)	2465 (20)
Wood-feeding	196 (8)	-	-	196 (8)
Multiple guilds	410 (17)	1 (1)	-	411 (18)
Other	8 (5)	216 (27)	1 (1)	225 (33)
Unknown guild	792 (6)	471 (23)	16 (9)	1279 (38)
<b>Sum</b>	<b>5756 (130)</b>	<b>7352 (133)</b>	<b>149 (26)</b>	<b>13257 (289)</b>

The majority of beetles trapped belong to a few highly abundant species. Five species, namely *Anthophagus omalinus*, *Eanus costalis*, *Elateroides dermestoides*, *Liotrichus affinis* and *Malthodes guttifer*, account for 63.5% of all observed individuals, of which only the three latter species are saproxylic. Only 18 species had more than 100 individuals found in the traps during the entire trapping period (appendix 1), and were the only species considered to be abundant enough for individual negative binomial modelling. Of these 18 species, 10 are categorized as saproxylic, and seven of these saproxylic species are known to utilize dead birch as a resource or habitat (appendix 1). 42.9% of the species found were represented by only one (81 species) or two (43 species) individuals in the samples (appendix 1).

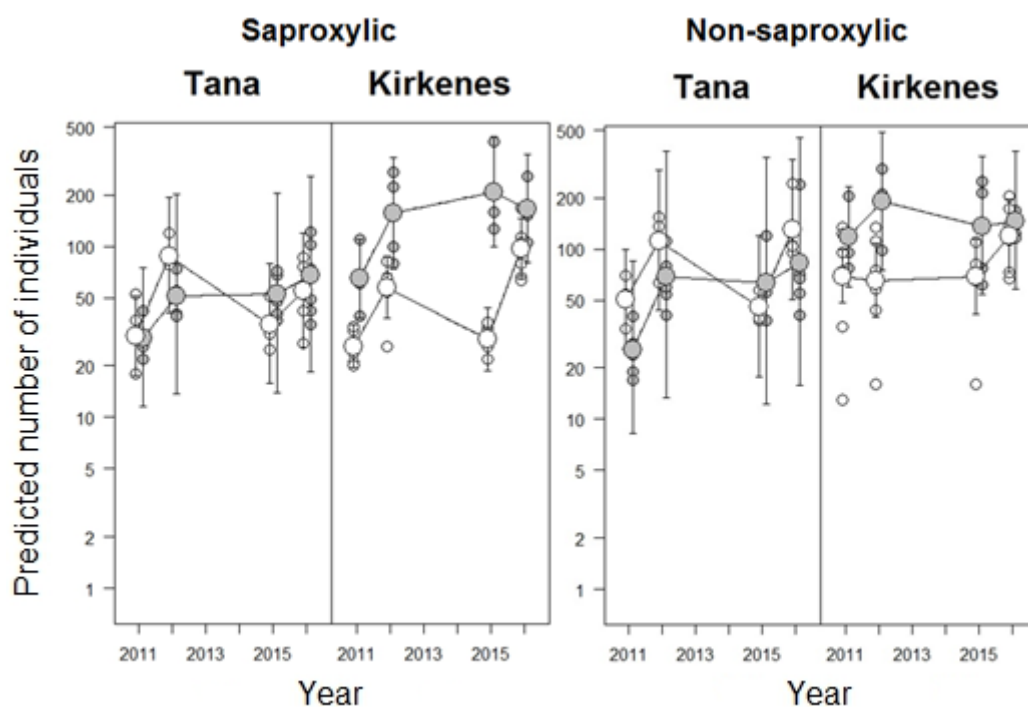
The results from the selected negative binomial models show that saproxylic beetles were in general more common in damaged than in undamaged forest (main effect of damage, table 2), but the amount differed between the transects and years. For the abundance of saproxylic beetles, there was in general less effect of damage in the Tana transect compared to the Kirkenes transect (damage  $\times$  transect interaction, table 2), and the effect in the Tana transect is seemingly very small (figure 4). Some variations in saproxylic beetle abundance between years also occurred, which seems to be relatively consistent in the undamaged forest (main effect of year 2012 and 2016, table 2, figure 4). However, the numerical response of the saproxylic beetle community to forest damage was greatest in 2015 (damage  $\times$  year interaction, table 2), and in 2016 there was clearly less saproxylic beetles in the Tana transect compared to the Kirkenes transect (negative interaction between transect  $\times$  year in 2016, table 2).

Non-saproxylic beetles indicated a weak trend towards higher abundance in damaged forest compared to undamaged forest in general (main effect of damage, table 2), and this effect was greater in Kirkenes compared to Tana (damage  $\times$  transect interaction, table 2). The general differences in beetle abundances of non-saproxylic beetles between damaged and undamaged forest were in addition greatest in 2012 (interaction between damage  $\times$  year in 2012, table 2). However, this year the Kirkenes transect had on average a lot more beetle individuals in damaged forest compared to Tana, even though the beetle abundance in damaged forest in Tana increased since the previous year (transect  $\times$  year interaction in 2012, table 2, figure 4).

The general patterns of the saproxylic and non-saproxylic beetle communities appeared to be quite similar in the Tana transect, with seemingly high variations in beetle abundances between years (figure 4). In the Kirkenes transect however, the differences between the two beetle communities were apparently greater. Both communities had higher beetle abundances in damaged forest compared to undamaged forest in the Kirkenes transect, but the saproxylic beetle community also seemed to have the greatest contrast between damaged and undamaged forest (figure 4).

**Table 2: Coefficients from selected negative binomial models showing relations between beetle counts of the saproxylic and non-saproxylic communities separately to predictor variables forest damage, transect and year.** The intercepts represents undamaged forest in the Kirkenes transect of 2011, with the estimates, standard errors and p-values. Significant codes: \*\*\* =  $p \leq 0.001$ ; \*\* =  $p \leq 0.01$ ; \* =  $p \leq 0.05$ ; . =  $p \leq 0.1$ .

Saproxylic community	Estimate	Std. Error	P-value
Intercept	3.22	0.15	< 0.001 ***
Damage	0.93	0.23	< 0.001 ***
Year (2012)	0.81	0.16	< 0.001 ***
Year (2016)	1.33	0.15	< 0.001 ***
Damage × Transect (Tana)	-0.96	0.33	0.004 **
Damage × Year (2015)	1.09	0.23	< 0.001 ***
Transect (Tana) × Year (2016)	-0.70	0.24	0.004 **
Non-saproxylic community	Estimate	Std. Error	P-value
Intercept	4.22	0.19	< 0.001 ***
Damage	0.54	0.29	0.067 .
Year (2016)	0.55	0.17	0.002 **
Damage × Transect (Tana)	-1.24	0.42	0.003 **
Damage × Year (2012)	0.55	0.28	0.049 *
Transect (Tana) × Year (2012)	0.86	0.29	0.003 **
Damage × Transect (Tana) × Year (2015)	0.88	0.41	0.033 *



**Figure 4: Variation in abundance of all saproxylic and non-saproxylic individuals across all sampling years in the two sampling transects.** Large symbols: predicted number of individuals from negative binomial models in damaged and undamaged forest in Tana and Kirkenes during 2011, 2012, 2015 and 2016. Error bars represent 95% confidence intervals. Small symbols: observed counts in specific stations. White circles represent undamaged forest, while grey circles represent damaged stations.

### 3.2 Single species:

Several of the saproxylic species selected for individual modelling were apparently affected positively by forest damage in terms of abundance (main effect of damage, table 3). However, only one species, the early successional saproxylic beetle *Elateroidea dermestoides*, showed a clear and consistent response to damage in both transects (table 3, figure 5A). One other species, the saproxylic *Sericus brunneus*, showed tendencies to a similar response, although much weaker (table 3, figure 5H). *Enicmus fungicola* was the only saproxylic species with a significant negative effect of damage, although *Podistra schoenherri* also had indications of a similar trend (table 3, figure 5G and E). *Denticollis linearis* and *Atheta hypnorum*, the two least abundant species selected for individual modelling, were the only selected saproxylic species that did not show any indications of an effect from forest damage (table 3, figure 5I and J). Neither of the two non-saproxylic species selected for individual modelling showed any indications of being affected by damage either (table 3, figure 5K and L).

Only two selected saproxylic beetle species had indications of a turnover from increasing in abundance in the first sampling years, to decreasing in the latter years in damaged forest. The effect of damage was significantly less in 2016 for the abundance of *Saplingus ruficollis* compared to the three previous years (negative interaction between damage  $\times$  year in 2016, table 3, figure 5D). The positive numerical response of *Rabocerus foveolatus* to forest damage was also reduced in the two latter years of this study (negative interaction between damage  $\times$  year in 2015 and 2016, table 3, figure 5F). A different response was found with *A. hypnorum*, which had a positive response to damage only in 2012 and 2016 (damage  $\times$  year interactions in 2012 and 2016, table 3), but no overall effect of damage (main effect of damage:  $p=0.135$ , table 3). Both of the selected non-saproxylic species had positive numerical reactions to forest damage during one year each; *Anthophagus omalinus* in 2012 (damage  $\times$  year interaction in 2012, table 3) and *Eanus costalis* in 2015 (damage  $\times$  year interaction in 2015, table 3). However, none of these two species had any significant numerical response to the overall effect of forest damage (main effect of damage, table 3).

The effect of forest damage on beetle abundances varied between transects for several of the affected species. For the saproxylic species *E. dermestoides*, *Liotrichus affinis* and *Malthodes guttifer*, which all seemingly had a general positive numerical response to forest damage, apparently also had the strongest positive responses to damage in the Kikrenens transect (damage  $\times$  transect interaction, table 3, figure 5A, B and C). The saproxylic species *E.*

*fungicola* were also less negatively affected by forest damage in the Tana transect compared to the Kirkenes transect (positive interaction between damage  $\times$  transect in Tana, table 3, figure 5G). The two non-saproxyllic beetle species *A. omalinus* and *E. costalis* were apparently both negatively affected by forest damage only in the Tana transect (negative interaction between damage  $\times$  transect in Tana, table 3, Figure 5K and L).

**Table 3: Coefficients from selected negative binomial models showing relations between total counts of all selected single species separately to predictor variables forest damage, transect and year.** The intercepts represents undamaged forest in the Kirkenes transect in 2011, with the estimates, standard errors and p-values. Significant codes: \*\*\* =  $p \leq 0.001$ ; \*\* =  $p \leq 0.01$ ; \* =  $p \leq 0.05$ ; . =  $p \leq 0.1$ . Whether the species is saproxylic or not is marked in parenthesis behind the species name, with S indicating saproxylic, and N indicating non-saproxylic.

<i>Elateroides dermestoides</i> (S)	Estimate	Std. Error	P-value
Intercept	0.09	0.35	0.801
Damage	3.05	0.41	< 0.001 ***
Year (2012)	1.30	0.27	< 0.001 ***
Year (2015)	1.50	0.29	< 0.001 ***
Year (2016)	1.49	0.29	< 0.001 ***
Damage × Transect (Tana)	-1.24	0.62	0.044 *
<i>Liotrichus affinis</i> (S)	Estimate	Std. Error	P-value
Intercept	1.50	0.28	< 0.001 ***
Damage	0.80	0.25	0.001 ***
Year (2012)	0.77	0.34	0.023 *
Damage × Transect (Tana)	-1.14	0.36	0.002 **
Transect (Tana) × Year (2012)	1.26	0.51	0.013 *
Transect (Tana) × Year (2015)	1.36	0.54	0.011 *
Transect (Tana) × Year (2016)	1.23	0.51	0.016 *
<i>Malthodes guttifer</i> (S)	Estimate	Std. Error	P-value
Intercept	0.38	0.46	0.402
Damage	1.29	0.62	0.036 *
Year (2016)	1.42	0.31	< 0.001 ***
Damage × Transect (Tana)	-2.49	0.88	0.004 **
<i>Salpingus ruficollis</i> (S)	Estimate	Std. Error	P-value
Intercept	-0.91	0.66	0.171
Damage	2.11	0.79	0.007 **
Transect (Tana)	-2.81	0.43	< 0.001 ***
Year (2012)	1.56	0.70	0.026 *
Year (2016)	3.41	0.66	< 0.001 ***
Damage × Year (2016)	-2.09	0.80	0.009 **
<i>Podistra schoenherri</i> (S)	Estimate	Std. Error	P-value
Intercept	1.13	0.23	< 0.001 ***
Damage	-0.57	0.33	0.089 .
<i>Rabocerus foveolatus</i> (S)	Estimate	Std. Error	P-value
Intercept	0.02	0.38	0.956
Damage	1.79	0.44	< 0.001 ***
Transect (Tana)	-1.18	0.27	< 0.001 ***
Year (2012)	1.46	0.37	< 0.001 ***
Year (2016)	1.20	0.39	0.005 **
Damage × Year (2015)	-2.20	0.63	0.001 ***
Damage × Year (2016)	-3.58	0.72	< 0.001 ***



**Table 3:** Continued from previous page.

<i>Enicmus fungicola</i> (S)	Estimate	Std. Error	P-value
Intercept	0.88	0.34	0.009 **
Damage	-1.49	0.35	< 0.001 ***
Transect (Tana)	-2.06	0.39	< 0.001 ***
Year (2016)	1.72	0.37	< 0.001 ***
Damage × Transect (Tana)	1.33	0.58	0.023 *
<i>Sericus brunneus</i> (S)	Estimate	Std. Error	P-value
Intercept	-1.72	0.55	0.002 **
Damage	1.39	0.56	0.012 *
Year (2012)	1.09	0.43	0.012 *
Year (2015)	1.44	0.43	< 0.001 ***
<i>Denticollis linearis</i> (S)	Estimate	Std. Error	P-value
Intercept	0.01	0.31	0.981
Damage	-0.35	0.25	0.168
Transect (Tana)	0.56	0.26	0.030 *
Year (2012)	0.66	0.32	0.039 *
<i>Atheta hypnorum</i> (S)	Estimate	Std. Error	P-value
Intercept	-0.17	0.44	0.692
Damage	-0.69	0.46	0.135
Transect (Tana)	1.25	0.50	0.012 *
Year (2016)	-1.61	0.80	0.042 *
Damage × Year (2012)	1.38	0.54	0.010 *
Damage × Year (2016)	2.02	0.70	0.004 **
Transect (Tana) × Year (2012)	-1.72	0.57	0.002 **
<i>Anthophagus omalinus</i> (N)	Estimate	Std. Error	P-value
Intercept	3.80	0.33	< 0.001 ***
Damage	0.53	0.51	0.301
Year (2012)	-1.64	0.30	< 0.001 ***
Damage × Transect (Tana)	-2.00	0.74	0.007 **
Damage × Year (2012)	1.39	0.44	0.001 ***
Transect (Tana) × Year (2012)	1.13	0.45	0.012 *
Damage × Transect (Tana) × Year (2012)	-1.54	0.66	0.019 *
<i>Eanus costalis</i> (N)	Estimate	Std. Error	P-value
Intercept	2.31	0.22	< 0.001 ***
Damage	0.17	0.34	0.609
Year (2012)	1.39	0.17	< 0.001 ***
Year (2015)	-0.53	0.21	0.013 *
Year (2016)	1.14	0.18	< 0.001 ***
Damage × Transect (Tana)	-1.28	0.41	0.002 **
Damage × Year (2015)	0.90	0.30	0.003 **

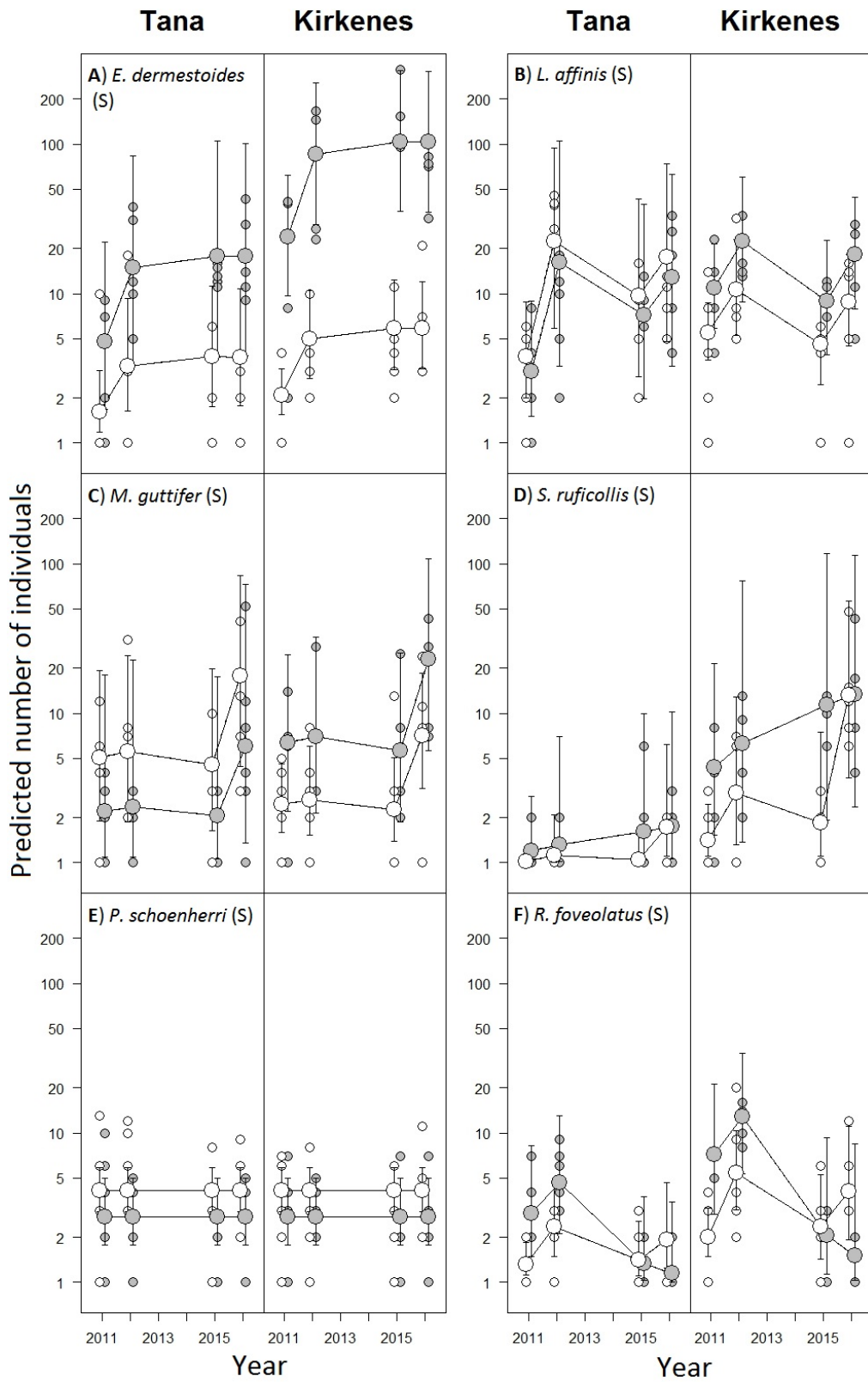
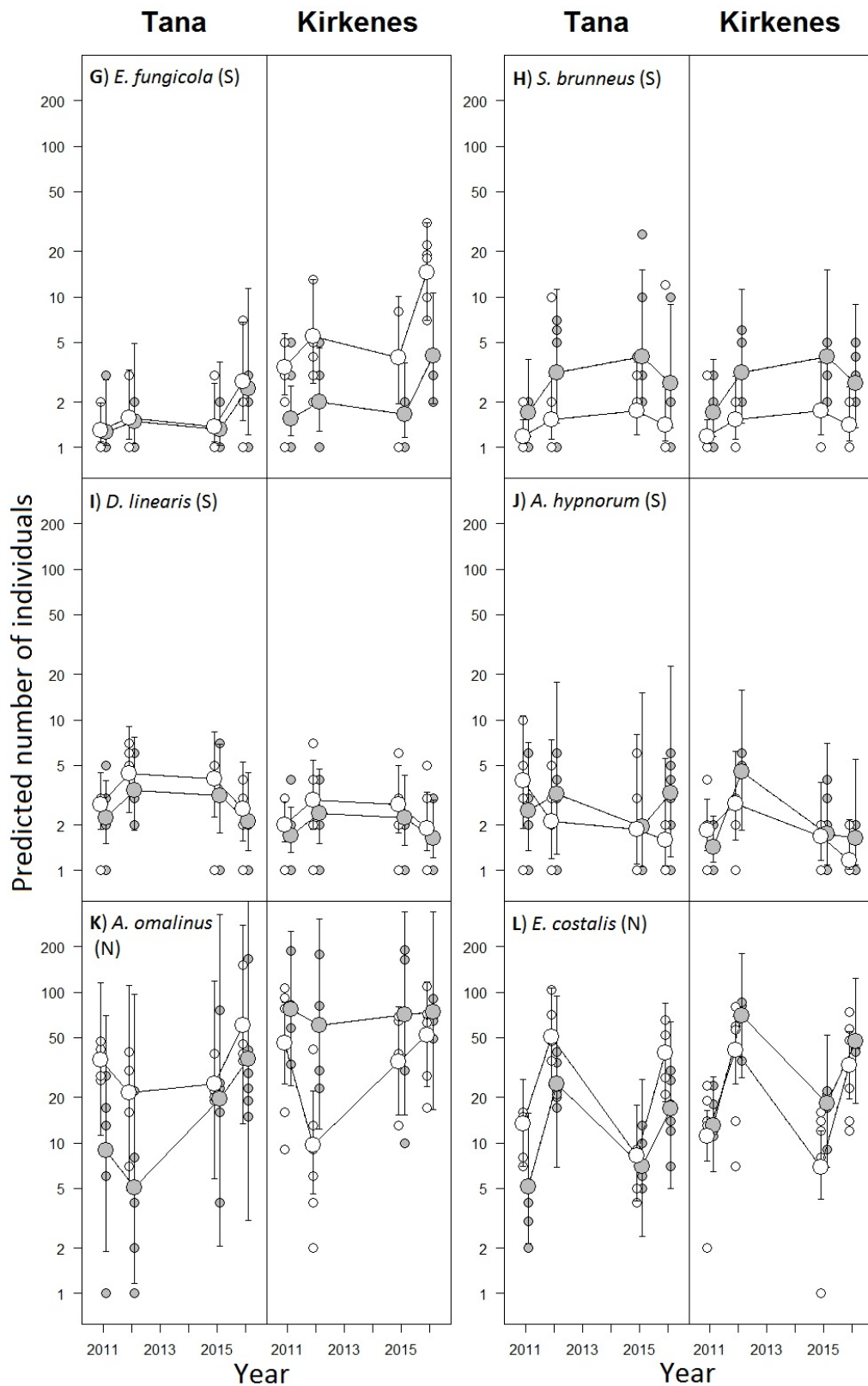


Figure 5: To be continued on next page.



**Figure 5: Variations in abundance of single beetle species across years in both transects.** Species included are *E. dermestoides*, *L. affinis*, *M. guttifer*, *S. ruficollis*, *P. schoenherri*, *R. foveolatus*, *E. fungicola*, *S. brunneus*, *D. linearis*, *A. hypnorum*, *A. omalinus* and *E. costalis*. Large symbols: predicted number of individuals from negative binomial models in damaged and undamaged forest in Tana and Kirkenes during 2011, 2012, 2015 and 2016. Error bars represent 95% confidence intervals. Small symbols: original datapoints. White circles represent undamaged forest, grey circles represent damaged stations. “S” stands for saproxylic, while “N” stands for non-saproxylic.

### 3.3 Insect galleries and exit-holes:

Of the 380 dead birch stems that were selected for observation of insect marks in this study, 104 of them were observed with one or more insect galleries, and 103 of them were observed with exit-holes. 245 of the observed stems had neither galleries nor exit-holes, and the majority of stems with insect marks had just a single or very few galleries or exit-holes. The amount of insect marks observed on a single stem varied from a single gallery or exit-hole to tens of galleries and several hundred exit-holes. The possibility for observing insect marks, independent of type or amount, increased with increasing diameter of the stem and damage (Table 4). Proportions of dead stems with observed insect galleries per surface area did also increase with stem diameter although the effect was much larger I Kirkenes than Tana. There was a tendency for less exit-holes per surface area in the damaged areas ( $p=0.074$ ) and the diameter did not affect this measurement. More exit-holes per surface area were also observed in Kirkenes compared to Tana (table4).

**Table 4: Coefficients of log-linear models showing relations between insect galleries and exit-holes to predictor variables forest damage, location and diameter of selected tree stems.** The intercepts represents damaged forest in the Kirkenes transect, with the estimates, standard errors and p-values. Significant codes: \*\*\* =  $p \leq 0.001$ ; \*\* =  $p \leq 0.01$ ; \* =  $p \leq 0.05$ ; . =  $p \leq 0.1$ .

Used/unused	Estimate	Std. Error	P-value
Intercept	-2.4905	0.58	< 0.001 ***
Damage (Undamaged)	0.9638	0.34	0.004 **
Diameter	0.2349	0.07	0.001 ***
Insect galleries per surface area	Estimate	Std. Error	P-value
Intercept	1.94222	0.45790	< 0.001 ***
Damage (Undamaged)	1.15089	0.28687	< 0.001 ***
Diameter	0.12106	0.05275	0.024 *
Damage (Undamaged) × Location (Tana)	-1.15640	0.50696	0.025 *
Exit-holes per surface area	Estimate	Std. Error	P-value
Intercept	3.55	0.48	< 0.001 ***
Damage (Undamaged)	-0.46	0.25	0.074 .
Location (Tana)	-0.82	0.25	0.001 **
Diameter	0.06	0.05	0.196

#### 4. Discussion:

As a consequence to the recent dead wood pulse, the numerical response of the saproxylic beetle community in Varanger has increased from 2012 to 2015. In 2016 however, no sign of this increase remained. In addition, the total response of the saproxylic beetle community to the dead wood abundance appears to be most prominent in the Kirkenes transect. Some of the most abundant saproxylic species responded most strongly in the Kirkenes transect as well, and these species seems to be driving the main patterns of the community. Most of the dominant species found in this study were the same species observed by Vindstad et al. (2014) as the most abundant species in the earliest sampling seasons, with *E. dermestoides* still as the most abundant saproxylic species as of 2016.

The resource pulse of dead wood generated by the most recent moth outbreaks in the Varanger region were expected to heavily promote the local saproxylic beetle community. Therefore, saproxylic beetles as a community, and especially the most abundant species of the region, were expected to experience a positive numerical response. The previous study on the same system showed only weak responses at the time, indicating a possible delay in the response of the local beetle community. This response was driven mainly by a few highly abundant species related to early successional stages (Schultze 2012; Vindstad et al. 2014). However, the numerical responses of the saproxylic beetle community was expected to continue to increase, and eventually shift from being dominated by early successional species to species related to the next successional stages in decomposition.

In the present study, there are some evidence for an increase in the numerical response of saproxylic beetles to the dead wood resource pulse since the previous study. The response still appears to be driven by a few highly abundant species that dominate the community, which are mostly the same as the species that dominated the community in the previous study. Most noticeably is *E. dermestoides*, which is an early successional species. This indicates that there has been little to no turnover in the successional stage of the damaged forest of the area during the period between 2012 and 2016.

There is a relatively clear effect of location on both the saproxylic and non-saproxylic beetle communities. The patterns found in both communities show clearly different trends between the two locations, but similar trends to each other within the Tana transect. The effect of forest damage is seemingly greater in the Kirkenes transect than the Tana transect for the saproxylic beetle community. The non-saproxylic beetle community, which only indicates a

weak trend towards a response to forest damage in general, does in addition respond more strongly to forest damage in the Kirkenes transect.

It may appear that local variations in habitats have a stronger effect on the local saproxylic beetle community of the Varanger region than any effects of the dead wood resource pulse left by the moth outbreaks. The effects of the outbreak does in addition appear to be stronger in the Kirkenes transect compared to the Tana transect. The reason for this may be that the Kirkenes transect extends through a more nutrient rich and diverse array of habitats than the Tana transect (Vindstad et al. 2014; Vindstad et al. 2015). Diversity in habitats commonly generates more niches, which again improves species diversity (Chesson 2000; MacArthur & MacArthur 1961; Ricklefs 1977). High saproxylic beetle diversity are often associated with high diversity in habitat types, including tree diameter, canopy cover, variations in topography and more (Azeria et al. 2012; Bouget et al. 2013; Janssen et al. 2016; Speight 1989). As a result, Kirkenes may contain habitats that are suitable for more species compared to Tana, and also more preferable habitats for the most abundant species found in the dataset. The numerical response of the saproxylic beetle community in Varanger therefore appear to be dependent, or at least strongly influenced by, factors related to locations.

In addition to a more diverse array of habitats, Kirkenes also has a higher proportion of birch trees with thicker stems. Stem thickness is known as an important factor for many saproxylic beetle species when selecting suitable dead wood habitats (Buse et al. 2008; Speight 1989; Stokland et al. 2012). The possibility of finding galleries and exit-holes made by saproxylic beetles on dead birch stems increased with the diameter of the stems, indicating that beetles tend to select thicker stems. Insect marks made by saproxylic beetles per surface area of stems also seemed to increase with diameter, which strongly suggest a preference for thicker stems as a resource. The utilization rate was also generally lower in Tana compared to Kirkenes. Considering the preference for thicker stems, and the fact that Tana in general has birch trees with lower stem diameter, it is reasonable to think of Tana as a location with poorer habitats for saproxylic beetles than Kirkenes.

The proportions of dead birch stems utilized by saproxylic beetles, marked by galleries or insect-holes, were generally higher in forest unaffected by the moth outbreaks compared to the heavily damaged forests. This may indicate that the amount of dead wood in the damaged forest areas are too high for the saproxylic beetle community to exploit all the resources. Instead, there seems to be a swamping-effect as the saproxylic beetles only utilize a small portion of the dead wood in the damaged forest, while in the undamaged forest they utilize a

much higher portion of the dead wood resources. Other reasons for higher proportions of utilized dead stems in undamaged forest may be due to a longer time since death or different mortality factors, which can make the trees more attractive for saproxylic beetles. The death of those trees are most likely not due to defoliation by the outbreaking moth species, and the time of death are therefore more uncertain, but might have happened before the outbreaks. If the cause of mortality were more sudden than by defoliation, the dead wood would probably be more nutrient rich than that of a slowly suffocating tree. A mortality cause which includes infectious fungi can also make dead wood more attractive since fungi often is a nutrient source for saproxylic beetles (Stokland et al. 2012; Ulyshen 2014). A longer time since death is however a less likely explanation since most insect marks on found in the area were made by *E. dermestoides*, which is related to the earliest successional stages of wood decay.

Only a few highly abundant species continue to dominate the saproxylic beetle community in the Varanger area. *E. dermestoides* was the most abundant saproxylic species in the dataset through all sampling years, and the species which had the most visible positive effect of damaged forest in both locations. Even though this species is related to the earliest successional stages of decomposition, it still retains a high abundance in 2016, indicating that the decomposition process has yet to proceed beyond the earliest successional stages in the study system. Some other saproxylic species, namely *L. affinis*, *M. guttifer*, *S. ruficollis*, *R. foveolatus* and *S. brunneus*, also showed evidence for a positive effect of damaged forest on their abundance. *R. foveolatus* and *S. brunneus* were the only of these species where the effect of forest damage were not weakened in the Tana transect. *R. foveolatus* were instead negatively affected by the Tana transect on a general basis. The effect of forest damage on the abundance of this species, which is related to early successional stages of wood decay, were also weakened during the two last sampling years. This is contrary to the response of *E. dermestoides*. A common species found in the dataset that are related to later stages of decay, namely *P. schoenherri*, were overall mostly found in undamaged forest, and showed no response to location or year. Another common species related to later successional stages, *D. linearis*, did not show any response to damage at all. This may support the other indications for slow decomposition rates as the dead wood is still apparently in the earliest successional stages.

Saproxylic insects play an important role in maintaining healthy forest ecosystems all over the globe. Their role may be even more crucial after large-scale disturbances generate massive resource pulses of dead wood. Insects can potentially generate large amounts of offspring, and

thereby quickly respond numerically to increased resource availability. It is possible that the cold climate of the study region has constrained the reproductive ability of the local beetle community, and thereby weakened their numerical response (Gullan et al. 2010). Considering the large size of the outbreak affected area, and the amount of beetle individuals required to aggregate from the surrounding areas to raise abundances significantly, it is likely that the reproductive response of the beetles are the most important driver of their total numerical response.

Accessibility of dead wood and time before colonization by other saproxylic organisms such as fungi may heavily depend on saproxylic insects, especially beetles, which thereby promotes decomposition (Dickie et al. 2012; Fukami et al. 2010; Stokland et al. 2012; Ulyshen 2014; Ulyshen et al. 2016). If saproxylic insects are unable to respond properly to increased dead wood, decomposition rates may be prolonged and the ecosystems may be heavily affected (Barbosa et al. 2012; Fukami et al. 2010; Gullan et al. 2010; Müller et al. 2010; Ulyshen 2014).

Combined effects of the sub-arctic climate with short productive seasons and the cause of death by defoliation can perhaps be the reason for why the numerical responses appears to be smaller than expected. The climate of the Varanger region may impair the decomposition process, since climate are known to be important for decay rates, with negative effects of colder temperatures (Chen 1999; Yatskov et al. 2003). Death by defoliation may be slow, and the actual time of death for the trees are probably later than when the outbreaks occurred. The fact that the wood killed by defoliation is left standing makes it more prone to weather effects and desiccation than fallen logs, which impairs the decomposition process. Long winters with low temperatures and high snow cover can reduce water content inside the trunks by freezing. Low temperatures over long times does in addition often result in lower survival rates and longer generation times for many insects (Chen 1999; Gullan et al. 2010; Hicks et al. 2003; Yatskov et al. 2003). The saproxylic beetle community are therefore less able to mount a numerical response sufficient enough to handle all of the resource pulse of dead wood. As a result, the dead wood created by the moth outbreak may spend longer time to decompose past the earliest successional stages than anticipated.



## 5. Conclusions:

Roughly a decade after the moth outbreaks produced a large scale resource pulse of dead wood, the saproxylic beetle community has yet to utilize all these resources in the area. The numerical response of the saproxylic beetle community in the region has continued to increase since 2012 until 2015. The wood appears, however, to remain in an early successional stage of decomposition, while saproxylic beetle species related to these still dominate the community. Most notably is *E. dermestoides*, which has remained dominant during all four sampling seasons of the entire study period, and is the species with the clearest response to the increase of dead wood in both study locations. Habitat variations between the locations does in addition appear to heavily affect most of the beetle community of the Varanger region. This includes both saproxylic and non-saproxylic beetles.

To better understand the effects of the moth outbreak and the massive tree death in the area, in addition to the amount of time needed for decomposition, more research on the development of the saproxylic beetle community can be useful. Since decomposition of wood is a highly diverse and dynamic process, potential future studies should try to include other saproxylic insect communities as well as microorganisms such as fungi. This can give important insights in the decomposition process in sub-arctic climates and the effects of insects outbreaks.

## References:

- Azeria, E. T., Ibarzabal, J., Boucher, J. & Hébert, C. (2012). Differential effects of post-fire habitat legacies on beta diversity patterns of saproxylic beetles in the boreal forest. *Écoscience*, 19 (4): 316-327.
- Barbosa, P., Letourneau, D. & Agrawal, A. (2012). *Insect outbreaks revisited*: John Wiley & Sons.
- Bouget, C., Larrieu, L., Nusillard, B. & Parmain, G. (2013). In search of the best local habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, 22 (9): 2111-2130.
- Buse, J., Levanony, T., Timm, A., Dayan, T. & Assmann, T. (2008). Saproxylic beetle assemblages of three managed oak woodlands in the Eastern Mediterranean. *Zoology in the Middle East*, 45: 55-66.

- Bylund, H. (1999). Climate and the Population Dynamics of Two Insect Outbreak Species in the North. *Ecological Bulletins* (47): 54-62.
- Carlton, R. & Goldman, C. (1984). Effects of a massive swarm of ants on ammonium concentrations in a subalpine lake. *The International Journal of Aquatic Sciences*, 111 (2): 113-117.
- Chalupa, Z. (1995). *Salpingus ruficollis* (Linnaeus, 1761) [Picture]. Available at: <http://www.biolib.cz/en/image/id237620/>.
- Chen, H. (1999). *Root decomposition in three coniferous forests: effects of substrate quality, temperature, and moisture*. Ph.D thesis. Oregon State University
- Chesson, P. (2000). General Theory of Competitive Coexistence in Spatially-Varying Environments. *Theoretical Population Biology*, 58 (3): 211-237.
- Collins, B. J., Rhoades, C. C., Battaglia, M. A. & Hubbard, R. M. (2012). The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *Forest Ecology and Management*, 284: 260-268.
- Davis, R. S., Hood, S. & Bentz, B. J. (2012). Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 42 (12): 2022-2036.
- Dickie, I. A., Fukami, T., Wilkie, J. P., Allen, R. B. & Buchanan, P. K. (2012). Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. *Ecology Letters*, 15 (2): 133-141.
- Ehnström, B. & Axelsson, R. (2002). *Insektsnag i bark och ved*. Uppsala: Artdatabanken, SLU.
- Elia, M., Laforteza, R., Tarasco, E., Colangelo, G. & Sanesi, G. (2012). The spatial and temporal effects of fire on insect abundance in Mediterranean forest ecosystems. *Forest Ecology and Management*, 263: 262-267.
- Franklin, J. F., Shugart, H. H. & Harmon, M. E. (1987). Tree Death as an Ecological Process. *BioScience*, 37 (8): 550-556.
- Fukami, T., Dickie, I. A., Paula Wilkie, J., Paulus, B. C., Park, D., Roberts, A., Buchanan, P. K. & Allen, R. B. (2010). Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. *Ecology Letters*, 13 (6): 675-684.
- Gullan, P. J., Cranston, P. S. & McInnes, K. H. (2010). *The insects : an outline of entomology*. 4th ed. ed. Chichester: Wiley-Blackwell.
- Hansen, V. (1954). *Biller : 17 : Rovbiller, 3. del*, vol. 17. København: G.E.C. Gads Forlag.

- Hicks, W. T., Harmon, M. E. & Griffiths, R. P. (2003). Abiotic controls on nitrogen fixation and respiration in selected woody debris from the Pacific Northwest, U.S.A. *Écoscience*, 10 (1): 66-73.
- Janssen, P., Cateau, E., Fuhr, M., Nusillard, B., Brustel, H. & Bouget, C. (2016). Are biodiversity patterns of saproxylic beetles shaped by habitat limitation or dispersal limitation? A case study in unfragmented montane forests. *Biodiversity and Conservation*, 25 (6): 1167-1185.
- Jepsen, J. U., Hagen, S. B., Ims, R. A. & Yoccoz, N. G. (2008). Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *Journal of Animal Ecology*, 77 (2): 257-264.
- Jepsen, J. U., Hagen, S. B., Høgda, K. A., Ims, R. A., Karlsen, S. R., Tømmervik, H. & Yoccoz, N. G. (2009). Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. *Remote Sensing of Environment*, 113 (9): 1939-1947.
- Jepsen, J. U., Hagen, S. B., Karlsen, S.-R. & Ims, R. A. (2009). Phase-Dependent Outbreak Dynamics of *Geometria* Moth Linked to Host Plant Phenology. *Proceedings: Biological Sciences*, 276 (1676): 4119-4128.
- Jepsen, J. U., Biuw, M., Ims, R. A., Kapari, L., Schott, T., Vindstad, O. P. L. & Hagen, S. B. (2013). Ecosystem Impacts of a Range Expanding Forest Defoliator at the Forest-Tundra Ecotone. *Ecosystems*, 16 (4): 561-575.
- Kamata, N. (2002). Outbreaks of forest defoliating insects in Japan, 1950-2000. *Bulletin of entomological research*, 92 (2): 109.
- Köhler, F. (2000). *Totholzkäfer in Naturwaldzellen des nördlichen Rheinlands: vergleichende Studien zur Totholzkäferfauna Deutschlands und deutschen Naturwaldforschung: LÖBF*.
- Letnic, M., Bobby, T. & Dickman, C. R. (2005). The Responses of Mammals to La Niña (El Niño Southern Oscillation)-Associated Rainfall, Predation, and Wildfire in Central Australia. *Journal of Mammalogy*, 86 (4): 689-703.
- MacArthur, R. H. & MacArthur, J. W. (1961). On Bird Species Diversity. *Ecology*, 42 (3): 594-598.
- Müller, J., Noss, R. F., Bussler, H. & Brandl, R. (2010). Learning from a “benign neglect strategy” in a national park: Response of saproxylic beetles to dead wood accumulation. *Biological Conservation*, 143 (11): 2559-2569.

- New, T. R. (2014). *Insects, Fire and Conservation*. Cham: Springer International Publishing.
- Perera, A. H., Sturtevant, B. R., Buse, L. J. & SpringerLink. (2015). *Simulation Modeling of Forest Landscape Disturbances*. 1st ed. 2015. ed.: Springer International Publishing : Imprint: Springer.
- Persson, Y., Vasaitis, R., Långström, B., Öhrn, P., Ihrmark, K. & Stenlid, J. (2009). Fungi Vected by the Bark Beetle *Ips typographus* Following Hibernation Under the Bark of Standing Trees and in the Forest Litter. *Microbial Ecology*, 58 (3): 651-659.
- Persson, Y., Ihrmark, K. & Stenlid, J. (2011). Do bark beetles facilitate the establishment of rot fungi in Norway spruce. *Fungal Ecology*, 4 (1): 262-269.
- Polis, G. A., Hurd, S. D., Jackson, C. T. & Piñero, F. S. (1997). El Niño effects on the dynamics and control of an island ecosystem in the gulf of California. *Ecology*, 78 (6): 1884-1897.
- Polish Biodiversity Information Network, (2008). *Biodiversity Map Database*. Available at: <http://baza.biomap.pl/en/db> (accessed: 2017, 07.03).
- Ricklefs, R. E. (1977). Environmental heterogeneity and plant species diversity: a hypothesis. *The American Naturalist*, 111 (978): 376-381.
- Sappington, J. M., Longshore, K. M. & Thompson, D. B. (2007). Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *Journal of Wildlife Management*, 71 (5): 1419-1426.
- Schultze, S., Ims, R., Jepsen, J. & Vindstad, O. P. (2012). *Do saproxylic beetles respond numerically to rapid changes in dead wood availability following moth outbreaks?*: Universitetet i Tromsø.
- Speight, M. C. D. (1989). *Saproxylic invertebrates and their conservation* Nature and Environment Series. Strasbourg, France Council of Europe 79 pp.
- Stokland, J. N. & Meyke, E. (2008). The saproxylic database: an emerging overview of the biological diversity in dead wood. *Revue d'écologie*: 37-48.
- Stokland, J. N., Siitonen, J. & Jonsson, B. G. (2012). *Biodiversity in Dead Wood*: Cambridge University Press.
- Thibault, M. & Moreau, G. (2016). The amplitude of dead wood resource pulses produced by plantation thinning mediates the assembly of wood-boring beetles. *Ecosphere*, 7 (2): e01215-n/a.
- Ulyshen, M. D. (2014). Wood decomposition as influenced by invertebrates. *Biological Reviews*, 91 (1): 70-85

- Ulyshen, M. D., Müller, J. & Seibold, S. (2016). Bark coverage and insects influence wood decomposition: Direct and indirect effects. *Applied Soil Ecology*, 105: 25-30.
- Vindstad, O. P. L., Schultze, S., Jepsen, J. U., Biuw, M., Kapari, L., Sverdrup-Thygeson, A. & Ims, R. A. (2014). Numerical Responses of Saproxyllic Beetles to Rapid Increases in Dead Wood Availability following Geometrid Moth Outbreaks in Sub-Arctic Mountain Birch Forest. *Plos One*, 9 (6).
- Vindstad, O. P. L., Jepsen, J. & Ims, R. (2015). Resistance of a sub-arctic bird community to severe forest damage caused by geometrid moth outbreaks. *European Journal of Forest Research*, 134 (4): 725-736.
- Weed, A. S., Ayres, M. P. & Hicke, J. A. (2013). *Consequences of climate change for biotic disturbances in North American forests*, 83. pp. 441-470.
- Wermelinger, B., Duelli, P. & Obrist, M. K. (2002). Dynamics of saproxyllic beetles (Coleoptera) in windthrow areas in alpine spruce forests. *Forest snow and landscape research*, 77 (1/2): 133-148.
- Yanai, S. & Kochi, K. (2005). Effects of salmon carcasses on experimental stream ecosystems in Hokkaido, Japan. *Ecological Research*, 20 (4): 471-480.
- Yang, L. (2006). Interactions between a detrital resource pulse and a detritivore community. *Oecologia*, 147 (3): 522-532.
- Yang, L. H., Bastow, J. L., Spence, K. O. & Wright, A. N. (2008). What can we learn from resource pulses. *Ecology*, 89 (3): 621-634.
- Yang, L. H., Edwards, K. F., Byrnes, J. E., Bastow, J. L., Wright, A. N. & Spence, K. O. (2010). A meta-analysis of resource pulse–consumer interactions. *Ecological Monographs*, 80 (1): 125-151.
- Yang, L. H. (2012). The ecological consequences of insect outbreaks. *Insect Outbreaks Revisited*: 197-218.
- Yatskov, M., Harmon, M. E. & Krankina, O. N. (2003). A chronosequence of wood decomposition in the boreal forests of Russia. *Canadian Journal of Forest Research*, 33 (7): 1211-1226.

## Appendices:

### Appendix 1:

*List of beetle species:*

**Table app. 1:** List of beetle species caught during the sampling periods of the study, with information on related dead wood association (DWA) group, known connection to birch, larval trophic guild, total abundance in dataset and the proportion of total beetle count each species account for (with a three decimal limit).

#### Keys:

**Saproxylic:** SO = obligate saproxylic, SF = facultative saproxylic, N = non-saproxylic, Unknown = unknown DWA-group. SO and SF are both treated equally as saproxylic in this study, which does not differ between obligate- and facultative saproxylic.

**Birch related:** Y = birch related, N = not birch related, Unknown = unknown if birch related or not, na = no data.

**Larval trophic guild:** Predator = predatory, Fungi = fungivorous, Herbivore = herbivorous, Wood = wood-feeding (separate from herbivores), Multiple = species belonging to more than one guild, Other = guilds that were rare in this study such as scavengers, coprophages and detritus-feeders, Unknown = unknown trophic guild (no information available).

#### Sources:

Köhler (2000); Stokland & Mayke (2008); Polish Biodiversity Information Network (2008).

Species	Saproxylic	Birch related	Larval trophic guild	Total abundance	Proportion of total count
<i>Cytillus sericeus</i>	N	na	Herbivore	1	< 0.001
<i>Carpelimus bilineatus</i>	N	na	Unknown	1	< 0.001
<i>Pteroloma forstromii</i>	N	na	Unknown	1	< 0.001
<i>Dienerella filum</i>	SF	N	Fungi	1	< 0.001
<i>Atomaria peltataeformis</i>	N	na	Fungi	1	< 0.001
<i>Colon serripes</i>	N	na	Fungi	1	< 0.001
<i>Hydnobius septentrionalis</i>	N	na	Fungi	1	< 0.001
<i>Phalacrus substriatus</i>	N	na	Fungi	1	< 0.001
<i>Mycetoporus erichsonianus</i>	Unknown	na	Fungi	1	< 0.001
<i>Acrotrichis rugulosa</i>	SF	Y	Fungi	1	< 0.001
<i>Scaphisoma agaricinum</i>	SF	Y	Fungi	1	< 0.001

<i>Anisotoma axillaris</i>	SO	Y	Fungi	1	< 0.001
<i>Anisotoma glabra</i>	SO	Y	Fungi	1	< 0.001
<i>Cis bidentatus</i>	SO	Y	Fungi	1	< 0.001
<i>Cryptophagus corticinus</i>	SO	Y	Fungi	1	< 0.001
<i>Latridius hirtus</i>	SO	Y	Fungi	1	< 0.001
<i>Synchita humeralis</i>	SO	Y	Fungi	1	< 0.001
<i>Eusphalerum lapponicum</i>	N	na	Herbivore	1	< 0.001
<i>Rhinoncus castor</i>	N	na	Herbivore	1	< 0.001
<i>Simpliocaria semistriata</i>	Unknown	na	Herbivore	1	< 0.001
<i>Athous subfuscus</i>	SO	na	Herbivore	1	< 0.001
<i>Deporaus betulae</i>	N	Y	Herbivore	1	< 0.001
<i>Amara hyperborea</i>	N	na	Unknown	1	< 0.001
<i>Calvia quatuordecimguttata</i>	N	na	Unknown	1	< 0.001
<i>Leiodes punctulata</i>	N	na	Unknown	1	< 0.001
<i>Lyprocorrhe anceps</i>	N	na	Unknown	1	< 0.001
<i>Notiophilus aquaticus</i>	N	na	Unknown	1	< 0.001
<i>Oulimnius tuberculatus</i>	N	na	Unknown	1	< 0.001
<i>Tachyporus pulchellus</i>	N	na	Unknown	1	< 0.001
<i>Thiasophila angulata</i>	N	na	Unknown	1	< 0.001
<i>Leiodes gyllenhalii</i>	Unknown	na	Unknown	1	< 0.001
<i>Neohyponus arcticus</i>	Unknown	na	Unknown	1	< 0.001
<i>Proteinus brachypterus</i>	SF	na	Unknown	1	< 0.001
<i>Atheta laevicauda</i>	Unknown	Unknown	Unknown	1	< 0.001
<i>Atheta spatuloides</i>	Unknown	Unknown	Unknown	1	< 0.001
<i>Quedius mesomelinus</i>	SF	Y	Unknown	1	< 0.001
<i>Acrotrichis silvatica</i>	N	na	Other	1	< 0.001
<i>Aploderus caelatus</i>	N	na	Other	1	< 0.001
<i>Atheta boleticola</i>	N	na	Other	1	< 0.001
<i>Atheta corvina</i>	N	na	Other	1	< 0.001
<i>Atheta cribrata</i>	N	na	Other	1	< 0.001
<i>Atheta intermedia</i>	N	na	Other	1	< 0.001
<i>Catops nigrita</i>	N	na	Other	1	< 0.001
<i>Eusphalerum minutum</i>	N	na	Other	1	< 0.001
<i>Gyrophypnus punctulatus</i>	N	na	Other	1	< 0.001
<i>Thanatophilus lapponicus</i>	N	na	Other	1	< 0.001
<i>Philonthus politus</i>	SF	na	Other	1	< 0.001
<i>Deliphrum tectum</i>	Unknown	Unknown	Other	1	< 0.001
<i>Gyrophaena affinis</i>	SF	Y	Other	1	< 0.001
<i>Lordithon lunulatus</i>	SF	Y	Other	1	< 0.001
<i>Agabus congener</i>	N	na	Predator	1	< 0.001
<i>Agonum consimile</i>	N	na	Predator	1	< 0.001
<i>Aleochara brundini</i>	N	na	Predator	1	< 0.001
<i>Atheta elongatula</i>	N	na	Predator	1	< 0.001
<i>Atheta setigera</i>	N	na	Predator	1	< 0.001
<i>Bembidion grapii</i>	N	na	Predator	1	< 0.001
<i>Eucnecosum brachypterus</i>	N	na	Predator	1	< 0.001

<i>Loricera pilicornis</i>	N	na	Predator	1	< 0.001
<i>Megarthritis nitidulus</i>	N	na	Predator	1	< 0.001
<i>Miscodera arctica</i>	N	na	Predator	1	< 0.001
<i>Omalius septentrionis</i>	N	na	Predator	1	< 0.001
<i>Oxypoda nigricornis</i>	N	na	Predator	1	< 0.001
<i>Philonthus corvinus</i>	N	na	Predator	1	< 0.001
<i>Tetartopeus zetterstedti</i>	N	na	Predator	1	< 0.001
<i>Encephalus complicans</i>	Unknown	na	Predator	1	< 0.001
<i>Stenus hyperboreus</i>	Unknown	na	Predator	1	< 0.001
<i>Arpedium quadrum</i>	SF	Unknown	Predator	1	< 0.001
<i>Gabrius appendiculatus</i>	SF	Unknown	Predator	1	< 0.001
<i>Tachinus lignorum</i>	SF	Unknown	Predator	1	< 0.001
<i>Bolitochara pulchra</i>	SF	Y	Predator	1	< 0.001
<i>Coryphium angusticolle</i>	SF	Y	Predator	1	< 0.001
<i>Epuraea binotata</i>	SF	Y	Predator	1	< 0.001
<i>Euplectus piceus</i>	SF	Y	Predator	1	< 0.001
<i>Quedius xanthopus</i>	SF	Y	Predator	1	< 0.001
<i>Paranopleta inhabilis</i>	SO	Y	Predator	1	< 0.001
<i>Pediacus fuscus</i>	SO	Y	Predator	1	< 0.001
<i>Placusa tachyporoides</i>	SO	Y	Predator	1	< 0.001
<i>Lordithon trinotatus</i>	N	na	Multiple	1	< 0.001
<i>Denticollis borealis</i>	SO	Y	Multiple	1	< 0.001
<i>Dinaraea aequata</i>	SO	Y	Multiple	1	< 0.001
<i>Glischrochilus quadripunctatus</i>	SO	Y	Multiple	1	< 0.001
<i>Gonotropis dorsalis</i>	SO	Y	Multiple	1	< 0.001
<i>Leptusa pulchella</i>	SO	Y	Multiple	1	< 0.001
<i>Hylastes brunneus</i>	SO	N	Wood	1	< 0.001
<i>Catops nigrita</i>	N	na	Other	1	< 0.001
<i>Eusphalerum minutum</i>	N	na	Other	1	< 0.001
<i>Gyrophypnus punctulatus</i>	N	na	Other	1	< 0.001
<i>Thanatophilus lapponicus</i>	N	na	Other	1	< 0.001
<i>Philonthus politus</i>	SF	na	Other	1	< 0.001
<i>Deliphrum tectum</i>	Unknown	Unknown	Other	1	< 0.001
<i>Gyrophaena affinis</i>	SF	Y	Other	1	< 0.001
<i>Lordithon lunulatus</i>	SF	Y	Other	1	< 0.001
<i>Agabus congener</i>	N	na	Predator	1	< 0.001
<i>Agonum consimile</i>	N	na	Predator	1	< 0.001
<i>Aleochara brundini</i>	N	na	Predator	1	< 0.001
<i>Atheta elongatula</i>	N	na	Predator	1	< 0.001
<i>Atheta setigera</i>	N	na	Predator	1	< 0.001
<i>Bembidion grapii</i>	N	na	Predator	1	< 0.001
<i>Eucnecosum brachypterum</i>	N	na	Predator	1	< 0.001
<i>Loricera pilicornis</i>	N	na	Predator	1	< 0.001
<i>Megarthritis nitidulus</i>	N	na	Predator	1	< 0.001
<i>Miscodera arctica</i>	N	na	Predator	1	< 0.001



<i>Omalius septentrionis</i>	N	na	Predator	1	< 0.001
<i>Oxypoda nigricornis</i>	N	na	Predator	1	< 0.001
<i>Philonthus corvinus</i>	N	na	Predator	1	< 0.001
<i>Tetartopeus zetterstedti</i>	N	na	Predator	1	< 0.001
<i>Encephalus complicans</i>	Unknown	na	Predator	1	< 0.001
<i>Stenus hyperboreus</i>	Unknown	na	Predator	1	< 0.001
<i>Arpedium quadrum</i>	SF	Unknown	Predator	1	< 0.001
<i>Gabrius appendiculatus</i>	SF	Unknown	Predator	1	< 0.001
<i>Tachinus lignorum</i>	SF	Unknown	Predator	1	< 0.001
<i>Bolitochara pulchra</i>	SF	Y	Predator	1	< 0.001
<i>Coryphium angusticolle</i>	SF	Y	Predator	1	< 0.001
<i>Epuraea binotata</i>	SF	Y	Predator	1	< 0.001
<i>Euplectus piceus</i>	SF	Y	Predator	1	< 0.001
<i>Quedius xanthopus</i>	SF	Y	Predator	1	< 0.001
<i>Paranopleta inhabilis</i>	SO	Y	Predator	1	< 0.001
<i>Pediacus fuscus</i>	SO	Y	Predator	1	< 0.001
<i>Placusa tachyporoides</i>	SO	Y	Predator	1	< 0.001
<i>Lordithon trinotatus</i>	N	na	Multiple	1	< 0.001
<i>Denticollis borealis</i>	SO	Y	Multiple	1	< 0.001
<i>Dinaraea aequata</i>	SO	Y	Multiple	1	< 0.001
<i>Glischrochilus quadripunctatus</i>	SO	Y	Multiple	1	< 0.001
<i>Gonotropis dorsalis</i>	SO	Y	Multiple	1	< 0.001
<i>Leptusa pulchella</i>	SO	Y	Multiple	1	< 0.001
<i>Hylastes brunneus</i>	SO	N	Wood	1	< 0.001
<i>Acrotrichis parva</i>	N	na	Fungi	2	< 0.001
<i>Acrotrichis strandi</i>	N	na	Fungi	2	< 0.001
<i>Atomaria hislopi</i>	N	na	Fungi	2	< 0.001
<i>Leiodes inordinata</i>	N	na	Fungi	2	< 0.001
<i>Leiodes obesa</i>	N	na	Fungi	2	< 0.001
<i>Atheta sodalis</i>	Unknown	na	Fungi	2	< 0.001
<i>Mycetoporus maerkeli</i>	SF	Unknown	Fungi	2	< 0.001
<i>Aspidiphorus orbiculatus</i>	SF	Y	Fungi	2	< 0.001
<i>Anisotoma castanea</i>	SO	Y	Fungi	2	< 0.001
<i>Cis submicans</i>	SO	Y	Fungi	2	< 0.001
<i>Triplax russica</i>	SO	Y	Fungi	2	< 0.001
<i>Amara apricaria</i>	N	na	Herbivore	2	< 0.001
<i>Atomaria lewisi</i>	N	na	Unknown	2	< 0.001
<i>Catops tristis</i>	N	na	Unknown	2	< 0.001
<i>Coccinella hieroglyphica</i>	N	na	Unknown	2	< 0.001
<i>Leiodes silesiaca</i>	N	na	Unknown	2	< 0.001
<i>Oxypoda lugubris</i>	N	na	Unknown	2	< 0.001
<i>Philonthus albipes</i>	N	na	Unknown	2	< 0.001
<i>Acrotrichis fascicularis</i>	Unknown	na	Unknown	2	< 0.001
<i>Atheta altaica</i>	Unknown	na	Unknown	2	< 0.001
<i>Philonthus varians</i>	Unknown	na	Unknown	2	< 0.001

<i>Atheta sparreschneideri</i>	Unknown	Unknown	Unknown	2	< 0.001
<i>Atheta atramentaria</i>	SF	Unknown	Unknown	2	< 0.001
<i>Sphaerites glabratus</i>	SF	Unknown	Unknown	2	< 0.001
<i>Aphodius depressus</i>	N	na	Other	2	< 0.001
<i>Atheta excelsa</i>	N	na	Other	2	< 0.001
<i>Cercyon quisquilius</i>	N	na	Other	2	< 0.001
<i>Clytra quadripunctata</i>	N	na	Other	2	< 0.001
<i>Cryptopleurum minutum</i>	N	na	Other	2	< 0.001
<i>Necrobia violacea</i>	N	na	Other	2	< 0.001
<i>Atheta vaga</i>	SF	Y	Other	2	< 0.001
<i>Atheta palleola</i>	N	na	Predator	2	< 0.001
<i>Atheta strandiella</i>	N	na	Predator	2	< 0.001
<i>Tachyporus chrysomelinus</i>	N	na	Predator	2	< 0.001
<i>Atheta celata</i>	Unknown	na	Predator	2	< 0.001
<i>Liogluta alpestris</i>	Unknown	na	Predator	2	< 0.001
<i>Bryophacis rufus punctipennis</i>	SF	Unknown	Predator	2	< 0.001
<i>Ischnoglossa prolixa</i>	SF	Y	Predator	2	< 0.001
<i>Mniusa incrassata</i>	SF	Y	Predator	2	< 0.001
<i>Atrecus pilicornis</i>	SO	Y	Predator	2	< 0.001
<i>Epuraea melina</i>	SF	N	Multiple	2	< 0.001
<i>Judolia sexmaculata</i>	SO	na	Wood	2	< 0.001
<i>Cis submicans</i>	SO	Y	Wood	2	< 0.001
<i>Placusa tachyporoides</i>	SO	Y	Predator	1	< 0.001
<i>Lordithon trinotatus</i>	N	na	Multiple	1	< 0.001
<i>Denticollis borealis</i>	SO	Y	Multiple	1	< 0.001
<i>Dinaraea aequata</i>	SO	Y	Multiple	1	< 0.001
<i>Glischrochilus quadripunctatus</i>	SO	Y	Multiple	1	< 0.001
<i>Gonotropis dorsalis</i>	SO	Y	Multiple	1	< 0.001
<i>Leptusa pulchella</i>	SO	Y	Multiple	1	< 0.001
<i>Hylastes brunneus</i>	SO	N	Wood	1	< 0.001
<i>Acrotrichis parva</i>	N	na	Fungi	2	< 0.001
<i>Acrotrichis strandi</i>	N	na	Fungi	2	< 0.001
<i>Atomaria hislopi</i>	N	na	Fungi	2	< 0.001
<i>Leiodes inordinata</i>	N	na	Fungi	2	< 0.001
<i>Leiodes obesa</i>	N	na	Fungi	2	< 0.001
<i>Atheta sodalis</i>	Unknown	na	Fungi	2	< 0.001
<i>Mycetoporus maerkeli</i>	SF	Unknown	Fungi	2	< 0.001
<i>Aspidiphorus orbiculatus</i>	SF	Y	Fungi	2	< 0.001
<i>Anisotoma castanea</i>	SO	Y	Fungi	2	< 0.001
<i>Cis submicans</i>	SO	Y	Fungi	2	< 0.001
<i>Triplax russica</i>	SO	Y	Fungi	2	< 0.001
<i>Amara apricaria</i>	N	na	Herbivore	2	< 0.001
<i>Atomaria lewisi</i>	N	na	Unknown	2	< 0.001
<i>Catops tristis</i>	N	na	Unknown	2	< 0.001
<i>Coccinella hieroglyphica</i>	N	na	Unknown	2	< 0.001

<i>Leiodes silesiaca</i>	N	na	Unknown	2	< 0.001
<i>Oxypoda lugubris</i>	N	na	Unknown	2	< 0.001
<i>Philonthus albipes</i>	N	na	Unknown	2	< 0.001
<i>Acrotrichis fascicularis</i>	Unknown	na	Unknown	2	< 0.001
<i>Atheta altaica</i>	Unknown	na	Unknown	2	< 0.001
<i>Philonthus varians</i>	Unknown	na	Unknown	2	< 0.001
<i>Atheta sparreschneideri</i>	Unknown	Unknown	Unknown	2	< 0.001
<i>Atheta atramentaria</i>	SF	Unknown	Unknown	2	< 0.001
<i>Sphaerites glabratus</i>	SF	Unknown	Unknown	2	< 0.001
<i>Aphodius depressus</i>	N	na	Other	2	< 0.001
<i>Atheta excelsa</i>	N	na	Other	2	< 0.001
<i>Cercyon quisquilius</i>	N	na	Other	2	< 0.001
<i>Clytra quadripunctata</i>	N	na	Other	2	< 0.001
<i>Cryptopleurum minutum</i>	N	na	Other	2	< 0.001
<i>Necrobia violacea</i>	N	na	Other	2	< 0.001
<i>Atheta vaga</i>	SF	Y	Other	2	< 0.001
<i>Atheta palleola</i>	N	na	Predator	2	< 0.001
<i>Atheta strandiella</i>	N	na	Predator	2	< 0.001
<i>Tachyporus chrysomelinus</i>	N	na	Predator	2	< 0.001
<i>Atheta celata</i>	Unknown	na	Predator	2	< 0.001
<i>Liogluta alpestris</i>	Unknown	na	Predator	2	< 0.001
<i>Bryophacis rufus punctipennis</i>	SF	Unknown	Predator	2	< 0.001
<i>Ischnoglossa prolixa</i>	SF	Y	Predator	2	< 0.001
<i>Mniusa incrassata</i>	SF	Y	Predator	2	< 0.001
<i>Atrecus pilicornis</i>	SO	Y	Predator	2	< 0.001
<i>Epuraea melina</i>	SF	N	Multiple	2	< 0.001
<i>Judolia sexmaculata</i>	SO	na	Wood	2	< 0.001
<i>Cis submicans</i>	SO	Y	Wood	2	< 0.001
<i>Cis comptus</i>	SO	Y	Fungi	3	< 0.001
<i>Olisthaerus megacephalus</i>	SO	Y	Fungi	3	< 0.001
<i>Lochmaea caprea</i>	N	Y	Herbivore	3	< 0.001
<i>Amara nigricornis</i>	N	na	Other	3	< 0.001
<i>Cercyon lateralis</i>	N	na	Other	3	< 0.001
<i>Gabrius trossulus</i>	N	na	Other	3	< 0.001
<i>Omalius rugatum</i>	SF	na	Other	3	< 0.001
<i>Dasytes obscurus</i>	SO	N	Predator	3	< 0.001
<i>Autalia puncticollis</i>	N	na	Predator	3	< 0.001
<i>Oxypoda haemorrhoea</i>	N	na	Predator	3	< 0.001
<i>Scymnus frontalis</i>	N	na	Predator	3	< 0.001
<i>Stenus geniculatus</i>	N	na	Predator	3	< 0.001
<i>Atheta euryptera</i>	Unknown	na	Predator	3	< 0.001
<i>Atheta laticollis</i>	SF	Unknown	Predator	3	< 0.001
<i>Rhizophagus dispar</i>	SO	Y	Predator	3	< 0.001
<i>Acrulia inflata</i>	SF	Y	Multiple	3	< 0.001
<i>Pityogenes chalcographus</i>	SO	N	Wood	3	< 0.001

<i>Agathidium arcticum</i>	SF	Y	Fungi	4	< 0.001
<i>Agathidium confusum</i>	SF	Y	Fungi	4	< 0.001
<i>Corticaria rubripes</i>	SF	Y	Fungi	4	< 0.001
<i>Atomaria affinis</i>	SO	Y	Fungi	4	< 0.001
<i>Gonioctena intermedia</i>	N	na	Herbivore	4	< 0.001
<i>Pheletes aeneoniger</i>	N	na	Herbivore	4	< 0.001
<i>Protaetia metallica</i>	N	na	Herbivore	4	< 0.001
<i>Lomechusoides inflatus</i>	N	na	Unknown	4	< 0.001
<i>Acrotona amblystegii</i>	Unknown	na	Unknown	4	< 0.001
<i>Aphodius fasciatus</i>	N	na	Other	4	< 0.001
<i>Atheta debilis</i>	N	na	Predator	4	< 0.001
<i>Megarthritis nigrinus</i>	N	na	Predator	4	< 0.001
<i>Nephus bipunctatus</i>	N	na	Predator	4	< 0.001
<i>Podabrus alpinus</i>	N	na	Predator	4	< 0.001
<i>Bisnius puella</i>	Unknown	na	Predator	4	< 0.001
<i>Lordithon speciosus</i>	SO	Y	Predator	4	< 0.001
<i>Atheta pilicornis</i>	SF	Unknown	Multiple	4	< 0.001
<i>Atomaria nitidula</i>	N	na	Fungi	5	< 0.001
<i>Mycetoporus mulsanti</i>	N	na	Fungi	5	< 0.001
<i>Corticarina minuta</i>	Unknown	na	Fungi	5	< 0.001
<i>Otiorhynchus nodosus</i>	N	na	Herbivore	5	< 0.001
<i>Atheta boreella</i>	N	na	Other	5	< 0.001
<i>Acrotona orbata</i>	N	na	Predator	5	< 0.001
<i>Atheta arctica</i>	N	na	Predator	5	< 0.001
<i>Coccinella trifasciata</i>	N	na	Predator	5	< 0.001
<i>Rhagonycha nigriventris</i>	N	na	Predator	5	< 0.001
<i>Aleochara moerens</i>	SF	na	Predator	5	< 0.001
<i>Atheta aeneipennis</i>	SF	Unknown	Predator	5	< 0.001
<i>Atheta myrmecobia</i>	SF	Unknown	Predator	5	< 0.001
<i>Bryoporus cernuus</i>	SF	Unknown	Predator	5	< 0.001
<i>Malthodes mysticus</i>	SO	Unknown	Predator	5	< 0.001
<i>Epuraea silacea</i>	SO	Y	Predator	5	< 0.001
<i>Ampedus nigrinus</i>	SO	Y	Multiple	5	< 0.001
<i>Enicmus lundbladi</i>	SO	N	Fungi	6	< 0.001
<i>Atheta taxiceroides</i>	SO	Y	Fungi	6	< 0.001
<i>Scymnus nigrinus</i>	N	na	Unknown	6	< 0.001
<i>Diacanthous undulatus</i>	SO	Y	Unknown	6	< 0.001
<i>Megasternum concinnum</i>	N	na	Other	6	< 0.001
<i>Lypoglossa lateralis</i>	N	na	Predator	6	< 0.001
<i>Tachinus pallipes</i>	N	na	Predator	6	< 0.001
<i>Dichelotarsus lapponicus</i>	Unknown	na	Predator	6	< 0.001
<i>Malthodes fuscus</i>	SO	Unknown	Predator	6	< 0.001
<i>Pityogenes bidentatus</i>	SO	N	Wood	6	< 0.001
<i>Atomaria apicalis</i>	N	na	Fungi	7	0.001
<i>Cryptophagus tuberculosus</i>	SO	Unknown	Fungi	7	0.001
<i>Agathidium rotundatum</i>	SF	Y	Fungi	7	0.001

<i>Aplocnemus tarsalis</i>	SO	N	Predator	7	0.001
<i>Dinaraea arcana</i>	SO	Y	Predator	7	0.001
<i>Byrrhus fasciatus</i>	N	na	Herbivore	8	0.001
<i>Notothecta flavipes</i>	N	na	Predator	8	0.001
<i>Olophrum consimile</i>	N	na	Predator	8	0.001
<i>Rhagonycha elongata</i>	N	na	Predator	8	0.001
<i>Euplectus karstenii</i>	SF	Y	Predator	8	0.001
<i>Acrotrichis intermedia</i>	N	na	Fungi	9	0.001
<i>Mycetophagus multipunctatus</i>	SO	Y	Fungi	9	0.001
<i>Cercyon melanocephalus</i>	N	na	Other	9	0.001
<i>Megarthritis prosseni</i>	SF	Unknown	Predator	9	0.001
<i>Epuraea rufomarginata</i>	SF	Y	Multiple	9	0.001
<i>Corticaria gibbosa</i>	Unknown	na	Fungi	10	0.001
<i>Latridius minutus</i>	SF	Y	Fungi	10	0.001
<i>Aphodius borealis</i>	N	na	Other	10	0.001
<i>Lordithon thoracicus</i>	SF	Y	Predator	10	0.001
<i>Nicrophorus vespilloides</i>	N	na	Other	11	0.001
<i>Bisnius nigriventris</i>	N	na	Predator	11	0.001
<i>Atheta procera</i>	SF	Unknown	Predator	11	0.001
<i>Dromius agilis</i>	SF	Y	Predator	11	0.001
<i>Orchesia minor</i>	SO	Y	Fungi	12	0.001
<i>Selatosomus melancholicus</i>	N	na	Herbivore	12	0.001
<i>Atheta depressicollis</i>	N	na	Predator	12	0.001
<i>Oxygaster skalitzkyi</i>	N	na	Predator	12	0.001
<i>Latridius consimilis</i>	SF	Y	Fungi	13	0.001
<i>Magdalis carbonaria</i>	SO	Y	Wood	13	0.001
<i>Mycetoporus lepidus</i>	N	na	Fungi	14	0.001
<i>Atheta excellens</i>	N	na	Predator	14	0.001
<i>Coeliodinus rubicundus</i>	N	na	Herbivore	15	0.001
<i>Amischa analis</i>	N	na	Predator	15	0.001
<i>Lordithon trimaculatus</i>	SO	Y	Predator	15	0.001
<i>Dadobia immersa</i>	SO	Y	Multiple	15	0.001
<i>Mycetoporus punctus</i>	SF	Unknown	Fungi	16	0.001
<i>Abdera affinis</i>	SO	Y	Fungi	16	0.001
<i>Acrotrichis cognata</i>	N	na	Fungi	17	0.001
<i>Corticaria ferruginea</i>	SF	Y	Fungi	17	0.001
<i>Tachinus laticollis</i>	N	na	Unknown	18	0.001
<i>Stenichnus bicolor</i>	SF	Y	Predator	18	0.001
<i>Catops alpinus</i>	N	na	Unknown	19	0.001
<i>Atheta melanocera</i>	N	na	Predator	19	0.001
<i>Euplectus signatus</i>	SF	Unknown	Predator	19	0.001
<i>Omalius strigicollis</i>	SF	Unknown	Predator	19	0.001
<i>Epuraea boreella</i>	SO	Y	Multiple	19	0.001
<i>Atheta diversa</i>	SO	na	Predator	20	0.002
<i>Corticaria orbicollis</i>	SO	Y	Fungi	21	0.002

<i>Trypodendron signatum</i>	SO	Y	Fungi.wood	21	0.002
<i>Atheta brunneipennis</i>	Unknown	na	Predator	21	0.002
<i>Latridius porcatus</i>	Unknown	na	Fungi	22	0.002
<i>Boreophilia islandica</i>	Unknown	na	Predator	22	0.002
<i>Malthodes brevicollis</i>	SO	Y	Predator	22	0.002
<i>Atheta cinnamoptera</i>	N	na	Predator	23	0.002
<i>Acrotrichis sericans</i>	N	na	Fungi	24	0.002
<i>Oxypoda brevicornis</i>	N	na	Predator	24	0.002
<i>Triplax aenea</i>	SO	Y	Fungi	25	0.002
<i>Epuraea angustula</i>	SO	Y	Multiple	26	0.002
<i>Atheta allocera</i>	SF	Unknown	Predator	27	0.002
<i>Rhagium mordax</i>	SO	Y	Wood	28	0.002
<i>Atheta subtilis</i>	Unknown	na	Fungi	29	0.002
<i>Tetratoma ancora</i>	SO	Y	Fungi	30	0.002
<i>Paraphotistus impressus</i>	SF	Unknown	Predator	32	0.002
<i>Phloeopora corticalis</i>	SO	Y	Predator	32	0.002
<i>Cryptophagus lapponicus</i>	SF	Y	Fungi	36	0.003
<i>Orchesia micans</i>	SO	Y	Fungi	37	0.003
<i>Cyphon padi</i>	N	na	Herbivore	42	0.003
<i>Atheta graminicola</i>	N	na	Predator	42	0.003
<i>Quedius plagiatus</i>	SF	Y	Predator	44	0.003
<i>Acidota crenata</i>	SF	Unknown	Predator	48	0.004
<i>Anaspis arctica</i>	SO	Y	Multiple	48	0.004
<i>Epuraea aestiva</i>	SF	Unknown	Multiple	49	0.004
<i>Cis boleti</i>	SO	Y	Fungi	54	0.004
<i>Bryophacis maklini</i>	N	na	Predator	56	0.004
<i>Triplax scutellaris</i>	SO	Y	Fungi	60	0.005
<i>Phratora vitellinae</i>	N	na	Herbivore	60	0.005
<i>Aphodius piceus</i>	N	na	Other	61	0.005
<i>Euplectus punctatus</i>	SO	Y	Predator	63	0.005
<i>Orthocis alni</i>	SO	Y	Fungi	68	0.005
<i>Euedectus giraudi</i>	SO	Y	Fungi	69	0.005
<i>Anthophagus alpinus</i>	N	na	Predator	75	0.006
<i>Acrostiba borealis</i>	N	na	Unknown	76	0.006
<i>Aphodius lapponum</i>	N	na	Other	79	0.006
<i>Cerylon ferrugineum</i>	SO	Y	Multiple	97	0.007
<i>Orithales serraticornis</i>	N	na	Unknown	100	0.008
<i>Acrotona fungi</i>	N	na	Predator	114	0.009
<i>Atheta hypnorum</i>	SF	Unknown	Predator	114	0.009
<i>Denticollis linearis</i>	SO	Y	Multiple	128	0.010
<i>Sericus brunneus</i>	SO	N	Wood	141	0.011
<i>Cyphon variabilis</i>	N	na	Herbivore	157	0.012
<i>Oxytelus laqueatus</i>	N	na	Predator	170	0.013
<i>Enicmus fungicola</i>	SO	Y	Fungi	196	0.015
<i>Rabocerus foveolatus</i>	SO	Y	Predator	201	0.015
<i>Polydrusus fulvicornis</i>	N	na	Herbivore	206	0.016

<i>Podistra schoenherri</i>	SO	Y	Predator	220	0.017
<i>Tachinus elongatus</i>	N	na	Unknown	228	0.017
<i>Salpingus ruficollis</i>	SO	Y	Predator	266	0.020
<i>Malthodes guttifer</i>	SO	N	Predator	485	0.037
<i>Liotrichus affinis</i>	SF	Y	Unknown	780	0.059
<i>Elateroides dermestoides</i>	SO	Y	Fungi.wood	1796	0.135
<i>Eanus costalis</i>	N	na	Herbivore	1938	0.146
<i>Anthophagus omalinus</i>	N	na	Predator	3415	0.258

## **Appendix 2:**

### *Biological information for selected single species:*

Biological information for all single species selected for individual negative binomial modelling in this study.

*Elateroides dermestoides* (Linnaeus 1761, family: Lymexidae, figure 5C) is an obligate saproxylic fungivorous species that occurs in the cambium under the bark of dead or dying deciduous trees, most commonly in birch (appendix 1, Schultze 2012). A total of 1796 individuals were caught during the sampling periods, which makes it the most abundant saproxylic species in the dataset.

*Liotrichus affinis* (Paykull 1800, family: Elateridae, figure 5D) is an herbivorous facultative saproxylic species that mostly occurs in trees (appendix 1, Schultze 2012). 780 individuals were in total caught during the sampling periods.

*Malthodes guttifer* (Kiesenwetter 1852, family: Cantharidae, figure 5E) is an obligate saproxylic predator that hunts in wood detritus. The preferred successional stage this species is unknown (appendix 1, Schultze 2012). 485 individuals were caught in total during the sampling periods.

*Salpingus ruficollis* (Linnaeus 1760, family: Salpingidae, figure 5F) is an obligate saproxylic predatory species that lives in dead woody material of deciduous trees (appendix 1, Polish Biodiversity Information Network, 2008). A total of 266 individuals of this species were caught during the sampling periods.

*Podistra schenherri* (Dejan 1837, family: Cantharidae, figure 5G) is an obligate saproxylic predator related to later successional stages of wood decomposition (appendix 1, Schultze 2012). A total of 220 individuals of this species were caught during the sampling periods.

*Rabocerus foveolatus* (Ljungh 1823, family: Salpingidae, figure 5H) is an obligate saproxylic predatory species that hunts underneath the bark of newly dead or dying trees (appendix 1, Schultze 2012). A total of 201 individuals of this species were caught during the sampling periods.



*Enicmus fungicola* (Thomson 1868, family: Latridiidae, figure 5I) is an obligate saproxylic fungivorous species often found on rotten wood and bark of tree trunks, stumps and thick branches lying on the ground (appendix 1, Polish Biodiversity Information Network, 2008). A total of 196 individuals of this species were caught during the sampling periods.

*Sericus brunneus* (Linnaeus 1758, family: Elateridae, figure 5J) is an obligate saproxylic species that live on wood (appendix 1). A total of 141 individuals of this species were caught during the sampling periods.

*Denticollis linearis* (Linnaeus 1758, family: Elateridae, figure 5K) is an obligate saproxylic species that are found in decaying tree trunks, stubs, logs and branches lying on the ground of both coniferous and deciduous trees (appendix 1, Polish Biodiversity Information Network, 2008). A total of 128 individuals of this species were caught during the sampling periods.

*Atheta hypnorum* (Kiesenwetter 1850, family: Staphylinidae, figure 5L) is a facultative saproxylic predatory species most commonly found on moist leaves, mosses and rotten stumps (appendix 1, Hansen 1954). A total of 114 individuals of this species were caught during the sampling periods.

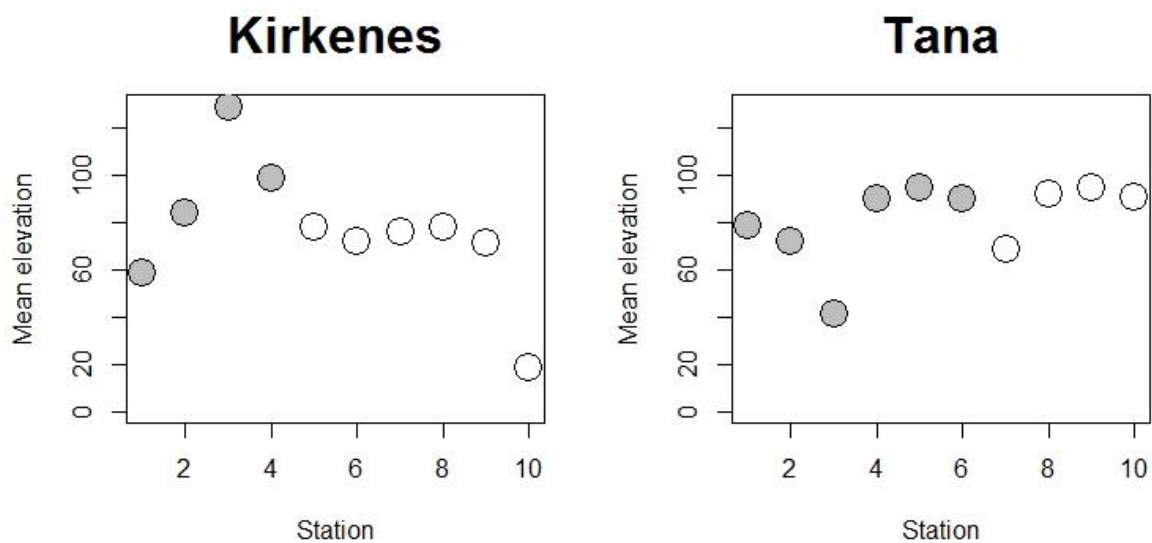
*Anthophagus omalinus* (Zetterstedt 1828, family: Staphylinidae, figure 5A) is a non-saproxylic predatory species living in herbs and flowers (appendix 1, Schultze 2012). With a total of 3415 individuals caught during the sampling periods, it is the most abundant species in the dataset.

*Eanus costalis* (Paykull 1800, family: Elateridae, figure 5B) is a non-saproxylic herbivore species (appendix 1, Schultze 2012), and with a total of 1938 individuals caught during the sampling periods, it is the second most abundant species in the dataset.

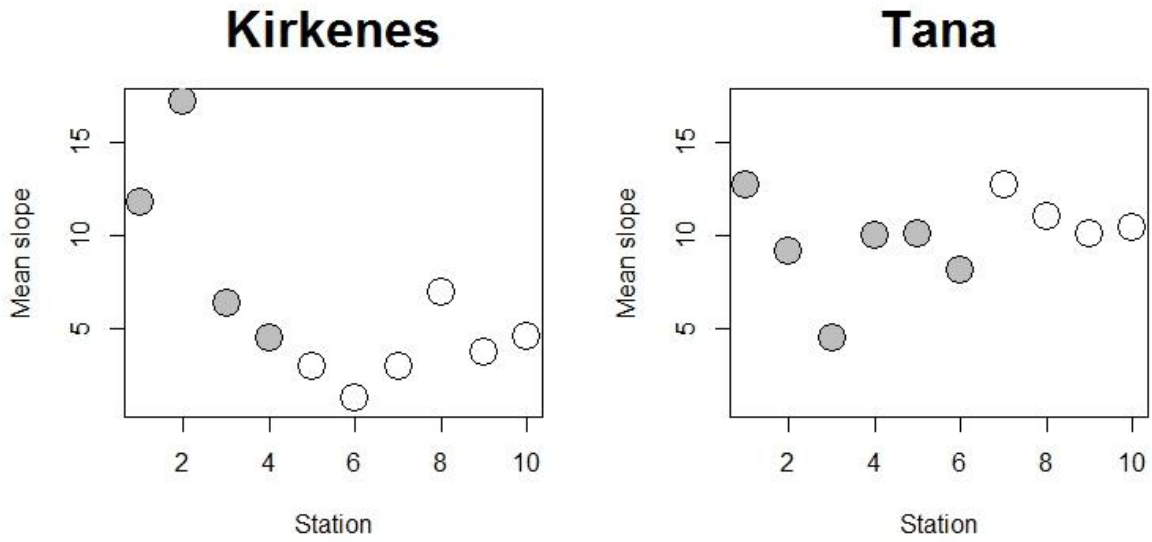
### Appendix 3:

#### *Terrain variables:*

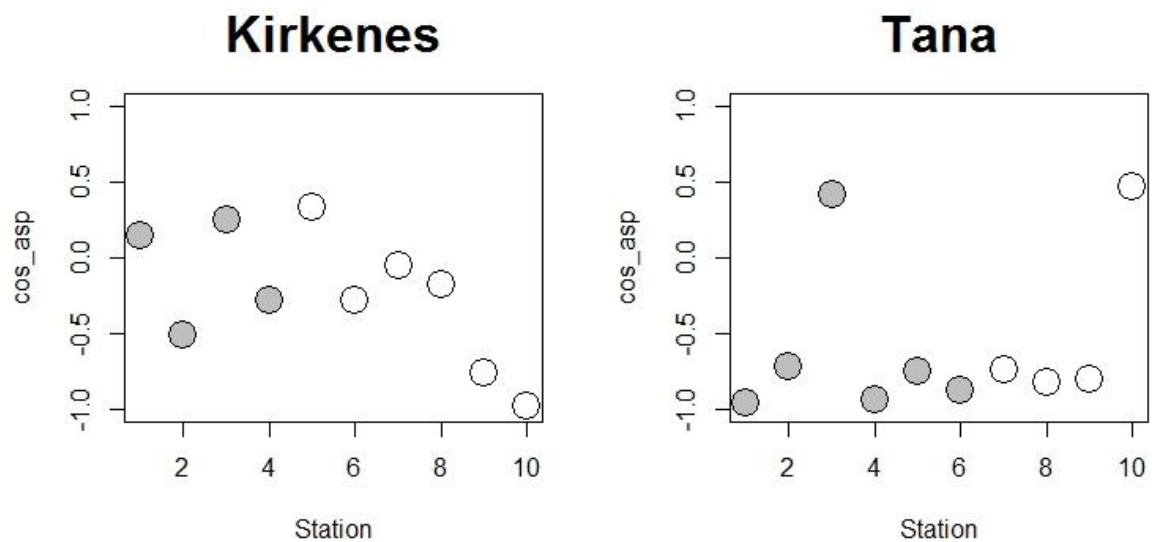
Additional abiotic terrain variables explaining the formation of the landscape on relatively small scale surrounding the sampling stations along both transects. Terrain information are based on a digital terrain model with 20 m pixel size explaining mean terrain values of 200 m surrounding each sampling station (Schultze 2012). The terrain variables included are elevation, slope, aspects of slope in directions north and east, and VRM (Vector Ruggedness Measure). Aspects of a slope described by  $\cos\_asp$ , which means “norhtness” (values range from 1, where the slope faces north, and -1 where the slope faces south), and  $\sin\_asp$ , which means “eastness” (values range from 1, where the slope faces east, and -1 where the slope faces west). By combining these two aspects one can describe 360° of all slopes. VRM is a measure of how “rough” a terrain is trough combining how steep the slopes of a given terrain is with its ruggedness (Sappington et al. 2007).



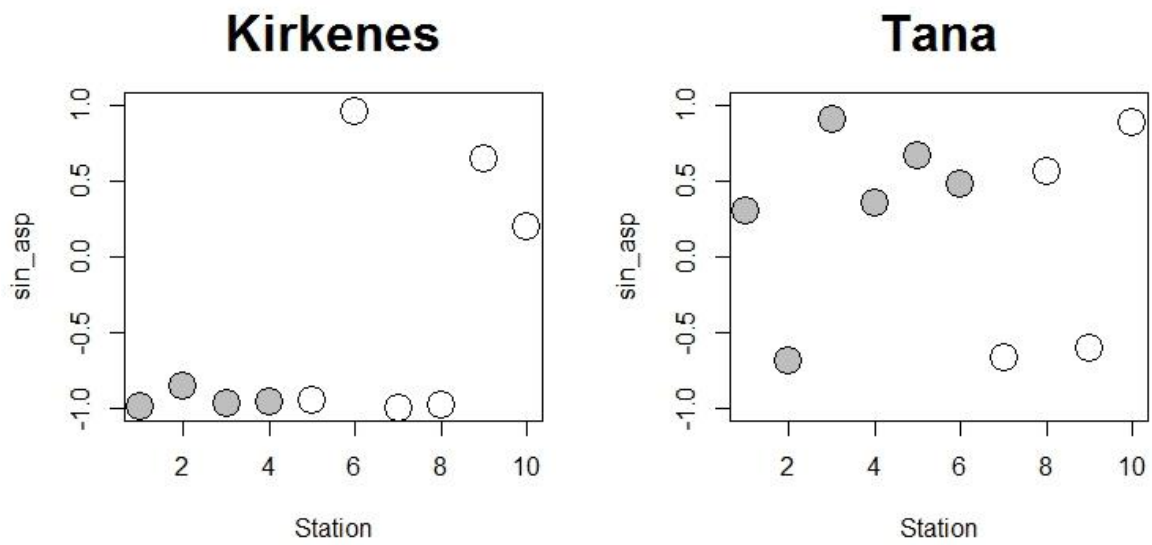
**Figure app. 1: Mean elevation for each sampling station along the sampling transects.** Each circle represent the mean elevation of 200 m surrounding the area of each sampling station. Filled circles represent sampling stations in damaged forest, and empty circles represent stations in undamaged forest.



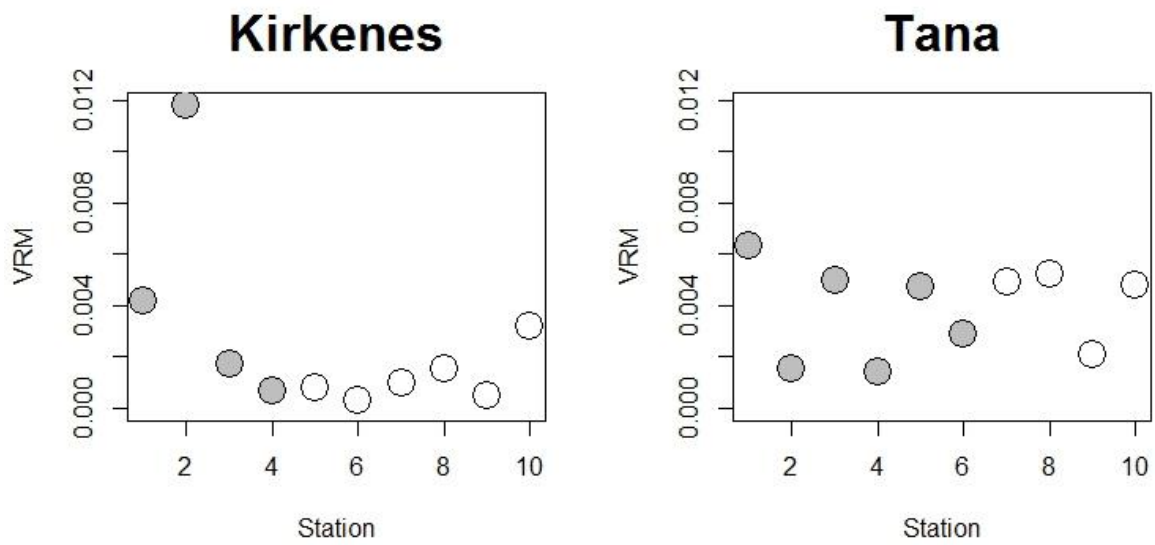
**Figure app. 2: Mean slope for each sampling station along the sampling transects.** Each circle represent the mean slope of 200 m surrounding the area of each sampling station. Filled circles represent sampling stations in damaged forest, and empty circles represent stations in undamaged forest.



**Figure app. 3: Mean northwards aspect of slope for each sampling station along the sampling transects.** Each circle represent the mean northwards aspect of slope 200 m surrounding the area of each sampling station. Filled circles represent sampling stations in damaged forest, and empty circles represent stations in undamaged forest.



**Figure app 4: Mean eastwards aspect of slope for each sampling station along the sampling transects.** Each circle represent the mean eastwards aspect of slope 200 m surrounding the area of each sampling station. Filled circles represent sampling stations in damaged forest, and empty circles represent stations in undamaged forest.



**Figure app. 5: Mean VRM score for each sampling station along the sampling transects.** Each circle represent the mean VRM score of 200 m surrounding the area of each sampling station. Filled circles represent sampling stations in damaged forest, and empty circles represent stations in undamaged forest.





Norges miljø- og biovitenskapelig universitet  
Noregs miljø- og biovitenskapelige universitet  
Norwegian University of Life Sciences

Postboks 5003  
NO-1432 Ås  
Norway