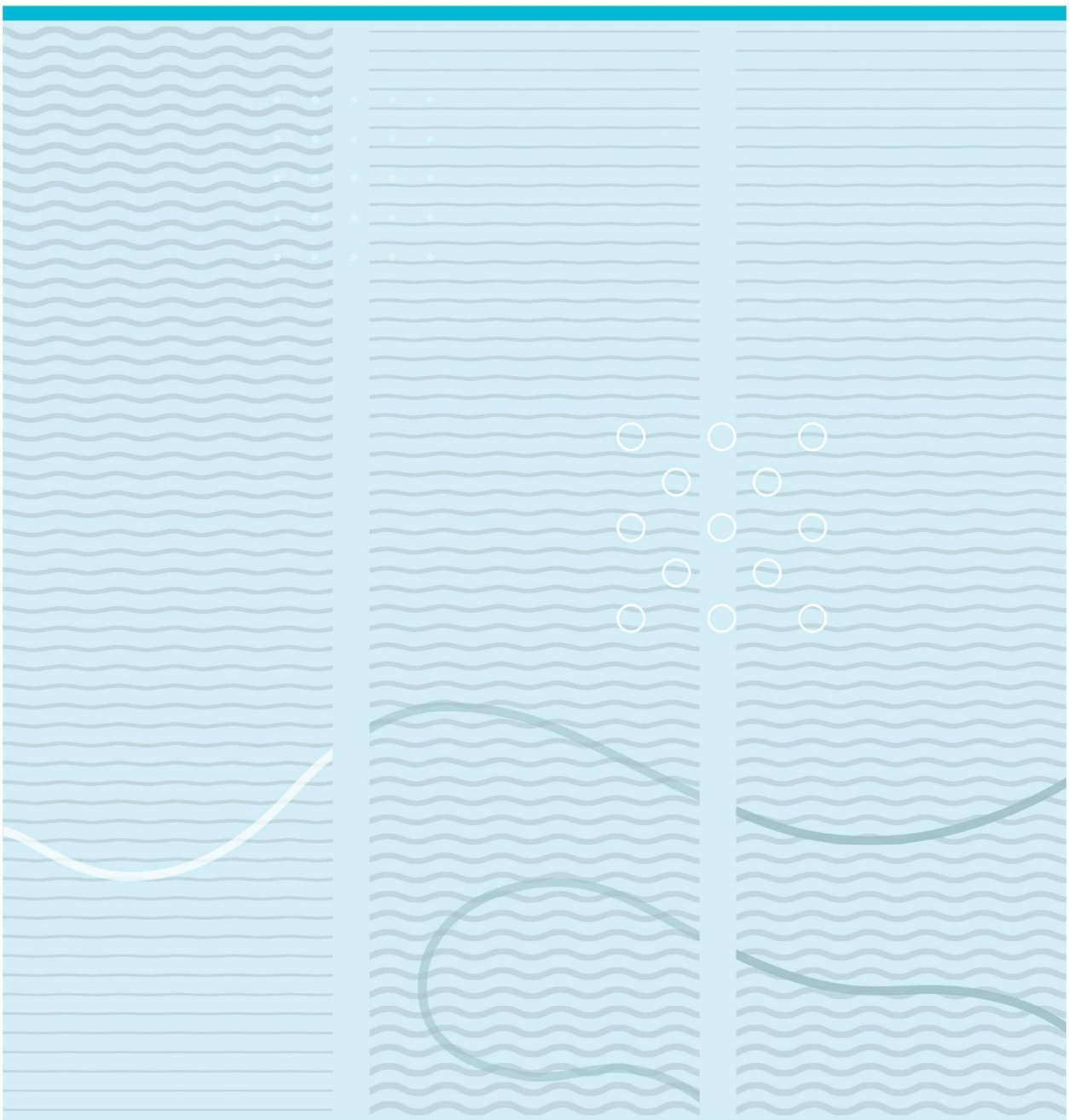# University of South-Eastern Norway

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Deadwood in beaver *(Castor fiber)* habitat – a study with focus on polypore fungi and saproxylic insects

This thesis is worth 60 study points

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1. Preface

I am thankful to my team of supervisors and helpers, family, and friends. I could not have done this without you around me.

2. Abstract

Deadwood is known as a diversity indicator in a forest, where 20-25 % of all forest species in the Nordic countries are dependent on deadwood. 10.7 % of the saproxylic beetles in Europe and 37 % of the polypore fungi in Finland is threatened, and forestry is a big threat. This study surveys to what extent the Eurasian beaver (*Castor fiber*) affects the number of available deadwood objects and the presence of polypore fungi- and saproxylic insect. The presence of saproxylic insects and polypore fungi is also surveyed up against several environmental factors to detect potential effects. The study was conducted by Gvarv and Saua river in Vestfold og Telemark county in Southeastern Norway in August and September 2019. Saproxylic insects and polypore fungi were registered together with several environmental variables in transects perpendicular on the riversides. For the polypore presence my results indicated a higher presence on both laying- and standing deadwood compared to stumps. My results also indicated a higher presence for later decomposition stages, and a positive effect of bark cover and tree diameter. For the presence of saproxylic insects my results indicated a higher presence in later decomposition stages. The death cause of the tree (beaver cut, human cut, natural death cause) was not found informative in describing the presence of neither saproxylic insects not polypore fungi. The deadwood will most likely not be very different independent of what caused the death of the tree. According to this study it does not seem like neither the presence of saproxylic insects or polypore fungi are directly affected by the fact that a beaver cut down the tree compared to a human or a natural death cause. However, the beaver might have an indirect effect in the long term.

Keywords: Deadwood, saproxylic insects, polypore fungi, beaver, *Castor fiber*

3. Introduction

All species are dependent on a suitable habitat, that sufficiently fulfils the requirements and needs of the species, enabling it to survive and reproduce (Hall et al. 1997). Saproxylic species need dead or weakened woody plants in order to fulfil all their stages of life (Grove 2002). Deadwood is known as an indicator for biodiversity (Hahn and Christensen 2005), and over 7500 species, which represent 20-25 % of all the forest species in the Nordic countries are saproxylic species (Siitonen 2001, Stokland and Siitonen 2012b). Among these are saproxylic insects and polypore fungi (Ehnström 2002, Ryvarden 2017).

These two groups have both generalist and specialist species, that depend on deadwood with different characteristics (Nordén et al. 2013). While for example the polypore red belt conk (*Fomitopsis pinicola*) is a real generalist, growing on both coniferous and deciduous tree species, the lemon-colored antrodiella (*Antrodiella citronella*) is a successor specialized to grow in natural coniferous forests, either right by or directly on red belt conks (Ryvarden 2017). Among the saproxylic insects the redbay ambrosia beetle (*Xyleborus cryptophagus*) is specialized on newly dead aspen trees (*Populus tremula*) with coarse bark, while the four-banded longhorn beetle (*Leptura quadrifasciata*) can utilise several different deciduous tree species with coarse bark in the middle stages of decomposition (Ehnström 2002).

The decomposition of a dead tree follows a succession of various polypore species (Niemelä et al. 1995). Preceding species in early decomposition stages makes brown rot (e.g. tinder fungus (*Fomes fomentarius*) on deciduous trees) or white rot (e.g. red belt conk on both deciduous and coniferous trees) that later decomposers are dependent on (Niemelä et al. 1995). The highest polypore diversity seems to be in the middle stages of decomposition before more specialized species colonize in the final stages (Niemelä et al. 1995, Junninen and Komonen 2011). Some polypore species depend on bark cover more than others. Weslien et al. (2011) from Sweden together with Ruokolainen et al. (2018) from Russia found that the preferred amount of bark cover varied between species, and that the

red belt conk was among the bark preferring species. Some polypores are more species specific than others when it comes to tree species, but the majority of polypore species grow either on coniferous- or deciduous trees (Junninen and Komonen 2011). Several articles have found a positive effect of larger diameters on polypore richness (Økland et al. 1996, Sippola et al. 2004), in contrast to Brūmelis et al. (2017) in Latvia, which found no effect. While some species prefer sun exposed deadwood, others prefer more shaded. The rusty gilled polypore (*Gloeophyllum sepiarium*) clearly prefers sun exposed substrates, while *Trechispora hymenocystis* is more shade tolerant (Pasanen et al. 2019). The form of deadwood is also important for what species dwell there. A log in contact with the ground has different microclimatic conditions than a standing dead tree, and it is easier for polypore species to colonize (Junninen and Komonen 2011, Brūmelis et al. 2017).

Similarly to the polypores, decomposition of a dead tree also follows a successional pattern among saproxylic insect species (Jonsell et al. 1998). The bark structure is most important in the first stages of decomposition, when it still is intact (Zuo et al. 2016, Dossa et al. 2018). The more bark types with various structure, the more potential habitats for saproxylic insects (Zuo et al. 2016). Deciduous trees normally have thinner bark than coniferous trees (Rosell et al. 2017). A thinner bark may results in a lower diversity of saproxylic insects, in contrast to a thick bark with a course and scaly structure (Rosell et al. 2017). The bark type has more to say than the tree species, but it is assumed that differences between some deciduous trees and coniferous trees still are considerable also at later decomposition stages (Stockland et al. 2012, Zuo et al. 2016). Among the first species to colonize a dead tree, are the bark beetles (Ehnström 2002, Gossner et al. 2016), which may also assist the polypore fungi dispersing from one tree to another (Strid et al. 2014). The saproxylic insects will have the highest diversity in the middle stages of decomposition (Gossner et al. 2016). A large tree diameter seems to have a positive effect on the abundance and diversity of saproxylic insect species according to Økland et al. (1996), but two studies from Sweden (Lindhe et al. 2005, Jonsell et al. 2007) agreed that diameter classes had a minor role for saproxylic insects, and that sun exposure had a larger effect

at least in the first stages of decomposition. While some species prefer sun exposed deadwood, others prefer more shaded. Among the saproxylic insects it seems like there are some more species preferring sun exposed compared to shaded deadwood objects (from now referred to as DWOs) (Lindhe et al. 2005). When it comes to form of deadwood, laying DWOs are closer to the ground, and which makes it easier for saproxylic insects to colonize (Gossner et al. 2016).

The dead tree will have different characteristics and species compositions depending on how and why the tree died (Renvall 1995, Lindblad 2002). Deadwood is created by biotic factors such as cutting, competition, and aging, and abiotic factors as wind, fire, and drought (Stokland and Siitonen 2012a). While aging, competition, and drought usually result in slow deaths with altered physical state and nutritional content, wind and cutting cause sudden deaths with all nutrients intact (Stokland and Siitonen 2012a). Deforestation and plantation forests have threatened many saproxylic species (Siitonen 2012, Calix et al. 2018) by removing future deadwood from the area, and ruining already present deadwood (Hautala et al. 2004). In the IUCN red list of saproxylic beetles from 2010 (Nieto and Alexander 2010), 10.7 % of saproxylic beetles in Europe were threatened, and in Finland 37 % of the polypore fungi was categorized as threatened or near threatened (Hottola et al. 2008). Due to research showing that the species richness of polypore fungi increases when deadwood is added to the area (Elo et al. 2019), commercial forestry are trying to improve their methods by leaving more deadwood behind (Davies et al. 2008). Despite this, by still using large machines for logging, it is difficult for commercial forestry sites to function as natural forests (Gibb et al. 2005, Junninen and Komonen 2011, Åström et al. 2019).

Another expert on cutting down trees, is the Eurasian beaver *(Castor fiber),* a monogamous and territorial herbivore, that is a potential contributor in adding deadwood to an area (Rosell et al. 2005). The beaver is well adapted to a life in and close by water (Jones et al. 1994), and it is cutting down trees to form its surroundings so that its needs for safety and food supply are fulfilled (Żurowski 1992). Trees are used for making lodges for shelter, dams for a stabile water level, and securing enough

winter supplies in a food cache (Żurowski 1992, Vorel et al. 2015). The Eurasian beaver is an opportunistic generalist (Vorel et al. 2015) with a diet consisting of grass and herbs, aquatic vegetation, and woody plants (Jenkins 1975, Nolet et al. 1995, Milligan and Humphries 2010). The preferred woody plants are willows *(Salix* spp.*),* poplars *(Populus* spp.*)*, rowan *(Sorbus aucuparia)* and birch *(Betula* spp.*)* (Pastor and Naiman 1992, Haarberg and Rosell 2006, Vorel et al. 2015). The beaver almost exclusively cut deciduous trees and very few coniferous trees (Haarberg and Rosell 2006, Vorel et al. 2015). They eat or take parts of the trees they cut with them, and leave the rest behind (Vorel et al. 2015). These are snags and coarse woody debris (CWD) that will increase the amount of deadwood in the area. The diameter of trees most frequently cut by the beaver is 5 cm or smaller, even though they also can take larger diameters than 50 cm (Rosell et al. 2005, Haarberg and Rosell 2006, Vorel et al. 2015). When trees are cut down, gaps in the canopy cover are created, causing more sunlight to penetrate. More sunlight on the forest floor will favour a different plant species composition, with less shade tolerant species (Pastor and Naiman 1992).

Research has been done on the foraging behaviour of beavers, but there are just a few studies on how the beaver affects the saproxylic community. A study from Finland on the Eurasian beaver found that the beavers increase the abundance and diversity of deadwood, and argues for that this creates favourable conditions for saproxylic species (Thompson et al. 2016). Another study in Canada on the North American beaver (*Castor canadensis*), found that bark beetles and longhorn beetles had a higher abundance on deadwood in beaver sites compared to control sites (Mourant et al. 2018). So, this maybe indicate that the situation is the same in Finland. That the beaver might increase the diversity of numerous deadwood dependent species. Both studies focus on deadwood in dammed beaver territories, but I have not found any research on beavers and saproxylic communities in undammed areas.

This study will investigate to what degree the beaver affects the saproxylic community in an undammed area by comparing beaver cut trees to human cut trees, and trees dying of natural causes.

The first aim will survey the distribution of deadwood objects (DWOs) in relation to distance from river, tree species, tree type, form of deadwood (form), decomposition stage, sun exposure, bark cover, and diameter. A second aim is to investigate if the presence of polypore fungi and saproxylic insects are affected by these variables. In the second aim I will predict that forms closer to the ground will have a positive effect on presence of polypores, together with a positive effect from later decomposition stages, and larger tree diameters. I also predict that the presence of saproxylic insects will be affected by tree type, together with a positive effect of forms closer to the ground, of later decomposition stages, and higher sun exposure, and a negative effect from more bark cover.

4. Materials and methods

4.1 Study area

The study was conducted at the riverbanks along the two rivers Saua (59°22´N, 9°15´E – 59°29´N, 9°18´E) and Gvarv (59°24´N, 9°8´E – 59°22´N, 9°12´E) in Vestfold and Telemark county in Southeastern Norway. Both rivers are part of Skiensvassdraget and are regulated to some extent (Pinto et al. 2009). They flow out into the northern part of Lake Nordsjø, Gvarv in west and Saua in east. Gvarv river is 45-130 m wide and Saua is 45-250 m wide (Pinto et al. 2009). The sediments are dominated by marine- and fluvial deposits in addition to glaciofluvial and some bare bedrock along Saua (Haarberg and Rosell 2006). The landscape is located between 72 and 116 MASL (Pinto et al. 2009). The annual mean temperature in the area for 2019 was 6.9^{0}C, and the annual precipitation was 1010.6 mm (Jensen 2007-2020). Both rivers meander through a landscape consisting of mixed forests, deciduous forests mostly dominated by grey alder *(Alnus incana)*, birch, and willow, and coniferous forests dominated by Norwegian spruce *(Picea abies)* and Scots pine *(Pinus sylvestris)* (Haarberg and Rosell 2006).

The river banks are largely impacted by agriculture and rural scattered settlements (Pinto et al. 2009). Logging is unusual in the riparian zone (Pinto et al. 2009), even though exceptions were

observed. The beaver has impacted the study area since the 1920s (Olstad 1937). Today, the population is at carrying capacity (Campbell et al. 2005, Mayer et al. 2019). The study area is distributed between 17 beaver territories: six in Gvarv and 11 in Saua (Figure 1). There are no beaver dams built in the study area due to too wide rivers, and a continuously good water access (Campbell et al. 2005, Haarberg and Rosell 2006, Hartman and Törnlöv 2006). However, there are exceptions in some narrower tributaries (Arnberg 2019).

4.2   Data collection

Data was collected in August and September 2019. Prior to that, coordinate points were placed for every 400 m in the centre of the two rivers. Every coordinate point represented two possible transects, one on each riverbank. Eleven out of 17 beaver territories were chosen randomly for the survey (five in Gvarv and six in Saua) (Figure 1). Ten of the 11 territories had four transects (also chosen randomly), while one had two due to the small territory size (Håtveit) (Figure 1, Appendix 1). The transects were perpendicular to the shoreline (Figure 2), 2 m wide (1 m on both sides of the transect band) and 50 m long. As previous research show, most of the beaver foraging occurs within 50 m from water (Gerwing et al. 2013, Graf et al. 2016), and we therefore chose to focus our survey within this distance.

Figure 1: Study area and the 17 beaver (*Castor fiber*) territories. Gvarv river is in west and Saua river in east.

Territories included in the study are marked in white. The map is provided by Google Maps (Kartdata 2020).
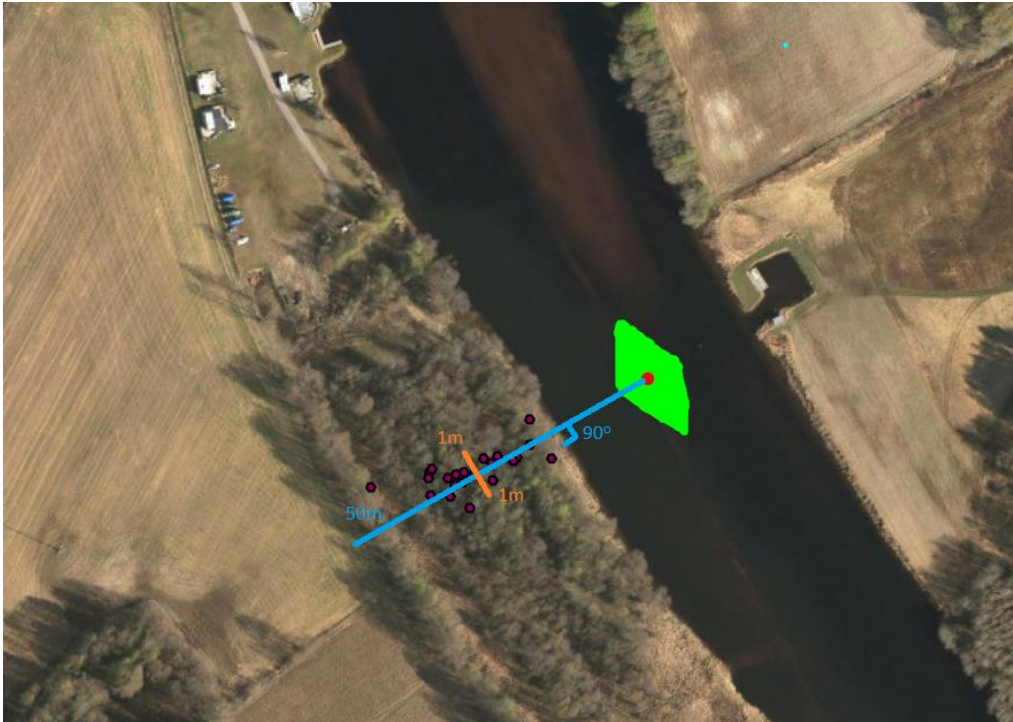
Figure 2: The field method illustrated with a boat (green) at the exact coordinate point (light red dot). The transect is placed perpendicular to the shoreline from the coordinate point, and stretches 50 m from the shoreline and away from the river (blue line). The whole transect is 2 m wide, 1 m to each side of the transect band (orange mark on the figure). The map is provided by the app Collector for ArcGIS (Ersi Inc. 2015-2018).

All DWOs touching inside the transect that were taller/longer than 10 cm and had a diameter 5 cm or larger were included. In total 42 transects were surveyed. Zero transects without any DWOs were not included in the analysis.

All data on each DWO were registered in the app Collector for ArcGIS (Ersi Inc. 2015-2018). Forest type was determined according to the surrounding tree species: grey alder dominated deciduous forest, coniferous forest, deciduous forest, deciduous forest with some broadleaf trees, and mixed forest. When possible, the deadwood was assigned a tree species and a tree type (deciduous / coniferous). Distance to the river was measured from the centre of the object. Form of deadwood (hereafter form) was divided into five levels: broken on stump (the log is still attached to the stump), laying (a log laying on the ground), hanging ($\geq$ 80 % of the object is above the ground), stump (standing object $\leq$ 130 cm), or standing (standing object > 130 cm). The length was measured from end to end.

Broken on stump was measured from the ground following the angle to the end. Standing or hanging objects were measured as far up as reachable, and the rest was estimated by eye, using the measured length as reference. The diameter was measured 10 cm above the ground or from the thickest end. If a stump was beaver cut lower than 10 cm, but the total height was 10 cm or higher (because of the characteristically pointy end), the DWO was measured on the highest whole diameter. The death causes, were divided into three categories and one unknown: beaver (characteristic teeth marks and pointy end), human (smooth, flat cut surface), and natural (natural through weather and wind, drought, aging, competition, illness and parasites). The percent of bark cover was estimated to the closest 5 % (where only 0 % and 1 % are lower). Decomposition stage (from one to five) was estimated by inserting a knife blade into the stem, and percentage of bark. The criteria for this estimation are based on Ehnström (2002), Staniaszek-Kik and Zarnowiec (2018) (Appendix 2). Sun exposure was measured by a spherical densiometer, model-A (Lemmon 1956) where the mean of four measurements (one in each cardinal direction from the centre of the object) gave the percentage of sun exposure coming through the canopy and affecting the DWO.

Polypore fungi and insect galleries were registered. Pictures, measurements, and notes were taken in the field and later used for species/taxa identification. Saproxylic insects were identified with three different levels of confidence: secure (s), unsecure (u), and very unsecure (vu). Polypore fungi were registered from the whole surface of the object, while the insect galleries were registered for the first 5 m (from the thickest end, or the end closest to the river when the diameter was the same).

4.3 Descriptive investigation of the data

To give an indication on how much deadwood that was found, an approximate volume of the deadwood was calculated by the formula:

$$V = \pi r^2 * h$$

V is DWO volume, r is DWO radius, h is DWO height. Further, to get an overview over how the deadwood was distributed among the different environmental variables, polypores and saproxylic insects, I made frequency tables in R-studio that were calculated further to percentage, standard deviation (SD) and mean values.

4.4 Statistical analysis

To investigate what factors that affect polypore- and saproxylic insect presence, I used generalized linear mixed effects models (GLMM) with Bernoulli distribution and logit link, using the glmmTMB package (Brooks et al. 2017). Territory and transect were included as crossed random effects to account for variability between territories and transect locations that might be caused by e.g. environmental differences and sampling frequency (Bolker et al. 2009). I made one global model for polypore presence, and one for the presence of saproxylic insects. Both included the same explanatory variables. These were tree type (deciduous/coniferous), death cause (beaver / human / natural), sun exposure (% light through the canopy), diameter (cm), bark cover (%), form (laying / hanging / standing / broken on stump / stump), and decomposition stage (first / second / third / fourth / fifth).

Decomposition stage was grouped (stage1 / stage2-3 / stage4-5) because of too few observations of different stages in some territories and transects. For death cause, the unknown observations were treated as NA and excluded from the analysis. I scaled and centered the variables to ensure model convergence. Tree type was included instead of tree species for both global models, as the tree species could in many cases not be identified.

Collinearity between variables was checked by using the functions corrplot-, corrgram-, and lattice package (Sarkar 2008, Wei and Simko 2017, Wright 2018). The threshold-based method for the collinearity plots and pairwise comparison was used with a correlation coefficient threshold of $|r| > 0.6$ (Dormann et al. 2013). The variables were also tested with variance inflation factor (VIF), by using the lattice package (Sarkar 2008) and a threshold value of > 3 (Zuur et al. 2010).

Model selection was done using the function dredge in the MuMIn package (Barton 2019) to compare candidate models based on Aikake's Information Criterion corrected for small sample size (AICc). I chose the most parsimonious of the candidate models with ΔAICc < 2 as my two top models.Variables that included zero in their 95 % confidence intervals were interpreted as uninformative. I validated my top models by inspecting the DHARMa scaled residual plots with the DHARMa package (Hartig 2020), and by plotting the residuals for each of the variables in the top models. To investigate if some of the levels of an informative categorical variable were different from each other considering the presence of polypores and saproxylic insects, I utilized the function emmeans in the package emmeans (Length 2020) for a pairwise comparison of the least square means. The program used for the statistical testing was R-studio version 3.6.3 (R Core Team 2020).

5 Results

5.1 Deadwood distribution

In total an approximate deadwood volume of 48 m^3 was found. The 42 transects had 532 DWOs, with a mean DWOs per transect of 12.7 ± 11.4 with a range between 0 – 43 (Appendix 4). Among these, seven were zero transects. In total: 54.0 % of the DWOs died of natural causes, 26.3 % were cut by human, 12.0 % were cut by beaver, and 7.7 % had an unknown death cause. The dominating cause of death was natural for seven of the 11 transects, while human was dominating for three, and beaver for one. Average distance from the river was 25.2 ± 14.2 m. Beaver cut trees had a mean distance of 22.9 ± 12.8 m from the river, human 28.4 ± 13.0 m, and natural 24.6 ± 14.8 m from the river. The dominating form of deadwood was laying followed by stumps, hanging, standing, and broken on stump. The mean diameter (cm) of DWOs was 13.2 ± 9.1 cm. Human cut trees had the highest mean diameter (cm) followed by natural-, and beaver cut trees. The DWOs were identified to sixteen different tree species or taxa. Of the identified DWOs, the four most frequently found were grey alder, birch, Norway spruce, and Scots pine. Birch was most frequently cut by beaver before grey alder, Scots pine, and Norway

spruce. Norway spruce was most frequently cut by humans before grey alder, birch, and Scots pine. Grey alder died most frequently because of natural causes followed by Norway spruce, birch, and Scots pine. The dominating tree type was deciduous trees before coniferous trees. A natural cause of death dominated over human cut- and beaver cut DWOs for both tree types. The mean sun exposure for the DWOs was 31.6 ± 27.9 %. The highest mean sun exposure was registered for human cut trees before natural dead trees, and beaver cut trees. The mean bark cover for the DWOs was 48.5 ± 40.7 %. The dominating decomposition stage among the DWOs were stage1 before stage2, stage4, stage5, and stage3. For beaver cut trees decomposition stage1 dominated over stage4, stage2, stage3, and stage5. For both trees that died of natural causes and human cut trees, decomposition stage1 dominated over stage2, stage4, stage5, and stage3.

5.2   Polypore fungi

Polypores were present on 17.1 % (91 / 532) of the DWOs with a range of 0 – 3 species per DWO. The polypore fungi were identified to 23 different species levels and three genus levels. The three most observed polypores were red belt conk, hairy bracket (*Trametes hirsuta*), and elbow-patch crust (*Fomitiporia punctata*), and the rose bracket (*Fomitopsis rosea*) that is on the Norwegian Red List for Species of 2015 as NT (near threatened), was also found (Appendix 5) (Henriksen and Hilmo 2015).

For GLMM models, the best model included bark cover (%), form, decomposition stage, and diameter (cm) (Appendix 3). Bark cover (%), decomposition stage4-5, and diameter (cm) were found to have a positive effect on the presence of polypores, while sumps had a negative effect (Figure 3, Table 1). Stump indicated a lower polypore presence than standing dead trees (estimate = -1.866, SE = 0.551, 95 % CI lower = 0.356, 95 % CI upper = 3.376) and laying (estimate = -1.328, SE = 0.420, 95 % CI lower = -2.478, 95 % CI upper = -0.177) DWOs. Decomposition stage1 indicated a lower polypore presence than stage4-5 (estimate = -1.037, SE = 0.413, 95 % CI lower = -2.010, 95 % CI

upper = -0.066). We found no effect for death cause, tree type, or sun exposure on the presence of polypores.

Table 1: Results from the GLMM with presence of polypores as the response variable, and bark cover (%), form, decomposition stage, and diameter (cm) as explanatory variables. For every explanatory variable there is estimate, standard error (SE), lower- (lwr) and upper (upr) 95 % confidence interval (CI). The informative explanatory variables (where 95 % CI does not include zero) have grey cells.

Response variable	Explanatory variable	Estimate	SE	95 % CI lwr	95 % CI upr
Presence of polypores	Intercept	-1.5901	0.5070	-2.5837	-0.5964
	Bark cover (%)	0.6335	0.1778	0.2849	0.9820
	From (Stump)	-1.8661	0.5515	-2.9469	-0.7853
	Form (Brokenonstump)	-1.0658	0.9747	-2.9761	0.8445
	Form (Hanging)	-0.9038	0.5838	-2.0480	0.2405
	Form (Laying)	-0.5385	0.4724	-1.4645	0.3875
	Decomposition stage (2-3)	0.3722	0.3837	-0.3799	1.1242
	Decomposition stage (4-5)	1.0373	0.4133	0.2273	1.8474
	Diameter (cm)	0.6301	0.1297	0.3759	0.8842
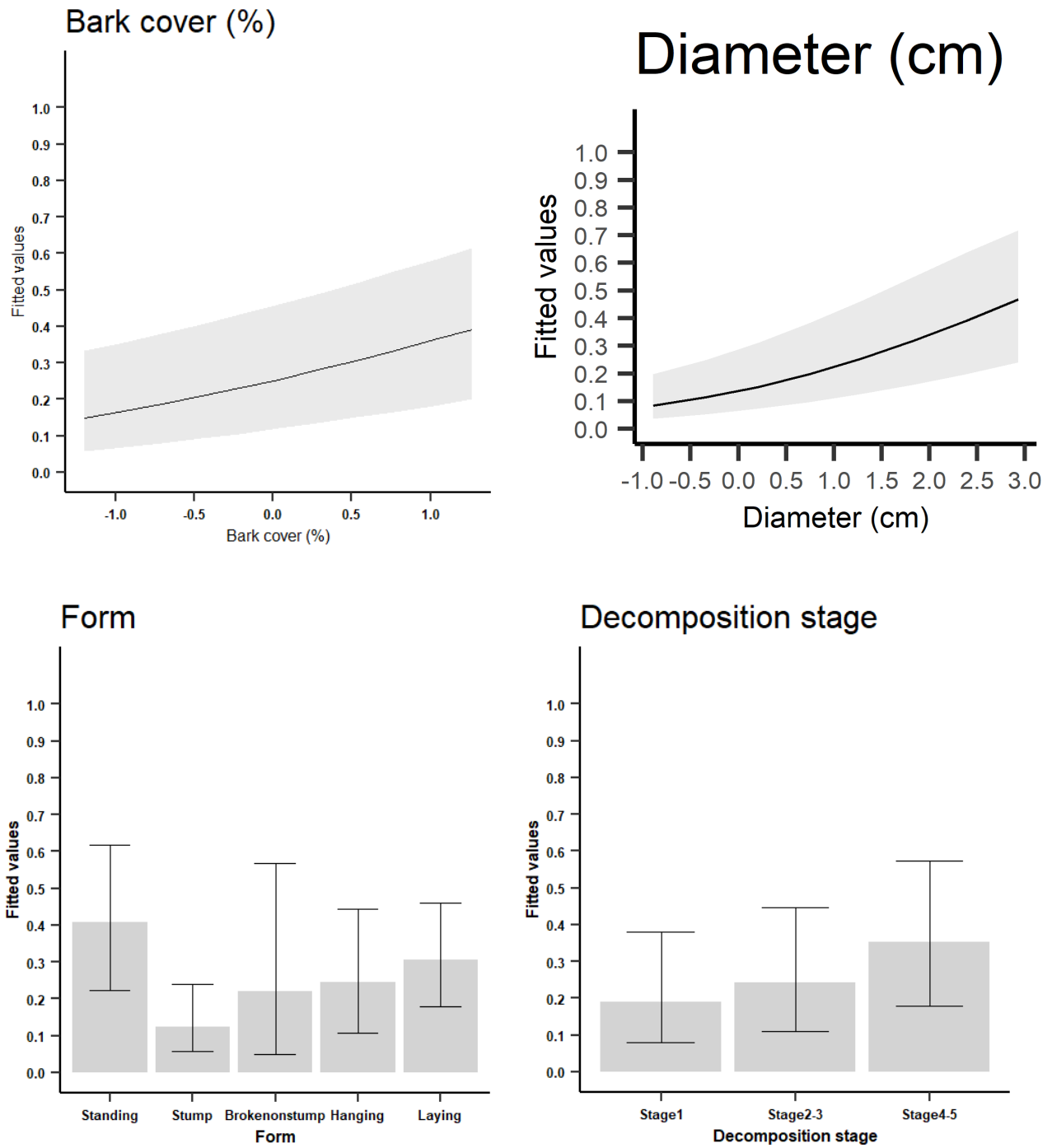
Figure 3: Predicted relationship ± 95 % confidence interval between each variable, and the presence of polypore fungi on deadwood objects (DWOs) located in beaver habitat. The 95 % confidence interval is marked with grey fields for diameter (cm) (up left) and bark cover (%) (up right), and error bars for form (down left) and decomposition stage (down right). The graphs are based on scaled and centered values.

5.3   Saproxylic insects

Insects were present on 94.0% (500 of 532) of the DWOs. Twenty-three different insect families were identified. Of these, 14 were identified with confidence (secure = s), while the rest had more uncertainty to them (unsecure = u, very unsecure = vu). The three most found insect families were snout beetles (*Curculionidae*), ants (*Formicidae*), and longhorn beetles (*Cerambycidae*) (Appendix 6).

In GLMM, the best model included sun exposure, decomposition stage, and diameter (cm) (Appendix 3, Table2). Decomposition stage2-3 and stage4-5 were found to have a positive effect on the presence of saproxylic insects (Table 2, Figure 4), while the rest was found non-informative (Table 2). Decomposition stage1 had a lower polypore presence than for both stage2-3 (estimate = -1.750, SE = 0.592, 95 % CI lower = -3.140, 95 % CI upper = -0.357) and stage4-5 (estimate = -2.800, SE = 1.056, 95 % CI lower = -5.280, 95 % CI upper = -0.314). Sun exposure and diameter (cm) were found non-informative in describing the presence of saproxylic insects, and tree type, death cause, bark cover (%), and form were not included in the best model.

Table 2: Results from the GLMM with presence of saproxylic insects as the response variable, and sun exposure, decomposition, and diameter (cm) as explanatory variables. For every explanatory variable, there is estimate, standard error (SE), lower (lwr)- and upper (upr) 95 % confidence interval (CI). Informative explanatory variables (95 % CI does not include zero) have grey cells.

Response variable	Explanatory variable	Estimate	SE	95 % CI lwr	95 % CI upr
Presence of saproxylic insects	Intercept	2.4620	0.4086	1.6612	3.2628
	Sun exposure	-0.4000	0.2220	-0.8351	0.0350
	Decomposition stage (2-3)	1.7499	0.5923	0.5890	2.9108
	Decomposition stage (4-5)	2.7961	1.0558	0.7269	4.8653
	Diameter (cm)	0.6679	0.3712	-0.0597	1.3955
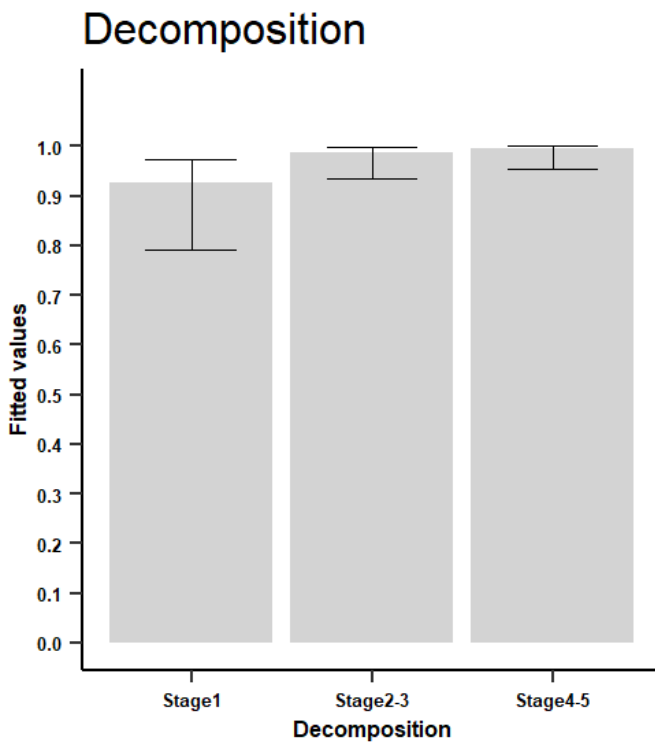
Figure 4: The predicted relationship (± 95 % confidence interval) between decomposition and the presence of saproxylic insects on deadwood objects (DWOs) located in beaver habitat. The error bars indicate 95 % confidence interval. The graph is based on scaled and centered values.

6 Discussion

The dominating cause of death for the DWOs was natural followed by human and beaver. The average distance from the river was smallest for the beaver cut trees followed by trees dying of natural causes, and largest for human cut trees. The beavers contributed most to deciduous trees together with the natural death cause, while humans contributed most to coniferous trees. The two most found deadwood forms were laying (natural 57.1 %) and stump (human 50.0 %), while the rarest form was broken on stump (beaver 70 %) (Appendix 4). As predicted form was informative in describing polypore presence, while it was not found informative for the saproxylic insect presence. The dominating decomposition stage was stage1 for all three death causes. A higher mean bark cover was found to

increase the polypore presence, while it was not found informative for presence of saproxylic insects. I did not have a prediction for the effect of bark cover on polypore presence, but my prediction of bark cover having a negative effect on presence of saproxylic insects was found to be wrong. The mean tree diameter was highest for human cut trees followed by trees dying of a natural death cause, and beaver cut trees. Diameter was found to be affect polypore presence positively, but was not found informative for the presence of saproxylic insects. This was as predicted for the polypore presence. It was some variation in mean sun exposure between the causes of death, but the variable was not found informative in describing neither polypore presence nor presence of saproxylic insects. Death cause alone was not found informative in describing neither polypore presence nor the presence of saproxylic insects. Uninformative variables will not be discussed further.

6.1   Tree selection

According to earlier research, the beaver's diet was dominated by grey alder, rowan, birch, willow and bird cherry (*Prunus padus*) (Haarberg and Rosell 2006). Even though grey alder was just as available as willows, willows was the most preferred (Haarberg and Rosell 2006). In my results grey alder, birch, Norway spruce, and Scots pine were found as the most dominating in the study area. Here, the species most cut by beaver was birch followed by grey alder, Scots pine, and then Norway spruce. This indicates the same preference as Haarberg and Rosell (2006). For human, the most frequently cut species was Norway spruce followed by grey alder, birch, and Scots pine. This may indicate that humans select for Norway spruce over other species. This is also supported by the Norwegian forestry industry (Sagen 2020). Natural death causes are much ruled by wind and weather, and the tree species` root system will decide how much force the tree can hold before it breaks or gets uprooted (Kucera 1998). Norway spruce has a superficial root system weak for rough weather, while birch and alder have deeper roots, followed by pine with even deeper roots that are more storm resistant (Kucera 1998). Other potential influencing factors except from the root system, are fungi attacking the root or

heart wood, and bark beetle attacks (Stokland and Siitonen 2012a). The results from the field indicate some of the same pattern where grey alder are the most dominated tree species followed by Norway spruce, birch, and Scots pine. A reason why grey alder was the dominated here, even though the root system is deeper than Norway spruce, might be because of the higher quantity of this species.

6.2 Polypores

The level stump was found to have a lower presence than both laying- and standing DWOs. Also as predicted laying DWOs had a higher presence most likely due to more contact with the ground (Junninen and Komonen 2011, Brūmelis et al. 2017). Stumps will, compared to its volume, have a higher contact with the ground than standing deadwood. However, a higher volume gives more hosting potential compared to a small volume stump (Stokland and Siitonen 2012a). Stumps also have a large open cut surface compared to its volume, that absorbs and evaporates easily, and cause varying moisture conditions that can be difficult living conditions for many decomposing fungi (Stokland and Siitonen 2012a). The results for decomposition stage matched my prediction, that later decomposition stages would have a positive effect on polypore presence. Decomposition stage has earlier been found important in describing the polypore diversity on deadwood, and that there are an increasing diversity among polypore species at later decomposition stages, when the most decomposed DWOs are excluded (Renvall 1995, Junninen et al. 2007). An succession from early decomposer to later decomposers has been explained, where the earliest decomposers overlap with the later decomposers in the middle decomposition stages (Renvall 1995). This causes the highest polypore diversity at these stages, something Junninen and Komonen (2011) also found a clear agreement on. My results indicate the same findings. Bark cover was found to have a positive effect on polypore presence. It was hard to predict the bark cover`s effect through literature search because there was no clear trend if most species preferred more or less bark cover. Of the identified polypore species in this study, the two most registered polypores were red belt conk and *Trametes* spp. These species are known as early

decomposers of deadwood (Heilmann-Clausen and Boddy 2005, Weslien et al. 2011), where the bark cover still is intact to a certain degree (Appendix 2). The red belt conk as mentioned earlier, has been found to prefer bark cover (Weslien et al. 2011). If there is a connection between polypore fungi on early decomposition deadwood and bark cover, and I think that a larger proportion of the unidentified polypores also are of early decomposers, then this might be a potential part of the reason why bark cover had a positive effect on the polypore presence. On the other hand, my data is not sufficient to make such a statement, and there is no prof for this hypothesis, and needs more research to find more out about it. A larger diameter was found to increase polypore presence, which agreed with my hypothesis. Earlier research have found that a larger diameter gives a higher diversity of polypores (Renvall 1995, Sippola et al. 2004). A higher diversity may indicate a larger chance of presence due to several potential species, and by that support the result of this study.

One of the polypores identified was categorized as NT (near threatened) on the Norwegian Red List for Species of 2015 (Henriksen and Hilmo 2015). This was the rose bracket fungi (*Fomitopsis rosea*), one of five polypore species that is used as indicator species for spruce forests with high continuity (Roesok 1998). These indicator species are considered to have different degrees of requirements for the continuity to be present in the area, where the rose bracket fungi is among the least demanding species (Roesok 1998). Besides, more than one indicator species needs to be in the area to call it a forest of high continuity (Roesok 1998).

6.3   Saproxylic insects

As predicted, a higher decomposition stage had a positive effect on the presence of saproxylic insects. Preceding species such as the bark beetles have made the resources more available in the first stages, which makes it easier also for other species to colonize the DWO at later decomposition stages (Ehnström 2002). Easier access to the deadwood resource combined with species overlapping between decomposition stages, causes an increasing diversity at later stages, and the highest diversity in the

middle stages (Ehnström 2002, Gossner et al. 2016). With a higher diversity of saproxylic insect species, there might also be a bigger chance of presence. Presence of saproxylic insects are registered from all visible insect galleries in the moment out in the field, together with the decomposition stage observed then. This may cause some false observations, because it is unknown which decomposition stage the insect made the gallery. This will not affect observations of decomposition stage 1, but may potentially increase later decomposition stages.

6.4   Beaver

The cause behind the death of a tree was not found as informative in describing the presence neither of polypores nor of saproxylic insects. There are no major differences between beaver cut trees compared to human cut trees or trees dying of natural causes. Beavers cut only fresh trees, and human cut trees and trees dying of natural causes are most often also quite fresh at the point of death (Haarberg and Rosell 2006, Stokland and Siitonen 2012a). A study from Finland found that by adding deadwood to an area, the abundance of polypores would increase, and by time also the species diversity (Elo et al. 2019). In this study the beaver contributed with only 12.0 % of the DWOs surveyed, which most likely not make much of a role. Through these results it does not seem like the beaver has a direct effect on the saproxylic community.

Other studies have discussed a more indirect effect of the beavers over time, where the beaver`s selective foraging changes the tree species composition of the forest vegetation close by the water. The beaver`s hardest foraging pressure is right by the shore, creating habitats well suited for early successor tree species, such as willows and alder that need more sun exposure. A bit further inward the land the beaver may cut down understory vegetation that which has a positive effect on later successor species as Norway spruce and Scots pine (Wright et al. 2002, Rosell et al. 2005). The same vegetation pattern was observed at several transects in this study as well. This changed composition of tree species may also change the composition of saproxylic insects and polypore fungi, due to different preferences

among them (Junninen and Komonen 2011, Stockland et al. 2012). Due to few identified species, it was hard to investigate the diversity of polypores and saproxylic species on beaver cut trees compared to trees dying of natural causes and human cut trees (Appendix 6 and 8).

7 Conclusion

According to this study it does not seem like neither the presence of saproxylic insects or polypore fungi are directly affected by the fact that a beaver cut down the tree compared to a human or a natural death cause. However, the beaver might have an indirect effect in the long term.

8 Acknowledgements

Supervisors: (Stefanie Reinhardt and Frank Narve Rosell): Thank you for giving me the opportunity of studying the life in deadwood, and for the help and support I got in the process.

Hanna Kavli Lodberg-Holm: Thank you for help with statistics (super seminar!), planning, app making, and the writing process.

Rasmus Mohr Mortensen: Thank you for all the help you gave me with the statistics!!

Mats Sletteng: Thank you for a great cooperation out in the field. You were a great field partner!

Torstein Kvamme: You are a cool guy! I am very grateful for the way you helped me with the insect part of the thesis, and for helping me to get in contact with Åke Lindelöw.

Åke Lindelöw: Thank you for helping me with identifying many of the insect galleries.

Rune Solvang: Thank you for the help with identifying many of the polypore species.

Tom hellik Hofton: Thank you for the polypore seminar you had in Bø this autumn, and for checking out some of the polypore species.

Leila Sunniva Berg: Thank you for being there for me through this master, and for helping me getting in contact with Rune Solvang. I appreciate our friendship through our time in Bø.

Marina Eraker Hjønnevåg: Thank you for being my partner in crime the last months, I really appreciate our friendship through these years in Bø.

Eirin Kvålo: My climbing partner. Thank you for all your support, and for keeping my head up.

Gullbring: Thank you for keeping me healthy both physically and mentally.

Parents: Thank you for always being there for me, and for helping med through life.

Last, but not least I want to thank family and friends for being there and having the belief in me.

9 References

Arnberg, M. P. 2019. The importance of vegetation availability in three scales on body condition, reproduction and territory size of the Eurasian beaver. Master thesis. University of South-Eastern Norway.

Barton, K. 2019. MuMIn: Multi-Model Inference.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J.-S. S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution **24**:127-135.

Brooks, M., E., K. Kristensen, K. van Benthem, J., A. Magnusson, C. Berg, W., A. Nielsen, H. Skaug, J., M. Mächler, and B. Bolker, M. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378–400.

Brūmelis, G., E. Oļehnoviča, U. Šūba, A. Treimane, S. Inne, E. Zviedre, D. Elferts, M. Dakša, and D. J. E. E. B. Tjarve. 2017. Bryophyte and polypore richness and indicators in relation to type, age and decay stage of coarse woody debris of Picea abies. **15**:95-103.

Calix, M., K. Alexander, A. Nieto, B. Dodelin, F. Soldati, D. Telnov, X. Vazquez-Albalate, O. Aleksandrowicz, P. Audisio, P. Istrate, N. Jansson, A. Legakis, A. Liberto, C. Makris, O. Merkl, R. Pettersson, J. Schlaghamersky, M. Bologna, H. Brustel, and L. Purchart. 2018. European Red List of Saproxylic Beetles.

Campbell, R. D., F. Rosell, B. A. Nolet, and V. A. A. Dijkstra. 2005. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behavioral Ecology and Sociobiology **58**:597-607.

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

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography **36**:27-46.

Dossa, G. G. O., D. Schaefer, J. L. Zhang, J. P. Tao, K. F. Cao, R. T. Corlett, A. B. Cunningham, J. C. Xu, J. H. C. Cornelissen, and R. D. Harrison. 2018. The cover uncovered: Bark control over wood decomposition. Pages 2147-2160.

Ehnström, B. 2002. Insektsgnag i bark och ved. Artdatabanken, SLU, Uppsala.

Elo, M., P. Halme, T. Toivanen, and J. S. Kotiaho. 2019. Species richness of polypores can be increased by supplementing dead wood resource into a boreal forest landscape. Journal of Applied Ecology **56**:1267-1277.

Ersi Inc. 2015-2018. Collector for ArcGIS. Page [Mobile application software]. ArcGIS Runtime SDK for .NET.

Gerwing, T. G., C. J. Johnson, and C. Alström-Rapaport. 2013. Factors influencing forage selection by the North American beaver (*Castor canadensis*). Mammalian Biology **78**:79-86.

Gibb, H., J. P. Ball, T. Johansson, O. Atlegrim, J. Hjältén, and K. Danell. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scandinavian Journal of Forest Research **20**:213-222.

Gossner, M. M., B. Wende, S. Levick, P. Schall, A. Floren, K. E. Linsenmair, I. Steffan-Dewenter, E.-D. Schulze, and W. W. Weisser. 2016. Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity? Biological Conservation **201**:92-102.

Graf, P. M., M. Mayer, A. Zedrosser, K. Hackländer, and F. Rosell. 2016. Territory size and age explain movement patterns in the Eurasian beaver. Mammalian Biology **81**:587-594.

Grove, S. J. 2002. SAPROXYLIC INSECT ECOLOGY AND THE SUSTAINABLE MANAGEMENT OF FORESTS. Annu. Rev. Ecol. Syst. **33**:1-23.

Haarberg, O., and F. Rosell. 2006. Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. Journal of Zoology **270**:201-208.

Hahn, K., and M. Christensen. 2005. Dead wood in European forest reserves—a reference for forest management. Monitoring and indicators of forest biodiversity in Europe—From ideas to operationality:181.

Hall, L. S., P. R. Krausman, and M. L. J. W. s. b. Morrison. 1997. The habitat concept and a plea for standard terminology.173-182.

Hartig, F. 2020. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.

Hartman, G., and S. Törnlöv. 2006. Influence of watercourse depth and width on dam-building behaviour by Eurasian beaver (*Castor fiber*). Journal of Zoology **268**:127-131.

Hautala, H., J. Jalonen, S. Laaka-Lindberg, and I. Vanha-Majamaa. 2004. Impacts of retention felling on coarse woody debris (CWD) in mature boreal spruce forests in Finland. Biodiversity & Conservation **13**:1541-1554.

Heilmann-Clausen, J., and L. J. M. e. Boddy. 2005. Inhibition and stimulation effects in communities of wood decay fungi: exudates from colonized wood influence growth by other species. **49**:399-406.

Henriksen, S., and O. Hilmo. 2015. Norsk rødliste for arter 2015.

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

Jenkins, S. H. 1975. Food selection by beavers. Oecologia **21**:157-173.

Jensen, I. S. 2007-2020. Gvarv, 2019 Oppsummert. NRK Meteorologisk institutt yr.no.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as Ecosystem Engineers. Oikos **69**:373-386.

Jonsell, M., J. Hansson, and L. Wedmo. 2007. Diversity of saproxylic beetle species in logging residues in Sweden – Comparisons between tree species and diameters. Biological Conservation **138**:89-99.

Jonsell, M., J. Weslien, and B. Ehnström. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity & Conservation **7**:749-764.

Junninen, K., and A. Komonen. 2011. Conservation ecology of boreal polypores: A review. Biological Conservation **144**:11-20.

Junninen, K., R. Penttilä, P. J. B. Martikainen, and Conservation. 2007. Fallen retention aspen trees on clear-cuts can be important habitats for red-listed polypores: a case study in Finland. **16**:475-490.

Kartdata. 2020. TerraMetrics. Google Maps.

Kucera, B. 1998. Treets oppbygning og vedanatomi. Norwegian University of Life Sciences, Ås.

Lemmon, P. E. J. F. s. 1956. A spherical densiometer for estimating forest overstory density. **2**:314-320.

Length, R. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lindblad, I. 2002. Død ved er levende liv. Naturen **126**:114-118 ER.

Lindhe, A., Å. Lindelöw, and N. Åsenblad. 2005. Saproxylic Beetles in Standing Dead Wood Density in Relation to Substrate Sun-exposure and Diameter. Biodiversity & Conservation **14**:3033-3053.

Mayer, M., S. Frank, A. Zedrosser, and F. Rosell. 2019. Causes and consequences of inverse density-dependent territorial behavior and aggression in a monogamous mammal. Journal of Animal Ecology.

Milligan, H. E., and M. M. Humphries. 2010. The importance of aquatic vegetation in beaver diets and the seasonal and habitat specificity of aquatic-terrestrial ecosystem linkages in a subarctic environment. Oikos **119**:1877-1886.

Mourant, A., N. Lecomte, and G. Moreau. 2018. Indirect effects of an ecosystem engineer: how the Canadian beaver can drive the reproduction of saproxylic beetles. **304**:90-97.

Niemelä, T., P. Renvall, and R. Penttilä. 1995. Interactions of fungi at late stages of wood decomposition. Annales Botanici Fennici **32**:141-152.

Nieto, A., and K. N. A. Alexander. 2010. European Red List of Saproxylic Beetles.

Nolet, B. A., P. J. Van Der Veer, E. G. J. Evers, and M. M. Ottenheim. 1995. A linear programming model of diet choice of free-living beavers. Netherlands Journal of Zoology **45**:315-337.

Nordén, J., R. Penttilä, J. Siitonen, E. Tomppo, and O. Ovaskainen. 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. Journal of Ecology **101**:701-712.

Olstad, O. 1937. Beverens (*Castor fiber*) utbredelse i Norge. Statens viltundersøkelser. Nytt Magasin for Naturvidenskapen **77**:217-273.

Pasanen, H., K. Juutilainen, and J. Siitonen. 2019. Responses of polypore fungi following disturbance-emulating harvesting treatments and deadwood creation in boreal Norway spruce dominated forests. Scandinavian Journal of Forest Research **34**:557-568.

Pastor, J., and R. J. Naiman. 1992. Selective Foraging and Ecosystem Processes in Boreal Forests. The American Naturalist **139**:690-705.

Pinto, B., M. J. Santos, and F. Rosell. 2009. Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. Canadian Journal of Zoology **87**:317-325.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Renvall, P. J. K. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. **35**:1-51.

Roesok, O. J. B. 1998. Lappkjuke Amylocystis lapponica i Norge, en indikatorart på artsrike kontinuitetsskoger. **56**:154-165.

Rosell, F., O. Bozser, P. Collen, and H. Parker. 2005. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mammal Review **35**:248-276.

Rosell, J. A., M. E. Olson, T. Anfodillo, and N. Martínez-Méndez. 2017. Exploring the bark thickness–stem diameter relationship: clues from lianas, successive cambia, monocots and gymnosperms. **215**:569-581.

Ruokolainen, A., E. Shorohova, R. Penttilä, V. Kotkova, and H. Kushnevskaya. 2018. A continuum of dead wood with various habitat elements maintains the diversity of wood-inhabiting fungi in an old-growth boreal forest. European Journal of Forest Research **137**:707-718.

Ryvarden, L. 2017. Poroid fungi of Europe. 2nd rev. ed. edition. Fungiflora, Oslo.

Sagen, A. 2020. Kapittel 14: Litt om skogindustrien. Pages 141-146. Norske takstolprodusenters forening

Sarkar, D. 2008. Lattice: Multivariate Data Visualization with R. Springer, New York.

Siitonen, J. 2001. Forest Management, Coarse Woody Debris and Saproxylic Organisms: Fennoscandian Boreal Forests as an Example. Ecological Bulletins:11-41.

Siitonen, J. 2012. Threatened saproxylic species. Pages 356-379 Biodiversity in dead wood.

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

Staniaszek-Kik, M., and J. Zarnowiec. 2018. Diversity of mosses on stumps and logs in the Karkonosze Mts (Sudetes Mts, Central Europe). Herzogia **31**:70-87.

Stockland, J. N., J. Siitonen, and B. G. Jonsson. 2012. Introduction. Pages 1-9 Biodiversity in dead wood.

Stokland, J. N., and J. Siitonen. 2012a. Mortality factors and decay succession. Pages 110-149 Biodiversity in dead wood.

Stokland, J. N., and J. Siitonen. 2012b. Species diversity of saproxylic organisms. Pages 248-274 Biodiversity in dead wood.

Strid, Y., M. Schroeder, B. Lindahl, K. Ihrmark, and J. Stenlid. 2014. Bark beetles have a decisive impact on fungal communities in Norway spruce stem sections. Fungal Ecology **7**:47-58.

Thompson, S., M. Vehkaoja, and P. Nummi. 2016. Beaver-created deadwood dynamics in the boreal forest. Forest Ecology and Management **360**:1-8.

Vorel, A., L. Válková, L. Hamšíková, J. Maloň, and J. Korbelová. 2015. Beaver foraging behaviour: Seasonal foraging specialization by a choosy generalist herbivore. Behavioral Ecology and Sociobiology **69**:1221-1235.

Wei, T., and V. Simko. 2017. R package "corrplot": Visualization of a Correlation Matrix.

Weslien, J., L. B. Djupström, M. Schroeder, and O. J. J. o. A. E. Widenfalk. 2011. Long-term priority effects among insects and fungi colonizing decaying wood. **80**:1155-1162.

Wright, J. P., C. G. Jones, and A. S. Flecker. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia **132**:96-101.

Wright, K. 2018. corrgram: Plot a Correlogram.

Zuo, J., M. P. Berg, R. Klein, J. Nusselder, G. Neurink, O. Decker, M. M. Hefting, U. Sass-Klaassen, R. S. P. Logtestijn, L. Goudzwaard, J. Hal, F. J. Sterck, L. Poorter, and J. H. C. Cornelissen. 2016. Faunal community consequence of interspecific bark trait dissimilarity in early-stage decomposing logs. Functional Ecology **30**:1957-1966.

Żurowski, W. 1992. Building activity of beavers. Acta Theriologica **37**:403-411.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1**:3-14.

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

Åström, J., T. Birkemoe, T. Ekrem, A. Endrestøl, F. Fossøy, A. Sverdrup-Thygeson, and F. Ødegaard. 2019. Nasjonal overvåking av insekter. Behovsanalyse og forslag til overvåkingsprogram. NINA Rapport. Norsk Institutt for Naturforskning. våtmark V1-C1 **4**:8.

10 Appendix

Appendix 1: Overview of all the DWOs (deadwood objects) surveyed in this study. The table shows the rivers (n = 2), beaver (*Castor fiber*) territories (n = 11), transects (n = 42), and the number of DWOs (deadwood objects) (n = 532).

River	Territories	Transects	Number of DWOs	Sum DWOs per territory
Gvarv	Nordsjø1	27A	23	62
		29B	9	
		30A	23	
		30B	7	
	GvarvbruaLower	31A	0	26
		31B	0	
		32A	26	
		32B	0	
	GvarvbruaMid	33A	0	33
		33B	28	
		34A	3	
		34B	2	
	Håtveit	36A	18	23
		36B	5	
	Evjutunet	37A	0	19
		37B	4	
		40A	14	
		40B	1	
Saua	Patmos0Upper	61B	28	55
		63B	13	
		64A	1	
		65A	13	
	Patmos1	58A	12	65
		59A	24	
		59B	19	
		60A	10	
	Patmos2A	54A	15	53
		54B	21	
		56A	17	
		56B	0	
	Patmos3A	87A	30	79
		87B	0	
		88A	40	
		88B	9	

		22A	1	
	BråfjordenB	22B	14	62
		78A	4	
		79A	43	
	Patmos5	72B	10	55
		73B	6	
		75A	11	
		76A	28	
Sum	**11**	**42**	**532**	

Appendix 2: Criteria defining the five stages of deadwood decomposition, using knife stabbing and bark percent.

Decomposition stage	Criteria
Stage 1	Knife stab < 1 cm deep, bark more or less intact.
Stage 2	Knife stab 1-2 cm deep, bark begun to loosen up (*Betula* sp. bark decompose slower than many other species).
Stage 3	Knife stab 3-5 cm deep, bark mostly gone, sapwood signs of fungal attack and decomposition.
Stage 4	Knife stab easily deep, but still some resistance, outer structures are changing.
Stage 5	Knife stab without resistance, easily falls apart in the hands.

Appendix 3: The candidate models (ΔAICc < 2) for presence polypores- and saproxylic insects. The candidate models marked in light grey are considered as the best models, and chosen for the GLMM. The model terms show which variables that are included, df (degrees of freedom), LogLik (log likelihood), AICc (Akaike`s Information Criterion c), Delta (ΔAICc), and weight based on all models present.

Response	Model terms	df	LogLik	AICc	Delta	Weight
Presence of polypores	Bark cover (%)+Form+Decomposition stage+Diameter (cm)	11	-198.795	420.2	0.00	0.216
	Bark cover (%)+Form+Decomposition stage+Diameter (cm)+Death cause	13	-197.488	421.8	1.61	0.097
	Bark cover (%)+Form+Decomposition stage+Diameter (cm)+Treetype	12	-198.72	422.1	1.96	0.081
Response	Model terms	df	LogLik	AICc	Delta	Weight
Presence of saproxylic insects	Sun exposure+Form+Decomposition stage+Diameter (cm)	11	-82.886	188.3	0.00	0.145
	Sun exposure+Decomposition stage+Diameter (cm)	7	-87.728	189.7	1.35	0.074
	Bark cover (%)+Sun exposure+Decomposition stage+Diameter (cm)	8	-86.922	190.2	1.81	0.059
	Bark cover (%)+Sun exposure+Form+Decomposition stage+Diameter (cm)	12	-82.742	190.2	1.82	0.059
	Sun exposure+Form+Decomposition stage+Diameter (cm)+Treetype	12	-82.800	190.3	1.93	0.055

Appendix 4: Descriptive results. n is quantity, SD is standard deviation, range shows minimum and maximum values, amount (%) shows the amount in percent, n/totaln shows the quantity of variable 1 per variable 2 of the total number of variable 1. DWOs is deadwood objects, natural is DWOs dying from natural causes, human is human cut DWOs, and Beaver is beaver cut DWOs. Laying, stump, hanging, standing, and broken on stump are the different deadwood forms. The rows marked in light grey, are not discussed further.

Variable 1 per variable 2		Unit	Mean ± SD	Range	Amount (%)	n/totaln
DWOs	Transect	n	12.7 ± 11.4	0 - 43	-	-
DWOs	Natural	n	-	-	54.0	287/532
DWOs	Human	n	-	-	26.3	140/532
DWOs	Beaver	n	-	-	12.0	64/532
DWOs	Unknown	n	-	-	7.7	41/532
DWOs	DistanceRiver	m	25.2 ± 14.2	0 - 50	-	-
Human	DistanceRiver	m	28.4 ± 13.0	0.45 - 50	-	-
Natural	DistanceRiver	m	24.6 ± 14.8	0 - 50	-	-
Beaver	DistanceRiver	m	22.9 ± 12.8	0.5 - 50	-	-
DWOs	Laying	n	-	-	57.0	303/532
DWOs	Stump	n	-	-	22.6	120/532
DWOs	Hanging	n	-	-	11.8	63/532
DWOs	Standing	n	-	-	6.8	36/532
DWOs	Brokenonstump	n	-	-	1.9	10/532
Beaver	Brokenonstump	n	-	-	70.0	7/10
Beaver	Stump	n	-	-	20.0	24/120
Beaver	Hanging	n	-	-	9.5	6/63
Beaver	Laying	n	-	-	8.9	27/303
Beaver	Standing	n	-	-	0.0	0/36
Human	Stump	n	-	-	50.0	60/120
Human	Laying	n	-	-	22.8	69/303
Human	Hanging	n	-	-	17.5	11/63
Human	Standing	n	-	-	0.0	0/36
Human	Brokenonstump	n	-	-	0.0	0/10
Natural	Standing	n	-	-	100.0	36/36
Natural	Hanging	n	-	-	73.0	46/63
Natural	Laying	n	-	-	57.1	173/303
Natural	Stump	n	-	-	24.2	29/120
DWOs	Length	m	3.4 ± 4.0	0.1 - 30	-	-
DWOs	Diameter	cm	13.2 ± 9.1	5 - 71	-	-
Human	Diameter	cm	14.6 ± 10.6	5 - 44	-	-
Natural	Diameter	cm	13.4 ± 9.1	5 - 71	-	-
Beaver	Diameter	cm	9.9 ± 4.7	5 - 29	-	-
DWOs	Grey alder	n	-	-	31.4	167/532
DWOs	Birch	n	-	-	13.5	72/532
DWOs	Norway spruce	n	-	-	13.5	72/532

DWOs	Scots pine	n	-	-	4.9	26/532
Beaver	Birch	n	-	-	40.6	26/64
Beaver	Grey alder	n	-	-	18.8	12/64
Beaver	Scots pine	n	-	-	1.6	1/64
Beaver	Norway spruce	n	-	-	0.0	0/64
Human	Norway spruce	n	-	-	27.1	38/140
Human	Grey alder	n	-	-	24.3	34/140
Human	Birch	n	-	-	13.6	19/140
Human	Scots pine	n	-	-	5.7	8/140
Natural	Grey alder	n	-	-	39.7	114/287
Natural	Norway spruce	n	-	-	10.1	29/287
Natural	Birch	n	-	-	7.7	22/287
Natural	Scots pine	n	-	-	5.9	17/287
DWOs	Coniferous	n	-	-	19.5	104/532
DWOs	Deciduous	n	-	-	76.9	409/532
Natural	Coniferous	n	-	-	47.1	49/104
Human	Coniferous	n	-	-	46.2	48/104
Beaver	Coniferous	n	-	-	1	1/104
Natural	Deciduous	n	-	-	56.2	230/409
Human	Deciduous	n	-	-	20.8	85/409
Beaver	Deciduous	n	-	-	15.4	63/409
DWOs	Sun exposure	%	31.6 ± 27.9	0 - 99.8	-	-
Human	Sun exposure	%	48.7 ± 33.3	0 - 99.8	-	-
Natural	Sun exposure	%	24.8 ± 23.1	2.6 - 99.8	-	-
Beaver	Sun exposure	%	23.8 ± 19.0	2.9 - 94.6	-	-
DWOs	Bark	%	48.5 ± 40.7	0 - 100	-	-
DWOs	Stage 1	n	-	-	33.8	180/532
DWOs	Stage 2	n	-	-	21.2	113/532
DWOs	Stage 4	n	-	-	18.6	99/532
DWOs	Stage 5	n	-	-	15.2	81/532
DWOs	Stage 3	n	-	-	11.1	59/532
Beaver	Stage 1	n	-	-	39.1	25/64
Beaver	Stage 4	n	-	-	25.0	16/64
Beaver	Stage 2	n	-	-	23.4	15/64
Beaver	Stage 3	n	-	-	9.4	6/64
Beaver	Stage 5	n	-	-	3.1	2/64
Human	Stage 1	n	-	-	54.3	76/140
Human	Stage 2	n	-	-	15.7	22/140
Human	Stage 4	n	-	-	10.7	15/140
Human	Stage 5	n	-	-	10.0	14/140
Human	Stage 3	n	-	-	9.3	13/140
Natural	Stage 1	n	-	-	26.8	77/287
Natural	Stage 2	n	-	-	23.9	66/287
Natural	Stage 4	n	-	-	19.5	56/287
Natural	Stage 5	n	-	-	17.8	51/287
Natural	Stage 3	n	-	-	12.9	37/287

Appendix 5: Polypore fungi (34.3 %, 67/102 of the present polypore species) identified to the closest taxonomic level (Order, Family, Genus and Species) with frequency of present polypores of each taxa (n). Status shows the species` category on the Norwegian Red List for Species 2015 (Henriksen and Hilmo 2015), where LC = Least Concern and NT = Near Threatened.

Order	(n)	Family	(n)	Genus	(n)	Species	(n)	Status
Polyporales	53	Fomitopsidaceae	28	Antrodia sp.	3	A.serialis	1	LC
						A.sinuosa	1	LC
				Fomitopsis	21	F.pinicola	20	LC
						F.rosea	1	NT
				Piptoporus	1	P.betulinus	1	LC
				Postia sp.	3	P.caesia	1	LC
						P.fragilis	1	LC
		Polyporaceae	25	Cerrena	2	C.unicolor	2	LC
				Datronia	1	D.mollis	1	LC
				Fomes	2	F.fomentarius	2	LC
				Lenzites	2	L.betulinus	2	LC
				Skeletocutis	1	S.papyracea	1	LC
				Trametes	12	T.hirsuta	8	LC
						T.ochracea	2	LC
						T.versicolor	2	LC
				Trichaptum	5	T.abietum	3	LC
						T.fuscoviolaceum	2	LC
Hymenochaetales	10	Hymenochaetaceae	10	Fomitiporia	4	F.punctata	4	LC
				Inonotus	2	I.radiatus	2	LC
				Phellinus spp.	4	P.laevigatus	2	LC
Gloeophyllales	3	Gloeophyllaceae	3	Gloeophyllum	3	G.sepiarium	2	LC
						G.odoratum	1	LC
Russulales	1	Bondarzewiaceae	1	Heterobasidion	1	H.paviporum	1	LC

Appendix 6: Polypore fungi (34.3 %, 67/102 of the present polypore species) identified, distributed on the deadwood object`s (DWO`s) death causes (natural, human, beaver, and DWOs with an unknown cause of death).

Polypores	Natural	Human	Beaver	Unknown	Total
F.pinicola	18	1	1	0	20
T.hirsuta	2	6	0	0	8
F.punctata	4	0	0	0	4
T.abietum	2	1	0	0	3
I.radiatus	2	0	0	0	2
L.betulinus	1	0	1	0	2
Phellinus_sp.	2	0	0	0	2
T.versicolor	1	1	0	0	2
P.caesia	0	0	0	1	1
A.seralis	0	1	0	0	1
F.fomentarius	1	0	1	0	2
F.rosea	1	0	0	0	1
C.unicolor	2	0	0	0	2
G.sepiarium	1	1	0	0	2
G.odoratum	1	0	0	0	1
S.papyracea	1	0	0	0	1
P.fragilis	1	0	0	0	1
Postia_sp.	1	0	0	0	1
T.ochracea	0	1	1	0	2
T.fuscoviolaceum	2	0	0	0	2
A.sinuosa	1	0	0	0	1
P.betulinus	1	0	0	0	1
P.laevigatus	2	0	0	0	2
Antrodia_sp.	0	0	1	0	1
H.paviporum	0	1	0	0	1
D.mollis	0	1	0	0	1
Sum	47	14	5	1	67

Appendix 7: Saproxylic insects (13.3 %, 133/ca. 1000 present saproxylic insect galleries) identified to the closest taxonomic level (Order, Family, Subfamily, Genus and Species). All the taxonomic levels have a column with the frequency of present insect galleries in each of the taxa (n), and a column showing the security of the identification (security: s = secure, u = unsecure, vu = very unsecure).

Order	(n)	Security	Family	(n)	Security	Subfamily	(n)	Security	Genus	(n)	Security	Species	(n)	Security
Coleoptera	106		Cerambycidae spp.	30	4/10 (s) 6/10 (u)	Lepturinae	9		Rhagium spp.	9	9/9 (u)			
						Lamiinae sp.	7	1/1 (s)	Acanthocinus spp.	2	2/2 (u)			
									Pogonocherus spp.	3	1/2 (u) 1/2 (vu)	P.hispidus	1	1/1 (s)
									Monochamus sp.	1	1/1 (u)			
						Lepturinae	1		Leptura	1		L.quadrifasciata	1	1/1 (s)
						Cerambycinae	3		Molorchus sp.	2	1/1 (u)	M.minor	1	1/1 (s)
									Xylotrechus sp.	1	1/1 (u)			
			Curculionidae spp.	44	19/19 (s)	Scolytinae sp.	21	1/1 (u)	Hylesinus	6		H.varius	6	6/6 (s)
									Dryocoetes	4		D.alni	4	3/4 (s) 1/4 (vu)
									Polygraphus spp.	2	2/2 (s)			
									Ips	1		I.typographus	1	1/1 (s)
									Hylurgops	1		H.palliatus	1	1/1 (u)
									Pityogenes spp.	3	2/2 (s)	P.chalcographus	1	1/1 (s)
									Scolytus	2		S.ratzeburgii	2	2/2 (s)
									Phleotribus	1		P.spinulosus	1	1/1 (s)
						Cossoninae	2		Rhyncolus spp.	2	2/2 (s)			
						Molytinae	2		Pissodes spp.	2	1/2 (s) 1/2 (u)			
			Ptinidae spp.	4	4/4 (s)									
			Lymexylidae	3		Hylecoetinae	3		Elateroides spp.	3	2/2 (s)	E.dermestoides	1	1/1 (s)
			Anobiidae sp.	1	1/1 (vu)									
			Mordellidae	1		Mordellinae	1		Tomoxia sp.	1	1/1 (u)			
			Lucanidae	3		Syndesinae	3		Sinodendron spp.	3	1/3 (s) 2/3 (u)			

Order	#		Family	#		Subfamily	#		Genus	#		Species	#	
			Anthribidae	2		Anthribinae	2		Platystomos	2		P.albinus	2	1/2 (u) 1/2 (vu)
			Trogossitidae	1		Peltinae	1		Ostoma sp.	1	1/1 (vu)			
			Pyrochroidae spp.	8	5/5 (s)	Pyrochroinae	3		Schizotus	3		S.pectinicornis	3	3/3 (u)
			Elateridae spp.	3	2/2 (s)	Elaterinae	1		Ampedus sp.	1	1/1 (s)			
			Ciidae spp.	2	2/2 (s)									
			Staphylinidae sp.	1	1/1 (u)									
			Tenebrionidae	2		Tenebrioninae	2		Bolitophagus	2		B.reticulatus	2	1/2 (s) 1/2 (u)
			Buprestidae	1		Agrilinae	1		Agrilus	1		A.viridis	1	1/1 (vu)
Lepidoptera	2		Cossidae	1		Cossinae	1		Cossus	1		C.cossus	1	1/1 (u)
			Tineidae	1		Scardiinae	1		Montescardia sp.	1	1/1 (s)			
Hymenoptera	19		Formicidae spp.	18	18/18 (s)									
			Ichneumonidae sp.	1	1/1 (s)									
Symphyta sp.	3	1/1 (s)	Xiphydriidae	2		Xiphydriinae	2		Xiphydria spp.	2	2/2 (vu)			
Diptera	2		Tipulidae spp.	2	2/2 (u)									
Raphidioptera	1		Raphidiidae	1					Raphidia_sp.	1	1/1 (s)			

Appendix 8: Saproxylic insects (13.3 %, 133/ca. 1000 present saproxylic insect galleries) identified, distributed on the deadwood object`s (DWO`s) death causes (natural, human, beaver, and DWOs with an unknown cause of death).

Saproxylic insects	Natural	Human	Beaver	Unknown	Total
Cerambycidae_sp.	5	4	0	0	9
Curculionidae_sp.	23	15	0	2	40
Formicidae_sp.	7	6	3	1	17
Ptinidae_sp.	3	0	1	0	4
Lucanidae_sp.	2	0	0	0	2
Lymexylidae_sp.	3	0	0	0	3
Pyrochroidae_sp.	1	4	0	0	5
Elateridae_sp.	0	2	0	1	3
Raphidiidae_sp.	1	0	0	0	1
Tineidae_sp.	1	0	0	0	1
Tenebrionidae_sp.	1	0	0	0	1
Ichneumonidae_sp.	0	0	1	0	1
Symphyta_sp.	0	1	0	0	1
Ciidae_sp.	1	1	0	0	2
Sum	48	33	5	4	90