

Conservation of spruce-associated saproxylic beetles: significance of management categories, environmental variables and fungi

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Preface

Finally, after one year of hard work, my master thesis has reached completion. Overall, I am very happy with the process, as it has been extremely enlightening, and because I believe the product can be useful for others. I was very lucky to be able to work with entomology and conservation ecology to begin with, and I sincerely hope that I will continue with this type of work in the future.

There are many who deserves my gratitudes for their involvement in my master thesis. First and foremost, I must thank my excellent supervisors Anne Sverdrup-thygeson and Tone Birkemoe for their friendliness, constant support, constructive feedback, and for their sincere interest in the work of their students. As others already have said, I could not have asked for better supervisors. Ronny Steen must be thanked for helping me with performing generalized linear mixed-effect statistics models. Thanks to him, I actually want to dig deeper into this topic now. Erik Juel, and all the workers at Selvik Bruk, must be thanked for being extremely helpful and kind when I did my fieldwork. They certainly made the fieldwork much easier and enjoyable. Egil Bendiksen must be thanked for his work on the fungi, and for answering all my questions related to this facinating taxonomic group. Sindre Ligaard must be thanked for his excellent work on identifying the species of almost 4000 beetles in only three monts. Leif Egil Loe also gave me some excellent advice on statistics, and he deserve my gratitude. Markus Sydenhamn and Christian Strømme often provided input of valuable insights, support and coffee, and I hope that I will be able to work with these people in the future. Last but not least, my dear Rannveig Jacobsen has my deepest gratitudes numerous ways she has assisted me with my thesis.

Abstract

Intensive modern forestry is a threat to beetles depending on dead wood (saproxylic beetles). To mitigate these negative effects, forests are regularly set aside as woodland key habitats or retention patches, as supplements to nature reserves. However, there are considerable uncertainties regarding the relative effectiveness of woodland key habitats and retention patches. In addition, it is important to know if these types of conservation are effective for organisms with different ecology and biology.

To explore these issues, the species richness, abundance and composition of spruce-associated saproxylic beetles was compared between 8 woodland key habitats, 9 retention patches and one nature reserve, in one production forest in Norway. Two types of flight intercept traps were used, which were placed on Norway spruce (*Picea abies*). Furthermore, I assessed if fungivores and cambium consumers of spruce-associated saproxylic beetles had similar responses to the management categories. Then I examined the relationship between the beetles and environmental variables. Lastly, it was tested for relationships between the species richness of saproxylic beetles and wood-decaying fungi found on the same logs as the traps.

My results were that woodland key habitats, but not retention patches, had a significantly different species richness of saproxylic beetles from the nature reserve. No significant differences were found in species abundance. Furthermore, no significant differences were found in species richness or abundance of fungivores and cambium consumers between the management categories. Also, dead-wood parameters and sun-exposure could not explain the variation in species richness. However, species composition differences between management categories were significant for saproxylic beetles, but not for fungivores or cambium consumers. Lastly, the species richness of fungi did neither correlate with the species richness of saproxylic beetles, nor with the different functional groups.

These results indicate that the conservation value of the woodland key habitats and the retention patches are useful supplements to the nature reserve, in terms of conserving spruce-associated saproxylic beetles in Selvik. Also, the correlation between spruce-associated saproxylic beetles and fungi appears to be weak on a relatively small temporal and spatial scale. However, it is unclear if the populations that were sampled in woodland key habitats and retention patches will be sustained over time, or if they will go extinct as a result of the relatively high degree of fragmentation in these management categories.

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1. Introduction

Intensive modern forestry is a major threat to organisms depending on dead wood (Grove 2002), i.e. saproxylic organisms (Speight 1989). This is because in many production forests the amount of dead wood has been reduced by over 90% compared to unmanaged old-growth forests (Siitonen 2001). At present, half of the species on the Norwegian red-list are associated with forests, and a large proportion of these are saproxylic beetles (Kålås et al. 2010). This is in conflict with the Norwegian government's target to stop the loss of biodiversity by 2020 (Liebe et al. 2011).

The proportion of total productive forest area protected by nature reserves in Norway is about 2% (Norwegian ministry of the environment 2013), although 4.6% (3360 km²) has been recommended in order to protect present diversity (Framstad et al. 2002). However, only protecting forests as nature reserves is not cost-effective (Wikberg et al. 2009).

To supplement nature reserves, more cost-effective strategies have been developed to mitigate the negative effects of forestry on biodiversity, such as setting aside forest areas in managed forests as woodland key habitats (hereby referred to as "key habitats") and retention patches (Lindenmayer & Franklin 2002). Retention patches are groups of live trees and dead wood which is left at the felling area, or at areas bordering lakes or bogs (Gustafsson et al. 2010). The setting aside of key habitats, on the other hand, is focused on conserving habitats in the forest landscape that is believed to be important for biodiversity (Haugset et al. 1996; Timonen et al. 2010).

Both of these management categories have been shown to have positive effects on the saproxylic beetle fauna. Martikainen (2001) found that retained aspen trees in Finland had clear differences in species composition of saproxylic beetles than old-growth forests. Similarly, Timonen et al. (2011) found by using a meta-analysis on several taxa that key habitats in Fennoscandian and Baltic forests contained both more species and red-listed species than production forests.

However, despite these positive qualities of key habitats and retention trees, there are still many uncertainties regarding how well these strategies supplements nature reserves in terms of species conservation (Gustafsson et al. 2010; Vatn et al. 2005). First of all, key habitats and retention patches consist of several small patches, instead of fewer but larger ones as with nature reserves. For instance, Komonen et al. (2000) found that fragmentation of old-growth forests reduced the number of levels in a food-chain from three to one. Reducing the average size of patches, but not the total area, has been argued to have potential negative effects on species richness (e.g. Diamond 1975), although the evidence is not conclusive (Tjørve 2010).

Secondly, even if a few studies already have examined how well these management categories conserve saproxylic beetles (e.g. Djupstrom et al. 2008; Sverdrup-Thygeson et al. Unpublished), it may be hard to extrapolate these results to other areas. There is a large variation in the quality and characteristics of key habitats and retention trees between countries (Gustafsson et al. 2010; Timonen et al. 2010) and production forests within a country (Gaarder et al. 2007). The mean size of key habitats varies between 0.7 ha in Finland and 4.6 ha in Sweden (Timonen et al. 2010). For retention patches in PEFC-certified forests, the number of retained trees per hectare is 10 in Norway and Sweden, but only 5 in Finland (Gustafsson et al. 2010).

The last reason for why the conservation efficiency of key habitats and retention patches is uncertain is that different taxa have different habitat preferences. For example, Gibb et al. (2006) found that fungivores had different associations with clear-cut areas than cambium consumers, when examining saproxylic beetles on Norway spruce (*Picea abies* L. Karst) logs. Similarly, saproxylic beetles and wood-decaying fungi have been shown to often have opposite relationships with dead wood at open areas or forest edges. Lindhe and Lindelow (2004) found that sun-exposure increased species density of saproxylic beetles on experimental snags of different tree species. Polypores adapted to old-growth forests, on the other hand, have been shown to be negatively associated with forest-edge conditions (Snäll & Jonsson 2001), although the responses are often complex (Siitonen et al. 2005). Consequently, effective conservation strategies covering all taxa are often not possible.

Associations have been found between fungivore beetles and fungi in numerous studies (Schigel 2011), including the common polypore *Fomitopsis pinicola* (Ratzeburg; Thunes et al. 2000). Komonen (2003) argues that polypore fruiting bodies are hotspots for insect diversity in boreal forests. Consequently, it would be interesting to see if these relationships are apparent at larger spatial scales. If that was the case, it could be useful for developing more effective management strategies.

In the present study, I have explored these issues by sampling saproxylic beetles in key habitats, retention patches and a nature reserve, in Selvik, Southern Norway. More specifically, the following research questions were asked:

1. Are retention trees and key habitats useful supplements to nature reserves in terms of saproxylic beetle conservation?
2. Is the response to key habitats, retention patches and nature reserves consistent between functional groups?
3. Can dead-wood variables and sun-exposure explain the responses of saproxylic beetles?
4. Can fungi species richness explain the response of saproxylic beetles?

2. Methods

2.1 Study area

The study was carried out within an area of about 2400 ha in a production forest in Buskerud and Vestfold, Norway. The elevation varies between 200 and 500 meters above sea level. The vegetation is mostly dominated by Norway spruce and aspen (*Populus tremula* L.), but with some deciduous forest in between. Several lakes and bogs are found in the area. The bedrock is magmatic.

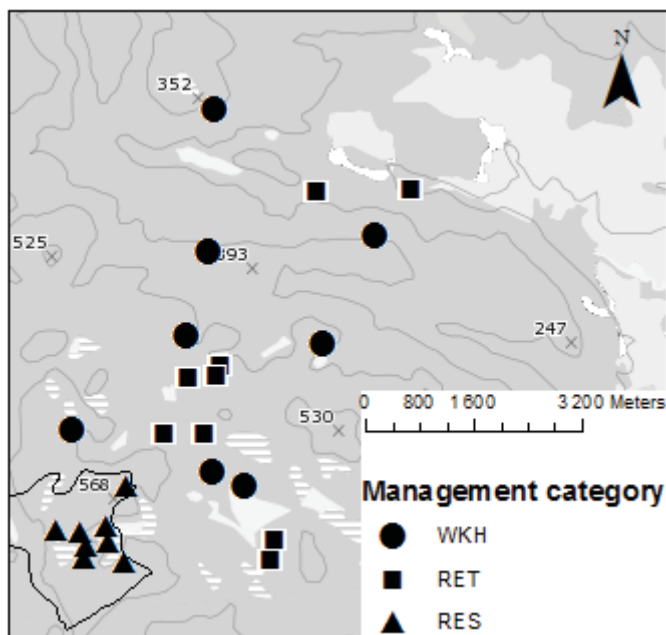


Fig. 1. Map over study area. Map symbols: x marks meters above sea level; striped fields mark bogs; light grey fields marks lakes; dark border marks Presteseter nature reserve. Abbreviations: WKH = woodland key habitats; RET = Retention patches; RES = nature reserve.

Presteseter nature reserve, which covers an area of 319.4 ha, is located at the southern edge of the study area (fig. 1). It is an old-growth high-productive spruce-dominated forest area, with a high diversity of lichen and other organisms (Forskrift om Presteseter naturreservat 2005). Buskerud county has one of the highest concentrations of red-listed species in Norway (Kålås et al. 2010).

2.2 Study design

Three management categories were compared: key habitats, retention patches and a nature reserve. Each of the management categories contained 8 study sites with 5 randomly chosen logs of spruce on which fungi had been identified.

The sites and logs were selected by Sverdrup-Thygeson et al. (Unpublished). The forests were managed by ISO 14001 standards, had a forest management plan and the PEFC Norway forest management standard. The key habitats were old spruce forest, with a considerable amount of lying or standing dead wood, had sizes between 10 and 300 da, and were located more than 200 meters from the nature reserve. The retention patches were located in a buffer-zone bordering a lake or bog, or on a clear-cutting. Additionally, the patches were surrounded by forest that was cut after year 2000. The nature reserve-sites were randomly

based on photos of the reserve. The reserve-sites were placed more than 300 meter away from each other, and more than 50 meters away from the reserve edge.

The 5 logs in each site were selected randomly by walking 10 m wide transects selecting the 5 first logs fitting the following criteria; not standing, diameters > 20 cm at breast height, minimum length of 3 meters and average decay stage between 3 to 5 (as described by Høiland and Bendiksen (1996). This signifies that least some bark has fallen off, and that at least the outer cm of the wood is soft, but that the log has not decayed to the stage where it has completely fallen apart. The logs should also have a minimum distance of 5 meters to a neighbouring study-log, and two study logs should not be connected by a third log.

2.3 Sampling

Two types of insect traps were used to increase the sampling-range of saproxylic beetle community (Wikars et al. 2005). One window trap was mounted above each study-log and two trunk window-traps were mounted at one randomly selected study-log at each site (fig. 2). Thus, one study-log at each site had both a window trap and two trunk window traps. The window traps were suspended over the middle of the log, hanging from 1-3 bamboos rods stuck in the ground. To catch beetles living in or at the log, the distance between the log and the window of the trap was never more than 40 cm. The trunk window traps were placed at 1/4th and 3/4th of the length of the selected log. The sampling period was from the beginning of June to mid-August, 2012, with one emptying of the traps at mid-July. The two sampling periods were pooled for each trap type prior to statistical analysis, as were the two trunk window traps mounted on the same log.

The window traps consists of two crossed transparent plastic plates (40 x 60 cm), mounted above a funnel with a 6 dl bottle for beetle collection (fig. 2). Drainage holes (diameter < 1 mm) for excess water were made in the top quarter of the bottle.

The trunk window traps had a transparent plastic window mounted directly on the log by iron nails (fig. 2). A plastic plate was mounted above the window to remove excess water. An open box, attached to the log by iron nails, was placed under the window. Drainage holes (diameter < 1 mm) were made near the top of the box. An inner box with an iron mesh (< 1 mm mesh size) in the bottom was used to make emptying easier.

Both window traps and trunk window traps were filled with 1 dl propylenglycol, a few drops of dish washing soap, and 0.2 dl water. The ratio between propylenglycol and water changed with rainfall. Some traps had most of the propylenglycol washed out before it was refilled, but did not seem to reduce the sample quality significantly.



Fig. 2. Example of a study-log, with two trunk window traps and one window trap.

Some traps were excluded from the analysis, as they had fallen over or were otherwise unreliable. The removal included one pair of trunk-window traps and 1 window traps in the retention patches, one pair of trunk window traps and 9 window traps in key habitats, and one window trap in the nature reserve. Thus, the number of window traps was 33, 38 and 39, while the number trunk window trap pairs were 7, 8 and 8, for key habitats, retention patches and nature reserves, respectively.

2.4 Study organism and grouping

All collected beetles were classified to species by an expert taxonomist (Sindre Ligaard). The nomenclature and systematics are based on Species Name Database drifted by Norwegian Biodiversity Information Centre (2012). The main target in my analysis were saproxylic beetles associated with spruce (hereby referred to as saproxylic beetles or species) as categorized by Dahlberg and Stokland (2004), as the beetles were caught above logs of spruce. These saproxylic beetles were further allocated to five functional groups:

- Early successional species (hereby referred to as “cambium consumers”), which prefer wood that has been dead for less than a year, according to Schmidl and Bußler (2004).

- Fungivores categorized as mycetophag, mould-eating mycetophag, or xylomycetophag by (Köhler et al. 2000).

I also split the saproxylic species into the following groups, which unfortunately had too few observations for further analysis:

- Red-listed species following (Kålås et al. 2010). Only 3 observed species with 7 individuals.
- Late successional species, which prefer wood with a stage of decay 4 or 5 following Dahlberg and Stokland (2004). Only 5 species with a total of 55 individuals.
- Species associated with white-rot fungi, following Dahlberg and Stokland (2004). Only 6 observed species with a total of 66 individuals.

In addition to beetle sampling, all logs were surveyed for fungi species, as specified by Sverdrup-Thygeson et al. (Unpublished). As most fungi species are difficult to identify in the field, each fruiting body was sampled and brought to a laboratory and identified with a microscope. As it was hard to quantify the number of individual fungi on each log, data on fungi were applied as presence/absence only.

2.5 Environmental variables

The length, diameter at breast height, sun exposure and decay-stage was measured for each study-log. The length and diameter was measured using a tape line. The sun exposure was measured by calculating basal area of trees per ha south of the log, by taking a 180° relascope count southwards. The decay stage was measured using method described by Høiland and Bendiksen (1996), where wood hardness was measured using a knife.

The volume of dead wood was estimated using the formula

$$V = \frac{1}{4}(\pi d^2 l) \quad (1)$$

where V is volume, d is diameter and l is length of the log (Fridman & Walheim 2000). The surface area of dead wood was estimated using the formula for cylinder volume:

$$S = 2\pi a(a+l) \quad (2)$$

where S is surface area, a is radius and l is length of the log. Note that both the volume and the surface area were overestimated. Firstly, the formula used to estimate volume assumed that the diameter was measured at the middle of the log, but I measured the diameter at breast height. Secondly, the formula used to estimate surface area assumed that both ends of the log had the same diameter, which was not the case. However, as I compared only relative surface area and volume, which probably was unaffected by the bias, the overestimation is unlikely to have affected my results.

Species richness (number of species) of fungi per square meter on the log (species density) was estimated. The surface area of the log was highly correlated with species richness of fungi. This is probably because when a large log is examined, the sampling effort is larger than when a small log is examined. Thus, the species richness of fungi is also a product of the size of the log, and not only actual habitat quality, i.e. the number of species per area unit (Heilmann-Clausen & Christensen 2004). The bias was adjusted for by detrending the correlation between log surface area and species richness of fungi on each log.

This was done in two steps. First, a logistic function was fitted to the trend between study-log volume and species richness of fungi:

$$y = 1.6376 \ln(x) - 1.5098 \quad (3)$$

where x is the surface area of the study-log, and y is the estimated species richness of fungi on that log. Then I subtracted the value of y estimated for a particular log from the species richness of fungi from that log. This resulted in a new estimate of fungi species richness which had no correlation with study-log surface area. This new variable was used as an estimate for fungal species density.

At each site, total dead-wood volume was measured, and the number of logs with a diameter over 30 cm at breast height (NumLargeLogs) was counted. The survey was done in a 400 m² quadrat, measured using a tape line. I ignored live trees, stumps and dead wood with a diameter at breast height < 10 cm, or length < 1 m, and any log parts outside the survey plot. The middle of the quadrat was 10 meters north of the centre of one randomly chosen study-log.

2.6 Data analysis

2.6.1 Generalized linear mixed effect model

To test what affected number of species (species richness) or number of individuals (species abundance) of the functional groups, I used a generalized linear mixed model (GLMM; using the lmer-function in the R-package lme4 (Bates et al. 2012)). All R-functions are part of the R-software (R Development Core Team 2012). The data on fungivores were overdispersed, so I used presence/absence as a response variable for this group.

I tested for differences in species richness and abundance between management categories for saproxylic beetles. The fixed effect was management category, and the three random effects were trap type, site and study-log. Study-log was nested under site, and trap-type was crossed with the nested variables (see model specification below). The model had a poisson error term, with a log link function. Z-values and p-values are only given when $p < 0.1$. The model was specified in R as

Response ~ ManagementCategory + (1 | Site / StudyLog) + (1 | TrapType).

To test which of the environmental variables that best could explain the variation in species richness, I used species richness as response variable for saproxylic beetles and cambium consumers (poisson error term, log link function) and incidence as a response variable for fungivores (binomial error term). The best subset of environmental variables was selecting by testing all combinations of fixed effects, and selecting the model with the lowest AIC (using the dredge function in R-package MuMIn (Barton 2013)). The environmental variables were NumLargeLogs, dead-wood volume, study-log volume, species density of fungi, and sun exposure. Additionally, decay stage of the study-log was included for cambium consumers, as I expected higher species richness of this group at early decay stages of the dead wood. Some environmental variables lacked observations for some logs, and then these logs were removed from these analyses. The four random effects in the models were study-log, nested under site, nested under management category, and additionally trap-type which was crossed with the nested variables (see model specification below). Furthermore, I tested if the presence/absence of *Fomitopsis pinicola* had a significant influence on the presence/absence of fungivores, where the random variables were identical to the previous test. The number of observations was not equal between all tests, as some environmental variables had missing observations at some traps, and then those traps were removed from the analysis when those environmental variables were included. The model for testing for relationship with environmental variables was specified in R as

Response ~ predictor + (1 | ManagementCategory / Site / StudyLog) + (1 | TrapType).

2.6.2 Rarefaction curves

Individual-based rarefaction curves were calculated for each functional group in each management category (using the rarc-function in the R-package rich (Rossi 2011)). Rarefaction curves are useful for evaluating how well the sampled species represented the true species richness in the area. Furthermore, they indicate if differences in species richness are caused by differences in sampled individuals or by ecological differences (Gotelli & Colwell 2011). Lastly, rarefaction curves represent total species richness, which is interesting to compare with mean species richness, as small differences in these two measures indicate low species turnover between sites (i.e. low beta diversity; see Krebs 2009). I used individual-based rarefaction curves, instead of sample-based rarefaction curves, as the number of sampled individuals varies between traps, which can be misleading. The permutations were run with replacement. I balanced the design, to make comparisons between categories more sound, by excluding traps using a random number generator. In total, four window traps and one pair of trunk window traps were excluded from retention

patches, and 6 window traps and one pair of trunk window traps were excluded from the nature reserve.

2.6.3 Differences in dead-wood volume

I tested if the average dead-wood volume differed between management categories, using ANOVA. To balance the design, three sites were excluded from the analysis randomly, using a random number generator: two from retention patches and one from the nature reserve. The data were log-transformed to attain normality. Furthermore, I verified that the variance was homogenous between categories, using a Barlett test, and that the residuals had a normal distribution.

2.6.4 Differences in sun exposure

It was tested if the sun-exposure was significantly different between management categories, using a linear mixed-effect model (using the lme-function in the R-package nlme (Pinheiro et al. 2012)). The response was sun-exposure, the predictor was management category, and site was used as a random effect. I verified that the response was normal distributed, and that residuals were independent of fitted values.

2.6.5 Permanova

To test for differences in species composition between management categories, a “Permutational Multivariate Analysis of Variance” (permanova) test was used (using the adonis-function in the R-package vegan (Oksanen et al. 2012)) on all saproxylic species associated with spruce as well as all the defined functional groups. Several pre-test adjustments were done. Firstly, the distance matrix was 4th root transformed, to increase the importance of less abundant species, without removing relative differences (Clarke 1993) page 38. Secondly, the ecological distance between traps was calculated using zero-adjusted Bray-Curtis dissimilarity. The zero-adjustment consisted of adding a dummy species to each test, which had one observation in each trap (Clarke 1993) page 44). Finally, ANOVA was used to test for multivariate homogeneity of groups dispersions (betadisper function, R-package vegan 2.0-5, (Oksanen et al. 2012). The permanova-test had management category as a predictor variable, and permutations were constrained within trap type. I had to assume that all traps were equally independent, as the adonis software did not support random effects. The assumption appeared to be valid, as I checked that traps from the same site were not clustered in a Nonmetric Multidimensional Scaling-ordination (see below for description of methodology. Results not included). A pairwise comparison of the species composition of the management categories was not done, as the permanova-test did not support this.

2.6.6 nMDS ordination

The results from the permanova tests were illustrated by plotting the results from a Nonmetric Multidimensional Scaling (nMDS) ordination test in two dimensions (using metaMDS function in R-packages vegan (Oksanen et al. 2012) and MASS (Venables & Ripley 2002)). This method was chosen because the count data were not normal distributed, and because nMDS has been used in many other studies, which makes comparisons easier (e.g. (Djupstrom et al. 2008) and (Stenbacka et al. 2010)). The pre-test adjustments and predictor variables were identical to the permanova tests, except that the data were untransformed. Spatial clustering of traps was not accounted for.

2.6.7 Simper

The relative contribution of each species to differences between management categories was tested separately on all saproxylic species associated with spruce as well as on the defined functional groups, using a similarity percentage (simper) test (using the simper-function in the R-package vegan (Oksanen et al. 2012)). As the window traps collected many more individuals than the trunk window traps, I ran the simper-test on the trap types separately for easier interpretation. The pre-test adjustments and predictor variables were identical to the permanova test.

3. Results

3.1 Species richness and abundance

The total sampling was 3955 individuals and 337 species (appendix A). Of these, 107 species (32% of total), with an abundance of 1714 individuals (43% of total) were classified as saproxylic beetles, which the rest of the study was based on. For simplicity, the term saproxylic beetles are used for this group in the rest of the thesis. Most of the saproxylic species were rare, as 40% were singletons or doubletons. In contrast, the five most abundant saproxylic species included 48 % of all individuals.

Cambium consumers were more abundant than fungivores (760 individuals against 278, respectively; appendix A). However, the species richness was similar (28 against 29, respectively). Fungivores and cambium consumers only had one species in common (*Dinaraea aequata* Erichson), with only one observation, so the two groups were considered unique to each other.

The rarefaction curves did not reach full asymptotes, showing that increased sampling effort would increase observed species richness (fig. 3). Furthermore, the rarefaction curves suggest that total species richness was lower in the nature reserve for all the functional groups, and especially for fungivores. These differences were probably not caused by differences in sampled individuals, as the rarefaction curve from the nature reserve declined faster than the other curves.

Fig. 3. Individual-based rarefaction curve for A: Spruce-associated saproxylic beetles, B: cambium consumers and C: fungivores. Cambium consumers and fungivores are sub-groups of spruce-associated saproxylic beetles. Both window traps and trunk window traps are included. 1000 randomizations. The design was balanced. Triangles = nature reserve, circles = woodland key habitats, squares = retention patches.

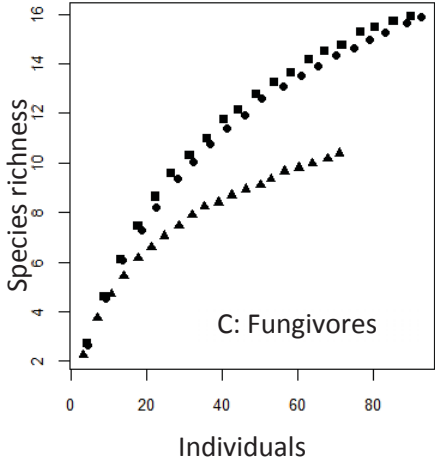
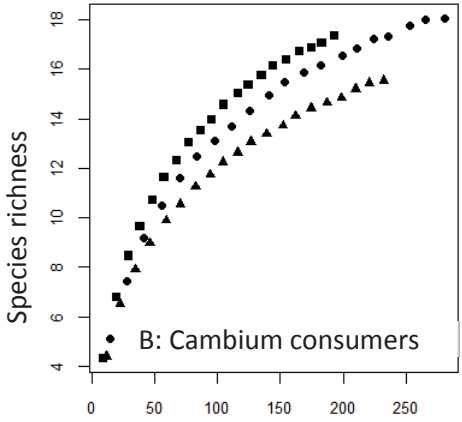
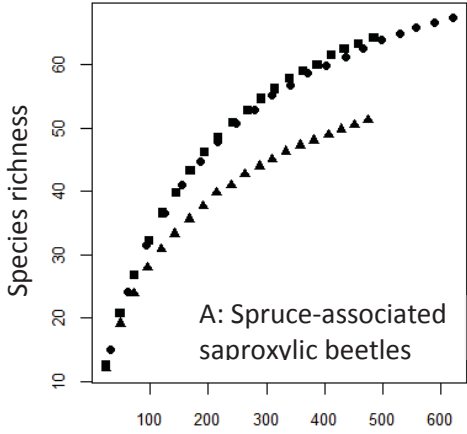


Table 1. Observed red-listed species in each management category, total number of observed individuals for each species, red-listed status, and whether the species is included in the spruce-associated saproxylic beetle group.

Species	Management category					
	WKH	RET	RES	Total	RL	SX
<i>Cacotemnus thomsoni</i> (Kraatz)	1	2	1	4	NT	Yes
<i>Atomaria subangulata</i> (Sahlberg)	0	1	0	1	NT	No
<i>Cis quadridens</i> (Mellié)	2	0	0	2	NT	Yes
<i>Corticaria polypori</i> (Sahlberg)	1	0	0	1	NT	No
<i>Amphicyllis globiformis</i> (Sahlberg)	0	1	0	1	NT	No
<i>Liodopria serricornis</i>	15	0	0	15	NT	No
<i>Mycetophagus fulvicollis</i> (Fabricius)	0	0	1	1	NT	Yes
Total individuals	19	4	2	25		
Total species	4	3	2	7		

Notes: Abbreviations: RL = red-listed status; SX = if the species was categorized as saproxylic in this study; WKH = woodland key habitats; RET = Retention patches; RES = nature reserve.

Regarding the total number of red-listed species, *Liodopria serricornis* (Gyllenhal) consisted of 19 of the 25 the observed individuals (Table 1), and was only present at woodland key habitat sites. However, this species was not classified as a saproxylic species. Apart from *L. serricornis* the differences in species richness and abundance of red-listed species were small between management categories.

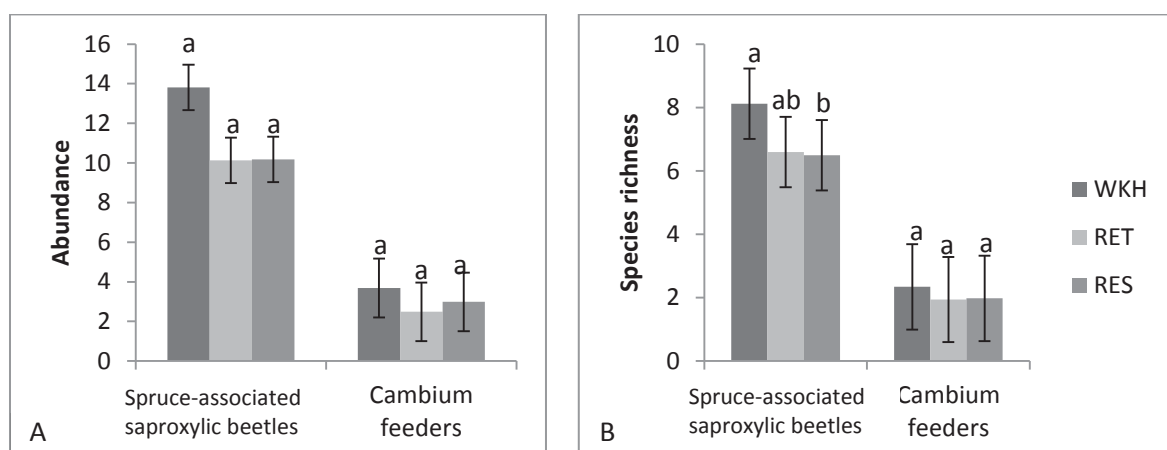


Fig. 4. Estimated mean \pm standard error (A) abundance and (B) species richness, for spruce-associated saproxylic beetles and cambium consumers in each management category. Cambium consumers are a sub-group of spruce-associated saproxylic beetles. Management categories not sharing the same letters within one functional group and one type of response are significantly different (p -value < 0.05, $n = 133$, GLMM). Abbreviations: WKH = woodland key habitats; RET = Retention patches; RES = nature reserve.

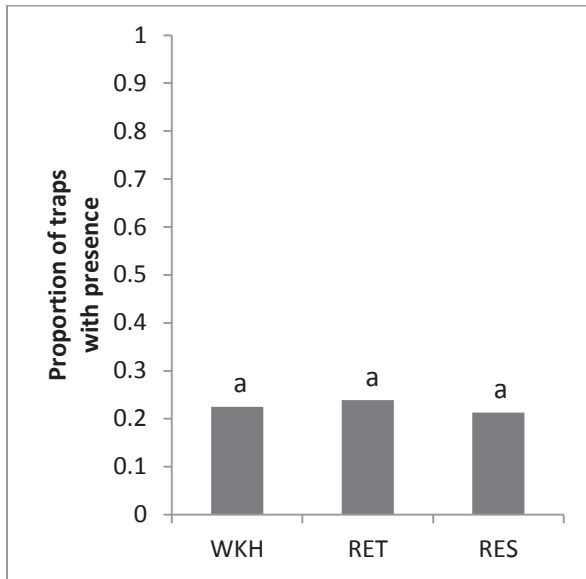


Fig. 5. Observed proportion of traps with presence of spruce-associated fungivore saproxylic beetles in different management categories. The letters signify that management categories did not differ significantly ($p > 0.6$, $n = 133$, GLMM). Abbreviations: WKH = woodland key habitats; RET = Retention patches; RES = nature reserve.

Estimated mean species richness of saproxylic beetles per trap in key habitat was significantly higher than in the nature reserve (z-value = -1.987, p-value = 0.0470) and marginally higher than in the retention patch (z-value = -1.855, p-value = 0.0637; fig. 4). There was no difference between retention patches and the nature reserve, after adjusting for random effects. Furthermore, the species richness of cambium consumers (fig. 4) and the presence/absence of fungivores (fig. 5) were similar between the management categories (p-value > 0.1).

The abundance of saproxylic beetles was marginally higher in key habitats than in the nature reserve (z-value = -1.807, p-value = 0.0708) and in the retention patches (z-value = -

1.837, p-value = 0.0662), after adjusting for random effects (fig. 4). No difference was found between retention patches and the nature reserve (p-value > 0.1), after adjusting for random effects. No significant differences in abundance for cambium consumers between categories were found (p-values > 0.1).

3.2 Relationship between environmental variables and species richness

None of the environmental variables correlated significantly with the species richness of any of the functional groups (table 2). LogsOver30 had a marginal negative correlation with species richness of saproxylic beetles, however. Presence/absence of *Fomitopsis pinicola* did not have a significant relationship with the probability of presence/absence of fungivores (table 3).

3.3 Dead-wood and sun-exposure

The mean m^3 dead-wood per ha (\pm standard deviation (SD)) was 58.35 (\pm 67.08), 127.11 (\pm 147.09) and 93.44 (\pm 39.89) for key habitat, retention patches and nature reserve respectively, but these differences were not significant (ANOVA, $p > 0.1$, $n = 21$). The mean number (\pm SD) of logs with a diameter over 30 cm per site differed similarly between the three management categories with 0.71 (\pm 1.49), 2.22 (\pm 2.68), and 2.00 (\pm 1.07), for key habitats, retention patches and the nature reserve respectively.

Table 2. Output for generalized linear models with the combination of fixed effects that gives the lowest AIC, for three groups of saproxylic beetles.

Response	Model output				
	Fixed effect factor	Estimate ± standard error	z-value	P-value	AIC
Spruce-associated saproxylic beetles ^a	Intercept	2.03 ± 0.11	18.58	<0.0001	161.3
	NumLargeLogs	-0.04 ± 0.02	-1.83	0.0670	
Cambium consumers ^b	Intercept	0.71 ± 0.29	2.49	0.0126	157.4
Fungivores ^c	Intercept	5.44 ± 1.18	4.60	<0.0001	118.9

Notes:

^a Response: Species richness. Poisson error term, with log link function.

^b Response: Species richness. Poisson error term, with log link function.

^c Response: Presence/absence. Binomial error term.

For model specification see text. No fixed effects were close to significant for cambium consumers and fungivores. A significant intercept signifies that the point of intersection is significantly larger than zero. Number of obs: 123. Critical level = $p < 0.05$. Fungivores and cambium consumers are sub-groups of spruce-associated saproxylic beetles.

Table 3. Output for a generalized linear model testing the relationship between presence/absence of *Fomitopsis pinicola* and the presence/absence of spruce-associated saproxylic fungivores on a log.

Response	Model output			
	Fixed effect factor	Estimate ± standard error	z-value	P-value
Spruce-associated saproxylic fungivores	(Intercept)	1.85 ± 0.35	5.20	<0.0001
	<i>Fomitopsis pinicola</i>	-0.73 ± 0.52	-1.41	ns.

Notes: Response was presence/absence. A significant intercept signifies that the point of intersection is significantly larger than zero. Binomial error term. $n = 123$. Critical level = $p < 0.05$

The mean estimated sun-exposure per study-log (\pm standard deviation) was 11 (± 3.55), 9.48 (± 3.69), and 10.04 (± 3.61) for key habitat, retention patches and nature reserve respectively, but these differences were not significant (mixed effect model, $p\text{-value} > 0.1$, $n=102$).

3.4 Species composition

A small but significant difference in species composition of saproxylic beetles was found between key habitats and both the nature reserve and retention patches (table 4). For the rest of the functional groups no significant differences in species composition between management categories were found. The assumption of the permanova was valid, as all functional groups had homogeneity of variance between management categories ($p\text{-values} > 0.1$).

Table 4. Results from PERMANOVA comparisons of spruce-associated saproxylic beetles, cambium consumers and fungivores in three different management categories.

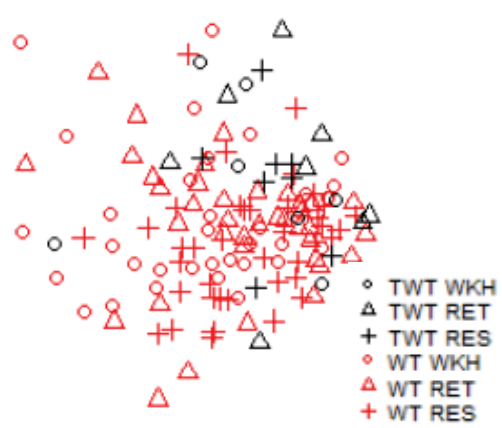
Source	D.f.	Sum of squares	Mean Square	F-value	R ²	P-value
Spruce-associated saproxylic beetles						
Management	2	1.0073	0.50365	2.1529	0.03206	0.0008
Residuals	130	30.4122	0.23394		0.96794	
Total	132	31.4195			1	
Cambium consumers						
Management	2	0.2987	0.14934	1.0162	0.01539	ns
Residuals	130	19.1044	0.14696		0.98461	
Total	132	19.4031			1	
Fungivores						
Management	1	0.2184	0.21837	1.6168	0.01888	ns
Residuals	84	11.3453	0.13506		0.98112	
Total	85	11.5637			1	

Notes: 4th root-transformed abundance data of individual species were used. 4999 randomizations, where randomizations were constrained within each of the two trap-types used for sampling. Critical level: $p < 0.05$. $n=133$.

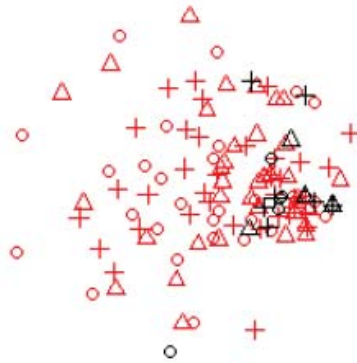
The permanova-results were supported by the nMDS ordination (fig. 6); the woodland key habitats were concentrated in the upper part of plot A whereas the other management categories were more evenly distributed. As for the fungivores, the apparent difference between the reserve and the other two categories is hampered by the low number of individuals (on average 1.36 per trap) and the lack of quantitative data. However, the 2D stress was less than 0.30 for all functional groups, indicating that there was a fair agreement between species dissimilarity and ordination distance.

The most abundant species contributed most to differences in species composition between management categories (appendix B). For the saproxylic beetles and cambium consumers these species were *Dryocoetes autographus* (Ratzeburg), *Hylastes cunicularius* (Erichson) and *Athous subfuscus* (Müller; appendix B). For fungivores, these species were mainly *Anisotoma castanea* (Herbst), *Elateroides dermestoides* (Linnaeus) and *Sepedophilus testaceus* (Fabricius).

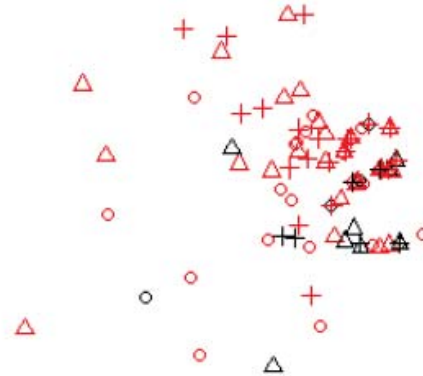
Fig. 6. Nonmetric multidimensional scaling (nMDS) scores of the species composition of A: Saproxylic beetles, B: Cambium consumers, C: Fungivores. Fungivores and cambium consumers are sub-groups of Spruce-associated saproxylic beetles. Each symbol represents one trap. Points closer together indicate more similar species compositions. Abbreviations: TWT = trunk window trap; WT = window trap; WKH = woodland key habitats; RET = Retention patches; RES = nature reserve. The figures have the same scale. The values on the X and Y axis has a range of ~2. The cluster of symbols indicate the centre of the ordination plot.



A: Saproxylic. 2D stress = 0.28



B: Cambium consumers. 2D stress = 0.22



C: Fungivores. 2D stress = 0.17

4. Discussion

4.1 Are retention patches and key habitats useful supplements to nature reserves in terms of saproxylic beetle conservation in Selvik?

The species richness of saproxylic beetles was higher in key habitats than the nature reserve, whereas the retention patches had similar species richness to the reserve. The abundance followed the pattern of the species richness, but the difference between key habitats and the reserve was only close to significant. As only spruce-associated species were included in the analysis, these patterns are unlikely to be caused by random visitors with no affinity to the collection site. Thus, the key habitats and retention patches appear to be useful supplements to the nature reserve in terms of saproxylic beetle conservation in Selvik.

Living in several small habitat patches rather than one large continuous habitat is likely to be unfavourable for a wide range of species (Diamond 1975). If the observed saproxylic beetles were negatively affected by living in the smaller and more fragmented fragments habitats or retention patches, the highest species richness would be expected in the nature reserve. As this was not the case, either the key habitats might represent some unique qualities on their own, or the species in question are not affected by fragmentation at the studied scale.

It is worth noting, however, that on a larger scale the old-growth forest in the nature reserve is also highly fragmented, as it is the only old-growth forest in the province (Forskrift om Presteseter naturreservat 2005). Thus, it is possible that many species associated with the nature reserve has already gone extinct due to fragmentation and habitat loss, and therefore the species richness in key habitat could be relatively high.

Previous studies have also failed to find higher species richness in nature reserves compared to retention patches and key habitats. Firstly, Sverdrup-Thygeson et al. (Unpublished) conducted an experiment in several Norwegian forest landscapes, of which one is the landscape of the present study, comparing beetles caught on aspen logs in nature reserves with beetles caught on similar logs in key habitats and retention patches. No overall difference between aspen-specialist species in the three management categories was found, which indicated that these species did not have problems with dispersal between forest patches. Secondly, Djupstrom et al. (2008) found no significant differences when comparing species richness of saproxylic beetles sampled on spruce logs in nature reserves with beetles sampled in key habitats or in retention patches in Sweden.

At least two important unanswered questions remain regarding the conservation effectiveness of these management categories. The first is whether the management categories are able to sustain

species populations over time. If many observed species populations have an extinction debt, i.e. will go extinct as the community reaches a new equilibrium after a disturbance (Kuussaari et al. 2009), the conservation effectiveness may be overestimated (Tilman et al. 1994). Extinction debt is considered to be a major challenge for species conservation (Kuussaari et al. 2009), although there are few studies that systematically investigate extinction debt for saproxylic beetles in boreal forests.

A second unanswered question about the value of retention patches and key habitats is whether the habitat quality remains stable over time. Retention patches has been shown to have large changes over time, as the tree-mortality is high. As trees dies, the supply of fresh dead wood declines and edge/interior ratio increases (Jönsson et al. 2007). This indicates that a steady supply of retention patches is necessary to uphold sufficient amounts of habitat created by this conservation strategy. Small key habitats may be susceptible to changes in the microclimate, e.g. due to nearby clear-cutting, but research on the persistence of the habitat over time is lacking (Timonen et al. 2011). The habitat quality of nature reserves, on the other hand, seems to increase over time after management is banned (Paillet et al. 2010).

Although number of sampled red-listed species was too low for statistical analysis, the distribution of red-listed species richness between management categories appeared to be similar to saproxylic species in general. That would support the results of similar studies examining management categories (Djupstrom et al. 2008; Sverdrup-Thygeson et al. Unpublished).

Interestingly, 15 individuals of the red-listed species *Liodopria serricornis* were observed, which is unusually high compared to other studies (i.e. Ødegaard et al. 2009). Furthermore, the observations were exclusively in key habitats, at four different sites, indicating that it is strongly associated with this type of habitat. Although it was not defined as saproxylic in my study, it is believed to be associated with slime moulds on dead wood and with old-growth forests (Ehnström & Waldén 1986). This indicates that key habitats in Selvik have some dead-wood qualities not found in the other management categories. It would be interesting to see how this species reacts to the management strategies in other areas.

Whether the results of my study can be extrapolated to other managed forests with similar conservation strategies is unknown. As previously mentioned, large variations in the characteristics of key habitats and retention patches exists both within (Gaarder et al. 2007) and between countries (Gustafsson et al. 2010; Timonen et al. 2010). Sverdrup-Thygeson et al. (Unpublished) found that the

species richness in my study area was significantly higher than two other managed forests in southern Norway. This indicates that my results should be extrapolated with caution.

4.2 Is the response to key habitats, retention patches and nature reserves consistent between functional groups?

No significant differences in species richness or abundance of cambium consumers or fungivores were found between management categories. Cambium consumers have been shown to prefer clear-cut areas over mature and old forests (Johansson et al. 2007). Fungivores, on the other hand, have been shown to be negatively associated with both fragmentation (Rukke 2000) and clear-cut areas (Gibb et al. 2006). Sverdrup-Thygeson et al. (Unpublished) found that study sites in retention patches were closer to open areas than study sites in key habitats and in nature reserves. Some of the sites were the same as in the present study. Thus, I had expected cambium consumers to be associated with retention patches, and fungivores to be associated with key habitats and the nature reserve. Instead, my results indicate that the management categories do not present large differences in habitat quality for these functional groups. However, the potential negative effects already mentioned for saproxylic beetles in general, such as extinction debt and habitat fragmentation, should also be considered for the conservation fungivores and cambium consumers.

It is unclear, however, whether other functional groups of saproxylic beetles will respond similarly to the management categories as the groups examined in this study. I found no studies that had compared the response of different groups to nature reserves, key habitats and retention patches. However, differences in the response of different functional groups to different forest types have been found for saproxylic beetles (Gibb et al. 2006). This indicates that the results from cambium consumers and fungivores in the present study should be extrapolated with caution to other functional groups.

Although no significant difference in presence/absence of fungivores was found between management categories, the total observed species richness of this group was lower in the nature reserve (not statistically tested). In other words, the fungivore species turnover between sites was lower in the nature reserve, compared to that in the key habitats and retention patches. Assuming that this pattern was not coincidental, it indicates that the inter-site habitat variation was lower in the nature reserve. This was probably due to the shorter distances between the sites in the nature reserve relative to the sites in the other two management categories. Thus, the number of shared species is likely to be higher, as it usually decreases as distance increases (i.e. Nekola & White 1999).

4.2.1 Differences in species composition

I found significant differences in species composition of saproxylic beetles between the management categories, but not for fungivores and cambium consumers. Although I was unable to test which pairs of management categories were significantly different, the differences were nevertheless small. Other studies have found similar effect sizes as my study, when examining differences in saproxylic beetle species composition between management categories (Djupstrom et al. 2008), and between thinned, mature and old-growth forests (Stenbacka et al. 2010). However, Johansson et al. (2006) found few differences in species composition between mature and old-growth forests, including for cambium consumers and fungivores.

It was surprising that the differences were not larger, as the different management categories are known to have important differences in structure and habitat types. Firstly, sun exposure has been shown to affect the species composition of saproxylic beetles, as some species are shade-tolerant while others prefer exposed areas (Hjalten et al. 2012; Lindhe et al. 2005) or recently disturbed areas (Martikainen 2001). Although the sun-exposure was not significantly different between management categories at the site level, retention patches are likely to have stronger edge-effects than key habitats and nature reserves. This will probably lead to more sun-exposed dead wood in retention patches, which could affect the species composition.

Secondly, key habitats are selected systematically, based on stand-level structural features and individual habitat elements (Timonen et al. 2010). It is likely that this will result in some unique habitat elements seldom found in the other management categories.

Lastly, the nature reserve is located in an old-growth forest, compared to key habitats and retention patches which are located mostly in production forests. Old-growth forests have been shown to support different a species composition of saproxylic beetles than production forests (Martikainen et al. 2000; Stenbacka et al. 2010).

Beetles are often found in other areas than where they reproduce and feed, due to random migration (Woiwod et al. 2001). This will reduce the apparent response to the environment, depending on the migration rate, migration distance and on which spatial scale the patterns were examined on. For instance, a Timonen et al. (2011) found by doing a meta-analysis that sessile organisms like fungi, plants and lichen responded more strongly to key habitats compared to production forests than saproxylic beetles.

It has been shown that many beetles probably are able to disperse between habitat patches in Selvik. Firstly, Jacobsen (2013) showed that the species richness of saproxylic beetles in my study

area was correlated with dead-wood volume within 2 km radius of the insect sampling sites, indicating that the insects travel between habitats on this spatial scale. Secondly, Jonsson and Nordlander (2006) tested how distance to an old-growth forest affected the colonization rate of fungivore beetles on fruiting bodies of *Fomitopsis pinicola*. No negative effect from distance up to 1610 meters was shown for most, but not all, of the species. Thirdly, Ranius et al. (2011) found that some aspen specialists were able to disperse several hundred meters. Lastly, Jonsell et al. (1999) found that most of the studied fungivores were likely to be able to survive if habitat was continually available on a one km scale. To conclude, a relatively high dispersal rate between patches is likely to have reduced the apparent difference in species composition of saproxylic beetles in Selvik.

However, some species might have low dispersal abilities, and may be negatively affected by fragmentation of patches. This was not tested in my study, but is important to remember in relation to species conservation. For instance, Thomas (2000) found that butterflies in England with low dispersal abilities had higher rate of population decline than those with high dispersal abilities. Furthermore, some saproxylic beetles appears to avoid open areas, indicating that not only distance between fragments is important, but also the landscape type of the matrix (Jonsell et al. 1999).

Regarding the simpser-test, abundance of the species seemed to have a larger influence on contribution to Bray-Curtis dissimilarity than differences in abundance between management categories. The species that scored highest on the simpser-test were the most abundant overall, and had little difference in abundance between management categories. For saproxylic beetles and for cambium consumers, these species were *Dryocoetes autographus* and *Hylastes cunicularius* and for fungivores these species were *Anisotoma castanea* and *Elateroides dermestoides*. *D. autographus* and *H. cunicularius* both prefer early decayed dead wood (Dahlberg & Stokland 2004). The abundance of *D. autographus* has been shown to be strongly affected by the amount of old-growth forests within 1-3 km (Olsson et al. 2012). Thus, that beetles with these preferences are generally most abundant indicates that Selvik in general is relatively suitable for beetles associated with less decayed dead wood and old-growth forests.

4.3 Can dead-wood variables and sun-exposure explain the responses of saproxylic beetles?

None of the environmental variables could explain the variation in species richness of saproxylic beetles or of the defined functional groups. This indicates that these variables do not have an important influence on the species richness of these groups on the spatial and temporal scale used. Although individual log volume, dead-wood volume and decay stage of dead wood, as well as sun-exposure, has shown to be important for many saproxylic beetles, not all studies find significant

relationships. Regarding individual log volume, my results agree with Jonsell et al. (2004), which found weak or no effect from log diameter. However, other studies have found that diameter is important for many species (Grove 2002; Lindhe et al. 2005). Similarly, dead wood volume has been shown to be important for saproxylic organisms. Martikainen et al. (2000) found a strong correlation between dead-wood abundance and species richness of saproxylic beetles, while Djupstrom et al. (2008) did not.

An important cause for these disparities is that the apparent strength of these relationships depends on which spatial scales they are examined on. The insects sampled in the window traps most likely reflected variations in the environment on a larger spatial scale than the environmental variables. Økland et al. (1996) showed that the correlation between saproxylic beetles and for example dead wood volumes became much stronger when they increased the spatial scale of observation. Thus, I might have observed stronger responses if the environmental variables had been measured at a larger spatial scale.

However, I had expected a stronger response from environmental variables measured at the substrate level on the sampling in the trunk-window traps. One possible explanation is that the variation in the environmental variables was too small to observe a significant response. I had, for example, expected a significant response from cambium consumers on decay stage of the log. However, cambium consumers were selected by association with logs in the earlier stages of decay, while most of the study-logs had medium to late stages of decay. Similarly, the study-logs had a minimum diameter of 20 cm. As the relationship between dead-wood volume and species richness of saproxylic beetles has been shown to be logarithmic (Martikainen et al. 2000), the relationship is likely to get weaker when dead-wood volume exceed certain amounts. To conclude, I would expect a stronger response if there was a larger variation in stages of decay and volume of the study-logs.

It should be mentioned that although the dead-wood survey plots in the present study had similar sizes as in other studies (e.g. Djupstrom et al. 2008), the distance between the survey plot and some of the study-logs was sometimes relatively large. The results might have been different if the distances were smaller, or if more survey-plots were used. However, the relationship did not get stronger if I only tested on the logs closest to the survey plot (results not included).

Lastly, that I found no relationship between sun-exposure and species richness of saproxylic beetles is supported by (Hjalten et al. 2012). One possible explanation is that some saproxylic beetles prefer sun-exposed areas, and others prefer shaded areas (Lindhe et al. 2005). Thus, the net effect of sun-exposure on species richness may be cancelled out by different groups reacting opposite to each

other. This implies that responses in species composition should be larger than differences in species richness.

4.4 Can fungal species richness explain the response of saproxylic beetles?

No significant correlation was found between species density of fungi and species richness of fungivores, cambium consumers or saproxylic beetles in general. Furthermore, presence/absence of *Fomitopsis pinicola* had no significant correlation with presence/absence of fungivores. These results indicate that the association between saproxylic beetles and fungi is weak at the investigated temporal and spatial scale.

These results were not surprising, as at least three other studies have found similar results. Firstly, Similä et al. (2006) found no significant correlation between fungi and saproxylic beetles, and the hot-spots of these two taxa did not overlap. Secondly, Johansson et al. (2007) found that logs inoculated with *F. pinicola* did not have a significant effect on fungivore saproxylic beetles, or any other tested functional beetle-group, compared to control logs. Thirdly, Olsson et al. (2012) found no significant effect on species richness of saproxylic beetles from baiting insect traps with wood containing *F. pinicola*.

A correlation between species richness of fungi and saproxylic beetles has been found in some studies (Jonsson & Jonsell 1999; Økland et al. 1996). As dead wood volume has been shown to be a significant predictor for saproxylic beetle richness (Martikainen et al. 2000; Økland et al. 1996), the correlation between fungi and beetles in Økland et al. (1996) and Jonsson and Jonsell (1999) might have been caused by a common correlation with dead wood volume. My assertion is supported by the fact that when Økland et al. (1996) included dead-wood volume in the site as a covariate, the correlation was insignificant.

A possible explanation for the lack of correlation could be that the number of fungus species with a visible fruiting body often correlates badly with the actual number of fungus species in the log (Rajala et al. 2012). This indicates that only fungivore beetles that are associated with the fruiting bodies of fungi should be expected to show a correlation in this study. Thus, it is possible that the correlation would be stronger if I selected fungivores only based on association with fruiting-bodies, instead of the current method.

A second possible explanation for the lack of correlation between saproxylic beetles and fungi could be differences in the ecological characteristics of the two study-organisms. Fungi are sessile, and species richness has been quantified by counting the fruiting bodies. A fruiting body present at a log shows that the fungus has been able to finish several steps of the life cycle on the substrate, which

indicates that the substrate is suitable for that species. Beetles, on the other hand, have been sampled at a motile life stage. Therefore, the presence of a beetle species on a substrate might have been a less precise indicator of habitat quality than for fungi, as the beetle may have no affinity to the habitat (“random visitor”). Consequently, I might have gotten different results if I had used sampling methods that reduce the number of random visitors, such as bark sieving or emergence traps (Jonsson et al. 2005; Wikars et al. 2005).

4.5 Conclusion

To conclude, I would recommend continued use of key habitats and retention patches as supplements to the nature reserve, in terms of conserving saproxylic beetles in Selvik. These management categories had relatively high species richness for spruce-associated saproxylic beetles, and most likely other positive characteristics not found in the nature reserve. However, it is uncertain how well these results can be extrapolated to other areas, or how these patterns change over time, which would be interesting to research further.

The dead-wood parameters, sun-exposure and fungi species richness were unable to explain the variation in species richness of the beetles, but are most likely important at different spatial and temporal scales than those examined in my study. Furthermore, examining other types of responses to these environmental variables, such as species composition, could reveal patterns not found in this study.

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Appendix A

Mean species richness and abundance \pm standard deviation (SD) for four different groups of beetles, sampled with two types of insect traps, in three types of management categories.

Trap type	Mng. cat.	All beetles		Spruce-associated saproxylic beetles		Cambium consumers		Fungivores	
		Mean Species richness \pm SD	Mean abundance \pm SD	Mean Species richness \pm SD	Mean abundance \pm SD	Mean Species richness \pm SD	Mean abundance \pm SD	Mean Species richness \pm SD	Mean abundance \pm SD
WT+TWT	Total	17.95 \pm 7.49	29.74 \pm 19.48	7.49 \pm 3.14	12.89 \pm 7.46	2.77 \pm 1.81	5.71 \pm 5.80	1.36 \pm 1.10	2.09 \pm 2.07
WT	Total	16.70 \pm 6.52	26.01 \pm 13.21	7.75 \pm 3.14	13.45 \pm 7.62	3.05 \pm 1.78	6.43 \pm 5.99	1.35 \pm 1.06	2.04 \pm 2.04
WT	WKH	18.76 \pm 6.67	30.39 \pm 14.37	8.91 \pm 3.01	16.42 \pm 7.64	3.33 \pm 1.99	7.70 \pm 6.50	1.39 \pm 1.00	2.18 \pm 2.21
WT	RET	16.37 \pm 6.45	25.87 \pm 13.18	7.45 \pm 3.49	12.45 \pm 7.77	2.97 \pm 1.67	5.53 \pm 5.53	1.39 \pm 1.22	2.08 \pm 2.12
WT	RES	15.28 \pm 6.18	22.44 \pm 11.30	7.05 \pm 2.65	11.90 \pm 6.90	2.87 \pm 1.72	6.23 \pm 5.96	1.26 \pm 0.97	1.87 \pm 1.82
TWT	Total	23.91 \pm 8.97	47.57 \pm 31.79	6.26 \pm 2.88	10.22 \pm 6.06	1.43 \pm 1.27	2.30 \pm 3.02	1.43 \pm 1.27	2.35 \pm 2.27
TWT	WKH	25.00 \pm 5.20	42.71 \pm 13.24	7.43 \pm 3.74	11.29 \pm 8.64	2.14 \pm 1.35	3.71 \pm 4.27	1.71 \pm 1.80	3.00 \pm 2.77
TWT	RET	19.75 \pm 10.11	37.13 \pm 26.49	5.13 \pm 2.70	9.50 \pm 6.28	0.75 \pm 1.16	1.38 \pm 2.77	1.25 \pm 1.04	2.38 \pm 2.50
TWT	RES	27.13 \pm 9.73	62.25 \pm 43.93	6.38 \pm 2.00	10.00 \pm 3.21	1.50 \pm 1.07	2.00 \pm 1.51	1.38 \pm 1.06	1.75 \pm 1.58

Cambium consumers and fungivores are sub-groups of spruce-associated saproxylic beetles.

Abbreviations: WT = Window traps; TWT = Trunk window traps; Mng. Cat. = management category; WKH = woodland key habitats; RET = Retention patches; RES = Nature reserve. The number of WT and TWT is 110 and 23, respectively.

Appendix B

Similarity percentage tests showing the top five species that contributed most to differences in species composition to each pair of management categories. Tested separately for three groups of beetles, and for two trap types.

Functional Group	Trap type	Mng. cat.	Species	Contribution to dissimilarity	Standard deviation of contribution	Ratio between contribution and st. dev.	Average abundance in A	Average abundance in B	Cumulative Sum of contribution
Spruce-associated saproxylic beetles	WT	WKH vs RET	<i>Dryocoetes autographus</i>	0.04	0.03	1.16	0.97	0.83	0.06
			<i>Athous subfuscus</i>	0.03	0.03	1.04	0.78	0.89	0.11
			<i>Hylastes cunicularius</i>	0.03	0.03	1.06	0.66	0.65	0.15
			<i>Epuraea pygmaea</i> (Gyllenhal)	0.03	0.03	0.96	0.55	0.34	0.20
			<i>Podistra schoenherri</i> (Dejean)	0.03	0.03	0.91	0.27	0.51	0.24
	WT	WKH vs RES	<i>Dryocoetes autographus</i>	0.04	0.04	1.12	0.97	0.81	0.06
			<i>Athous subfuscus</i>	0.03	0.03	1.13	0.78	0.45	0.11
			<i>Hylastes cunicularius</i>	0.03	0.03	1.10	0.66	0.66	0.16
			<i>Podistra schoenherri</i>	0.03	0.03	1.05	0.27	0.64	0.21
			<i>Epuraea pygmaea</i>	0.03	0.03	0.98	0.55	0.42	0.26
WT	RET vs RES	<i>Dryocoetes autographus</i>	0.04	0.04	1.13	0.83	0.81	0.06	
		<i>Athous subfuscus</i>	0.04	0.04	1.18	0.89	0.45	0.13	
		<i>Podistra schoenherri</i>	0.04	0.04	1.03	0.51	0.64	0.18	
		<i>Hylastes cunicularius</i>	0.04	0.04	1.06	0.65	0.66	0.24	
		<i>Elateroides dermestoides</i>	0.03	0.03	0.91	0.36	0.45	0.29	
Spruce-associated saproxylic beetles	TWT	WKH vs RET	<i>Hylastes cunicularius</i>	0.06	0.04	1.52	0.95	0.13	0.08
			<i>Podistra schoenherri</i>	0.04	0.04	1.00	0.46	0.67	0.15

Salpingus ruficollis
(Linnaeus)

WT	RET vs RES	0.04	0.06	0.68	0.25	0.22	0.63
	<i>Dryocoetes autographus</i>	0.09	0.08	1.09	0.83	0.81	0.18
	<i>Hylastes cunicularius</i>	0.08	0.08	1.02	0.65	0.66	0.33
	<i>Elateroides dermestoides</i>	0.06	0.07	0.89	0.36	0.45	0.46
	<i>Epuraea pygmaea</i>	0.06	0.07	0.87	0.34	0.42	0.58
	<i>Salpingus ruficollis</i>	0.04	0.06	0.59	0.14	0.22	0.65

TWT WKH vs RET

Cambium consumers	TWT	WKH vs RET	0.17	0.11	1.60	0.95	0.13	0.36
<i>Hylastes cunicularius</i>			0.17	0.11	1.60	0.95	0.13	0.36
<i>Dryocoetes autographus</i>			0.11	0.10	1.09	0.60	0.19	0.60
<i>Hyllobius pinastri</i> (Gyllenhal)			0.04	0.08	0.54	0.22	0.15	0.69
<i>Epuraea pygmaea</i>			0.04	0.08	0.52	0.14	0.13	0.78
<i>Rhizophagus dispar</i> (Paykull)			0.04	0.08	0.53	0.14	0.13	0.86

TWT WKH vs RES

	TWT	WKH vs RES	0.12	0.11	1.12	0.95	0.59	0.28
<i>Hylastes cunicularius</i>			0.12	0.11	1.12	0.95	0.59	0.28
<i>Dryocoetes autographus</i>			0.10	0.10	0.97	0.60	0.38	0.50
<i>Hyllobius pinastri</i>			0.03	0.07	0.40	0.22	0.00	0.57
<i>Epuraea pygmaea</i>			0.03	0.07	0.40	0.14	0.00	0.63
<i>Polygraphus poligraphus</i> (Linnaeus)			0.02	0.06	0.40	0.14	0.00	0.68

TWT RET vs RES

	TWT	RET vs RES	0.12	0.13	0.96	0.13	0.59	0.29
<i>Hylastes cunicularius</i>			0.12	0.13	0.96	0.13	0.59	0.29
<i>Dryocoetes autographus</i>			0.10	0.12	0.82	0.19	0.38	0.51
<i>Elateroides dermestoides</i>			0.05	0.09	0.51	0.13	0.13	0.62
<i>Hyllobius piceus</i> (Degeer)			0.03	0.07	0.37	0.00	0.13	0.68
<i>Ischnoglossa prolixa</i> (Gravenhorst)			0.03	0.07	0.37	0.00	0.13	0.74

Functional Group	Trap	Mng. cat.	Species	Contribution	Standard	Ratio	Average	Average	Cumulative
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type		to	deviation of	between	abundance	abundance	Sum of		
		dissimilarity	contribution	contribution	in A	in B	contribution		
				and st. dev.					
Fungivores	WT	WKH vs RET	<i>Anisotoma castanea</i>	0.11	0.12	0.89	0.43	0.32	0.22
			<i>Elateroides dermestoides</i>	0.09	0.11	0.80	0.25	0.36	0.41
			<i>Curtimorda maculosa</i> (Naezen)	0.04	0.08	0.44	0.07	0.13	0.49
			<i>Scaphisoma agaricinum</i> (Linnaeus)	0.03	0.08	0.38	0.12	0.05	0.55
			<i>Micrambe abietis</i> (Paykull)	0.03	0.07	0.41	0.06	0.12	0.61
Fungivores	WT	WKH vs RES	<i>Anisotoma castanea</i>	0.11	0.12	0.89	0.43	0.29	0.23
			<i>Elateroides dermestoides</i>	0.10	0.12	0.87	0.25	0.45	0.46
			<i>Hallomenus binotatus</i> (Quensel)	0.04	0.08	0.51	0.12	0.14	0.55
			<i>Micrambe abietis</i>	0.04	0.08	0.50	0.06	0.18	0.64
			<i>Scaphisoma agaricinum</i>	0.04	0.08	0.45	0.12	0.10	0.72
Fungivores	WT	RET vs RES	<i>Elateroides dermestoides</i>	0.11	0.12	0.92	0.36	0.45	0.24
			<i>Anisotoma castanea</i>	0.10	0.12	0.79	0.32	0.29	0.45
			<i>Micrambe abietis</i>	0.05	0.09	0.55	0.12	0.18	0.56
			<i>Scaphisoma agaricinum</i>	0.03	0.07	0.39	0.05	0.10	0.62
			<i>Hallomenus binotatus</i>	0.03	0.07	0.39	0.03	0.14	0.68
Fungivores	TWT	WKH vs RET	<i>Anisotoma castanea</i>	0.11	0.14	0.79	0.57	0.00	0.21
			<i>Sepedophilus testaceus</i>	0.06	0.10	0.63	0.14	0.25	0.33
			<i>Gyrophaena boleti</i>	0.04	0.09	0.50	0.14	0.18	0.41
			<i>Curtimorda maculosa</i>	0.04	0.11	0.36	0.00	0.20	0.49
			<i>Cis dentatus</i> (Mellié)	0.04	0.08	0.53	0.14	0.13	0.56
Fungivores	TWT	WKH vs RES	<i>Anisotoma castanea</i>	0.13	0.14	0.98	0.57	0.56	0.28
			<i>Sepedophilus testaceus</i>	0.04	0.08	0.53	0.14	0.13	0.37

<i>Scaphisoma agaricinum</i>	0.04	0.07	0.55	0.00	0.25	0.46
<i>Elateroides dermestoides</i>	0.03	0.08	0.35	0.00	0.13	0.52
<i>Corticaria rubripes</i> (Mannerheim)	0.03	0.08	0.35	0.00	0.13	0.58
<i>Anisotoma castanea</i>	0.10	0.11	0.95	0.00	0.56	0.20
<i>Sepedophilus testaceus</i>	0.06	0.10	0.63	0.25	0.13	0.33
<i>Scaphisoma agaricinum</i>	0.05	0.08	0.66	0.13	0.25	0.43
<i>Elateroides dermestoides</i>	0.05	0.10	0.50	0.13	0.13	0.53
<i>Curtimorda maculosa</i>	0.04	0.12	0.37	0.20	0.00	0.61

Notes: Based on 4th root transformed data. Therefore, raise the specified average abundance to the power of 4 to get the actual mean abundance. Fungivores and cambium consumers are sub-groups of Spruce-associated saproxylic beetles. Abbreviations: WT = Window traps; TWT = Trunk window traps; Mng. Cat. = management category; WKH = woodland key habitats; RET = Retention patches; RES = Nature reserve. n = 133.