The importance of Ecoparks for saproxylic beetles

– A study on general ecological hypotheses in differently managed landscapes

Albin Larsson Ekström

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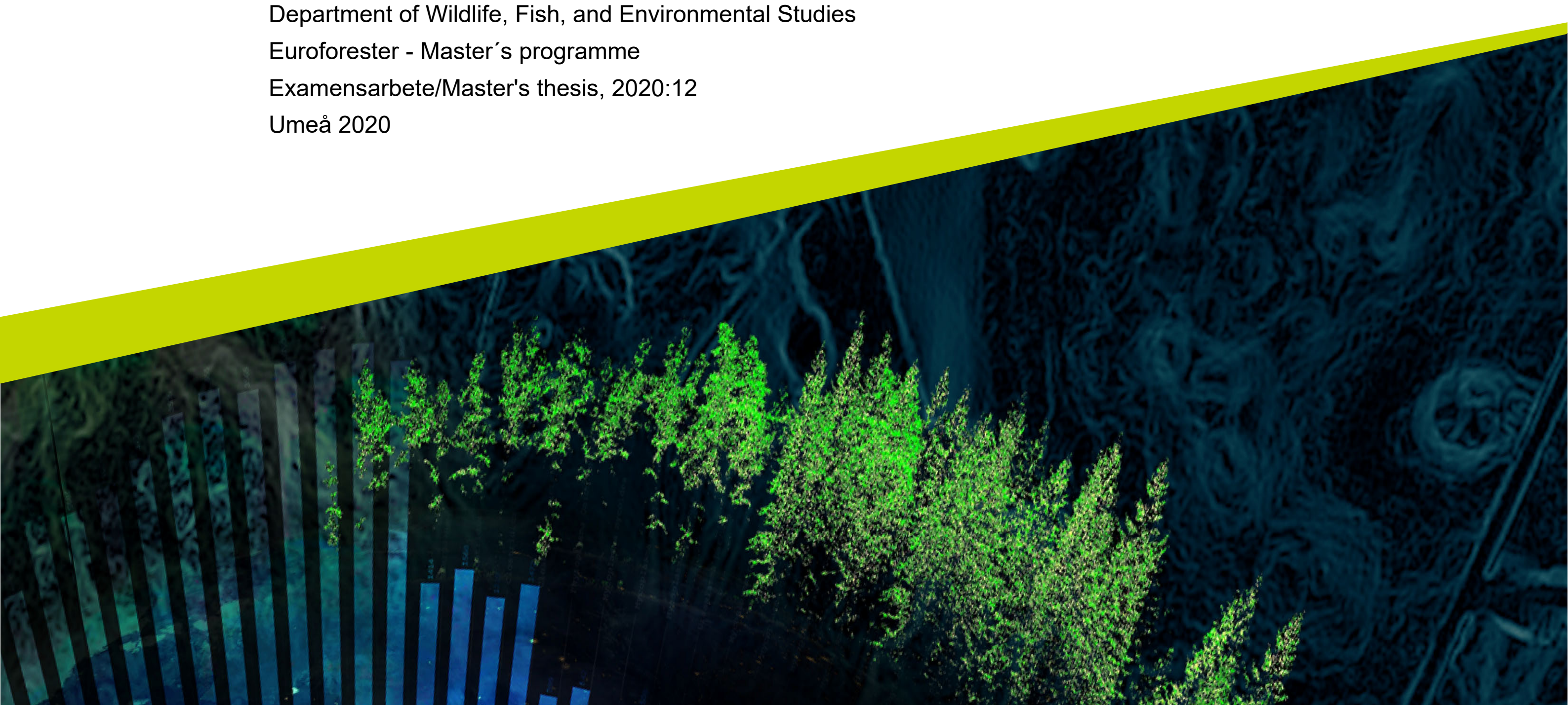

The importance of Ecoparks for saproxylic beetles – A study on general ecological hypotheses in differently managed landscapes

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Abstract

Current forestry practices have led to a decline of deadwood availability in Swedish forests. Even though deadwood has increased somewhat in Swedish forests in later years, it is still far from estimated deadwood threshold levels and of those found in natural systems. This has in turn led to a decline in species associated with deadwood e.g. saproxylic beetles, which will be the focus group of this study. In order to halt this development, it is essential to study how different landscape management systems might influence saproxylic beetles. It is also of great importance to understand the major drivers of biodiversity, such as habitat amount or habitat heterogeneity. Ecoparks are Sveaskog's landscape parks with a majority of the forest land being of conservation concern. Two of Sveaskog's Ecoparks, one in northern and one in southern Sweden were the selected sites of this study, representing a multi-purpose driven forest landscape. Ecoparks are landscape-scale forest parks where at least 50% of the forest land is exempt from forestry measures. Reference sites where chosen to represent conventionally managed landscapes, but with similar properties as respective Ecoparks. Beetles were collected during 3 years in sun-exposed plots, where local (20m radius) habitat structure data was collected as well. Ecoparks held larger abundance and richness of red-listed beetles, but not of all saproxylic (deadwood dependent) beetles, compared to reference sites. Ecoparks contained different beetle community assemblages from reference sites. Deadwood amount had a positive relationship with the abundance of saproxylic beetles, as well as richness of facultative saproxylics in southern Sweden. Abundance of red-listed beetles also showed positive relationship with deadwood amount in southern Sweden. Deadwood diversity showed no conclusive effect other than being important for southern Sweden beetle community assemblages. Deadwood amount showed negative relationships to abundance within Ecoparks, compared to reference sites. Results show that more diverse and complex landscapes host different saproxylic community assemblages and larger amounts of red-listed beetles. This study supports the habitat amount hypothesis but not the habitat heterogeneity hypothesis. There are also indications that landscape complexity might influence local deadwood responses, giving support to the landscape intermediate-complexity hypothesis. The results suggest that deadwood amount, in conventionally managed landscapes, should be increased at local levels. In more diverse landscapes, maintaining diversity and habitat size should be the main focus.

Keywords: deadwood, saproxylic beetles, habitat amount hypothesis, habitat heterogeneity hypothesis, landscape ecology, landscape intermediate complexity hypothesis

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1. Introduction

Degradation, fragmentation and loss of habitats as a result of human impact has led to species going extinct or being threatened, and are some of the greatest threats to biodiversity (Wilcox & Murphy 1985, Wilson 1989, Tilman et al 1994, Wilcove et al 1998, Harrison & Bruna 1999, Convention on Biological Diversity 2010, Haddad et al 2015). Lack of deadwood, caused by current forestry practices, promoting even-aged monocultures that are felled at lower ages and bereft of natural disturbances such as fire has in turn led to a decline in species bound to deadwood (Zackrisson 1977, Zackrisson & Östlund 1991, Niklasson & Granström 2000, Sandström et al 2015, Seibold et al 2015). In result, 30 and 50 percent of species present in the Finnish and Swedish red-list, respectively, are forest-dwelling (ArtDatabanken 2015, Hyvärinen et al 2019).

Although there has been a slight increase in national deadwood volumes from the middle of the 90's from 6.1 m3 per hectare to 8.3 m3 per hectare today (Jonsson et al 2016, Forest statistics 2018), it is still far from levels found in natural boreal forests, ranging from 50-120 m3/ha (Siitonen 2001, Rouvinen et al 2002). It is estimated that levels of 20-50 m3/ha are required to support the majority of forest-dwelling taxa (Müller & Bütler 2010).

Beetles are one of the organism groups with the highest number of species (Gaston 1991). Many of these are saproxylic, which means that they are deadwood dependent during part of their lifecycle (Speight 1989), whether they are facultative or obligate saproxylics (Dahlberg & Stokland 2004).

Saproxylic beetles play a vital part in ecosystem functioning through tree decomposition and nutrient cycling (Harmon et al 1986, Grove 2002). Their abundance, richness and species composition in boreal forests vary with the amount and diversity of deadwood (Jonsell et al 1998, Martikainen et al 2000, Siitonen 2001, Hjältén et al 2007, Lassauce et al 2011, Hjältén et al 2012, Gao et al 2015, Seibold et al 2016).

There are several theories regarding the major drivers and influencers of biodiversity, which is essential to understand in order to make the right decisions in terms of conservation and restoration.

Island theory (MacArthur & Wilson 1963, 1967) has been a cornerstone in ecological research alongside with patch size and isolation theories. The general theory is that with larger patch sizes, abundance and in that, richness, increases.

This has been challenged by Fahrig, stating that the patch size theory is mainly driven by sample size and introducing the habitat amount hypothesis (HAH), which suggests that the abundance increases with amounts of habitat, regardless of the patch size (Fahrig 2013). Although HAH cannot fully disprove island theory, HAH has still proven to be a useful baseline in ecological studies (Seibold et al 2017, Martin 2018). Another hypothesis, the habitat heterogeneity hypothesis (HHH) states that with increased habitat heterogeneity, species richness increases (Whittaker 1972, González-Megías et al 2011, Seibold 2016, Hamm & Drossel 2017).

In more recent years, the surrounding landscape has gained more attention in ecological studies, proving to be influential on forest biodiversity (Edman 2008, Rubene et al 2015, Hallinger et al 2018). Extensive harvesting in the landscape can have negative effects on species communities (Ranlund & Viktorsson 2018) by homogenizing the forest landscapes and decreasing the amount of mature forests and volumes of decaying wood. At the same time, harvesting creates sun-exposed landscapes that can be beneficial for early successional, open-habitat or disturbance favoured beetles (Koivula et al 2002, Lindhe et al 2005, Selonen et al 2005, Gibb et al 2006). Restoration measures in the stand scale can have positive effects on insect communities (Hekkala et al 2014, Hägglund et al 2015, Hjälten et al 2017), but the success of restoration measures might be affected by the structure and complexity of the landscape, according to e.g. the intermediate-landscape-complexity hypothesis (Tscharntke et al 2005, Kouki et al 2012, Tscharntke et al 2012).

Although beetles are a well-studied group, together with their habitat associations, investigating general ecological hypotheses together with the effect of the surrounding landscape is not as well-studied (Tscharntke et al 2012, Seibold et al 2015, Hekkala & Roberge 2018). Sveaskog, the Swedish state-owned forest company, have created so called Ecoparks in order to maintain a multifunctional forest landscape. Ecoparks ('ECO' from hereon) consist of at least 50 percent set-aside forests for conservation and restoration, where the remaining forests are being managed with more conventional methods (Angelstam & Bergman 2004). At the same time, Business as usual landscapes ('BAU') are mainly used for production with only general consideration of valuable habitats.

This paper will use the HAH and HHH as the leading stones, to investigate the main drivers of abundance, richness and species communities of saproxylic beetles. These hypotheses will be tested in two Ecoparks and their reference sites, as well as for the entire landscape, to see if the landscape structure have an influence on these hypotheses. This study is a part of a long-term project to evaluate the effects of Sveaskog's Ecoparks on biodiversity.

The aims of this study were to determine whether or not (I) ECO-parks hold higher species richness and abundance of saproxylic, facultative and obligatory, and red-listed beetles than their respective reference BAU-sites, (II) species richness and abundance of facultative and obligatory saproxylic as well as red-listed beetles increase with increasing deadwood diversity (HHH), (III) species richness and abundance of facultative and obligatory saproxylic and red-listed beetles increase with increasing volumes of deadwood (HAH), and (IV) ECO-parks contain different beetle community assemblages than BAU-sites determined by local substrate factors (deadwood).

2. Materials & Methods

2.1. Study areas & sites

This study is part of a long-term project with the aim to investigate the effects of landscape scale management on biodiversity, running from 2009-2033, called Effekt 20. The study was conducted in two Ecoparks and two commercially managed reference landscapes in Sweden.

Reference sites were chosen for their likeness to their respective ECO and where conventional forestry methods are carried out, so called business as usual (BAU) sites. In northern Sweden, Ecopark Käringberget with its reference site Vindeln in the central boreal zone (Ahti et al 1968) was chosen as study sites. Ecopark Hornsö with reference site Hälleskog in the hemiboreal zone (Ahti et al 1968) was chosen for the study site in southern Sweden (Figure 1). Detailed maps of each site can be found in Appendix 1, figures 2-5.

Ecopark Hornsö was established in 2004 due to its importance to insect communities and to preserve and restore habitats in the area. It is mainly dominated by Scots pine (*Pinus sylvestris L.)* with pedunculate oak (*Quercus robur L.)* and beech (*Fagus sylvatica L.)* occurring frequently as well. Up until the 1900's, fire was a frequent disturbance in this landscape, which has greatly affected the state of this landscape (Sveaskog 2008).

Ecopark Käringberget was established in 2005, also having a long tradition of fires. It is dominated by Scots pine but also Norway Spruce (*Picea abies L. H.Karst)* with some elements of birch (*Betula pendula Roth., Betula pubescens Ehrh.)* and aspen (*Populus tremula L.).* The Ecoparks are structurally different or hold significant natural values compared to the surrounding landscape, and even if much of the set-aside areas are trivial today, restoration measures are being taken to further increase their natural values in the long term (Sveaskog 2005).

Both Ecoparks have similar distributions of forests of conservation concern and production forests, with a majority of conservation forests being restoration sites, whereas BAU-sites are dominated by production forest sites (Table 1). Both Ecoparks have greater proportions of forests in higher age classes than their respective reference (BAU) sites (Figure 6). Production forests refer to forests that have active forestry activity, conservation concern refers to all productive forest land exempted from forestry. Within conservation concern there are three further classifications: Restoration, where measures are being taken to restore natural values or structures; Set-aside, areas that are voluntarily set-aside from forestry; and Protected, areas that are legally protected from exploitation.

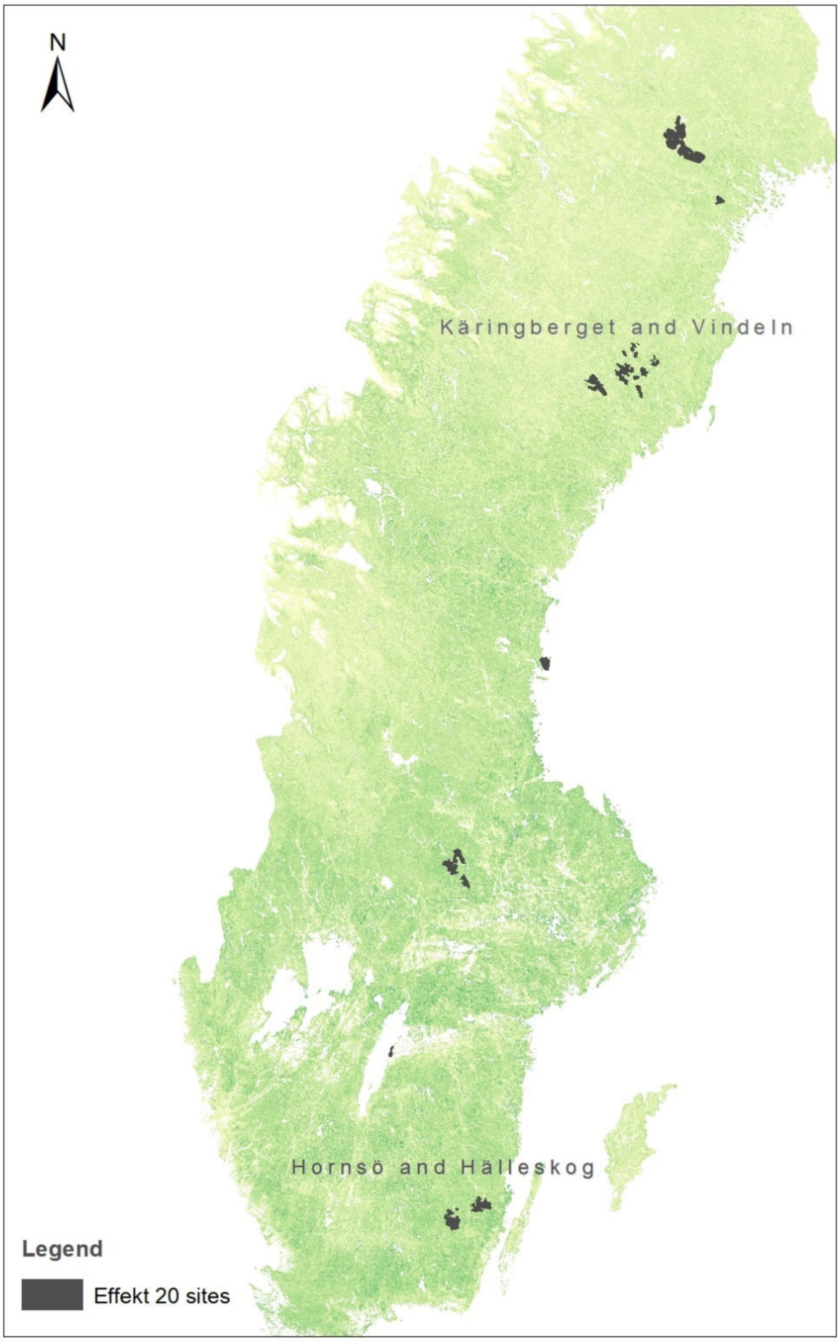

Figure 1. Location of study sites within the "Effekt 20" project. Study sites highlighted with grey markings. Sites used in this study highlighted with names.

Table 1. Location, area distribution and dominating vegetation for each study site. The size includes all land, productive and non-productive. Other areal distribution information is productive forest land. Percentages of restoration, set-aside and protected areas are calculated from the total of conservation concern areas. BAU=Business as usual. ECO=Ecopark.

Area	Northern Sweden		Southern Sweden	
Treatment	ECO	BAU	ECO	BAU
Site	Käringberget	Vindeln	Hornsö	Hälleskog
Coordinates	64° 04' N; 18° 41' E	64° 03' N; 18° 43' E	57° 00' N; 16° 09' E	56° 50' N; 15° 39' E
Mean annual temperature	2.5 C°	2.5 C°	7.8 C°	7.8 C°
Mean annual precipitation	705mm	705mm	513 mm	513 mm
Size (ha)	13963	21181	9242	9144
Production	5786 (54%)	20066 (95%)	4438 (53%)	8570 (94%)
Conservation concern	4989 (46%)	1115 (5%)	4014 (47%)	574 (6%)
-Restoration	2817 (26%)	18 (0%)	3227 (38%)	124 (1%)
-Set-aside	1615 (15%)	331 (2%)	485 (6%)	381 (4%)
-Protected	557 (5%)	766 (4%)	302 (4%)	69 (1%)
Dominating vegetation	VT(38%), MT(27%)	VT(46%), MT(27%)	CT(38%), MT(35%)	CT(46%), MT(12%)

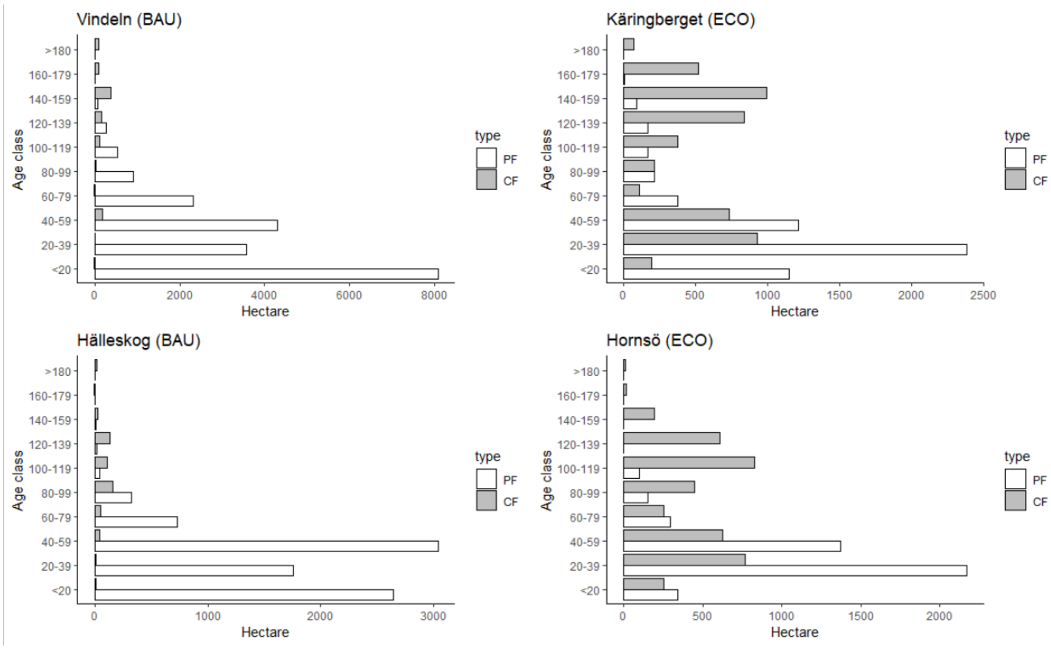

Figure 6. Production and nature forest area per age class for different sites. PF = Production forests. CF = Conservation forests. Mind the different axis-scales.

2.2. Sampling design

In each landscape, 26 plots were chosen with at least 1 km between each plot, to diminish spatial correlation of insect trappings (See Appendix 1, Figures 2-5). Each plot was chosen for its exposure to the south and west. In more closed plots, in order to open up the canopy, trees were removed to expose the plot to the sun in these directions. Plots were also chosen for their representativity of the site and accessibility from roads. In each plot, high stumps were created in pairs in 2010 for northern Sweden and 2011 for southern Sweden. Each pair of high stumps consisted of pine and birch, but in some cases pine and pine or birch and birch were chosen. The height of each high stump was 2.5 meters, diameter 14-42 cm, and they were placed with ca 1-5 meter apart from each other.

2.3. Insect sampling and classification

Insects were sampled with two trunk-attached window traps per high stump (Kaila 1993). The window traps consisted of a 10 x 20 cm, 2 mm thick, transparent plexiglass sheet that was attached to the trunk of each high stump, with a 0.5-litre aluminium mould to capture insects. Propylene glycol diluted to ca 60 percent with a small amount of detergent was used as preserving liquid in the traps. The traps were placed on 1.1 and 1.6 meters from the ground, facing south. The traps were set at the end of May and removed at the end of July. The traps were emptied twice each sampling season for 3 consecutive years, 2010-2012 in northern and 2011-2013 in southern Sweden. Insects were then identified to species or genera level, separate for each high stump. The main purpose of species identification was to identify saproxylic beetles with high conservation value, thus some known non-saproxylics were not identified at all. Precision of species identification was higher in northern than southern Sweden where some families such as Staphylinidae were not fully identified, and bark beetles were identified to genera-level (Appendix 2). Thus, the species counts in northern and southern study areas are not comparable, while within the area, comparisons between BAU and ECO are valid.

Mean temperatures during the months (June-August) of beetle collection was 13.6 C° in N Sweden and 16.2 C° in S Sweden (Swedish Meteorological and Hydrological Institute 2019).

2.4. Field measurements

Measurements on tree stand structure were carried out in circular sample plots (20 m radius) in 2019. The centre of each plot was placed between the two high stumps and the sample plots' borders were measured using an ultra-sound distance measuring device.

Living tree diameters at breast height(1.3m, DBH) were recorded for each tree with a DBH >4.5 cm and a height of >1.3m as well as their respective tree species. *B. pendula* and *pubescens* were both measured and classified as birch, and *Q.robur and Q. petraea (Matt., Liebl.)* as oak.

In order to measure canopy closure/gap, hemispherical photos were taken using a fish-eye lens. These photos were then processed in ImageJ (Schneider et al 2012) using the plugin Hemispherical 2.0 (Beckschäfer 2015) to obtain values for canopy closure/gap.

The species, DBH, height and decay class were recorded for standing dead trees and snags. For lying dead trees, also the top (to minimum value 4.5 cm) and bottom diameters were recorded for trees over 4.5 cm in diameter and at least 1.3 m in length. Type of substrate was also recorded, whether it was a standing dead tree, snag or lying deadwood log.

Four decay classes were used to describe the decomposition stage of deadwood logs, adjusted from Gibb et al 2005: (1) Hard wood with intact bark >50%, (2) Hard wood with smooth surface beginning to soften, <50% bark remaining, (3) crevices and holes, soft wood surface, free of bark, (4) soft wood, possibly with a hard core remaining, hard to define surface and outline. The broadleaves in later decay stages were classified according to decay classes (3) and (4), disregarding the percentage cover of bark. Standing trees and snags were classified according to Jung et al 1999 and Parker & Thomas et al 1979. Field vegetation was classified using Cajander's vegetation classification (Cajander 1926). The dominating vegetation type was chosen, in cases where the vegetation type was shifting, the two most dominating types were chosen.

2.5. Calculations

Both living trees and all deadwood were divided into 10 cm diameter classes, starting from 4,5 cm up to >50cm, totalling in six different diameter classes. Basal area and deadwood volumes were calculated to per hectare values for each plot. Living tree and deadwood diversity index was calculated, modified by Siitonen et al 2000 and Hekkala et al 2016. Living tree diversity was calculated as different combinations of tree species and diameter class for each plot. Deadwood diversity was calculated similarly as for living trees with tree species, diameter class adding deadwood type or decay class for deadwood. Deadwood diversity would then be the number of different combinations of species, size and decay class for each plot. Volumes of intact standing dead trees (classes 3-5, Parker & Thomas 1979) was calculated based on diameter and height. Brandel's functions for pine, spruce and birch for Northern and Southern Sweden were used (Brandel 1990). Birch functions were used for all broadleaves >6m (Brandel 1990). Volumes of logs, snags and high stumps were calculated as cylinders based on diameter and height/length. Broadleaves <6 m were calculated as cylinders using DBH. See formulas used for calculations in appendix 3. Red-listed beetles were classified according to 2010's red list (Gärdenfors 2010).

Classification of facultative and obligate saproxylics was made using a datafile with compiled data on saproxylic classification (Hjältén unpublished), based on literature and expert opinions (Appendix 2).

2.6. Analysis

All insect trappings were pooled for each plot (four traps per plot), divided by site and year. Only plots with pine and birch stump-pairs were used, resulting in 22-24 pairs used per landscape. Species richness and abundance for all red-listed, all saproxylic, obligate and facultative beetles was calculated. R version 3.5.1 was used for all analysis (R core team 2018).

Linear models (LM) were used to test differences in tree stand structures between Ecoparks and reference sites. GLM (generalised linear model) and GLMER (generalized linear mixed effect model) using the lme4-package (Bates et al 2014) with Poisson distribution were used to explore relationships and differences in species richness and abundance between deadwood volume (HAH) and diversity (HHH) as well as between Ecoparks and their reference sites. ECO or BAU is henceforth referred to as treatment. GLMER was used to test treatment and deadwood effects on saproxylics, using year as a random factor to account for repeated measures. When testing treatment and deadwood effects for red-listed beetles, GLM was used for each year of collected insect data separately, to ensure model convergence.

Using the bblme package (Bolker 2017), Akaike Information Criterion (AIC) was compared between models from the same dataset. Models with ΔAIC ranging between 0-2 were considered the best models.

Deadwood volumes were log-transformed prior to testing. Separate models were made for each saproxylic classification, facultative and obligate.

Beetle community assemblages were visualized by Non-metric multidimensional scaling (NMDS) using the vegan package, and then analysed with Permutational Multivariate Analysis of Variance Using Distance Matrices, Adonis (Oksanen et al 2007), using year as stratified variable (Species ~ Treatment, strata=Year. Permutations = 1000).Northern and southern study areas were analysed separately. Environmental (deadwood amount and diversity) vectors were fitted to the NMDS plots (Oksanen et al 2017).

In order to test hypothesis (I) treatment (ECO or BAU) was used as fixed effects. To test hypothesis (II), treatment*deadwood diversity and/or treatment+deadwood diversity. Hypothesis (III), treatment*deadwood amount and/or treatment+deadwood amount. To test hypothesis (IV), NMDS was used to illustrate the community assemblages and Adonis was used to test the differences in assemblages.

3. Results

In total, 43263 individuals of 230 saproxylic beetle species and 214 individuals of 23 red-listed beetle species were found in northern Sweden. In southern Sweden, respective numbers were 11067 individuals of 120 saproxylic beetle species and 423 individuals of 42 red-listed beetle species. *Hylastes brunneus* was the most numerous species in northern Sweden, making up 18% of individuals, followed by *Trypodendron lineatum* (15%) and *Rhizophagus ferrugineus* (7%). *Enicmus rugosus* made up (18%), *Ampedus balteatus* (9%) and *Hylobius abietis* (5%) in southern Sweden (Appendix 2).The mean richness and abundance of all saproxylic species decreased over years in northern Sweden and increased in southern Sweden (Figure 7). Mean values of species richness and abundance of saproxylic beetles between years of insect trappings can be found in Figure 3, of red-listed beetles in Figure 8. Deadwood volume and diversity were greater in Ecoparks in both northern and southern study areas, in the south also living tree diversity and basal area were greater in the Ecopark in comparison to BAU (Table 2).

Table 2. Stand structure data. Mean±SE for stand structures. p-value results from LM models provided under "p-value". Numbers highlighted as bold hold significance, p <0.05. BAU=Business as usual. ECO=Ecopark.

	Southern Sweden		**p**	**Northern Sweden**		**p**
Treatment	BAU	ECO		BAU	ECO	
Site	Hälleskog	Hornsö		Vindeln	Käringberget	
Basal area (m2/ha)	9.4±0.5	14.6±0.7	**0.001**	10±0.8	12.7±0.6	0.05
Living tree diversity	8.3±0.3	12.2±0.4	**<0.001**	7.6±0.4	9±0.3	0.1
Deadwood volume (m3/ha)	4.4±0.2	9.3±0.6	**0.02**	6.6±0.6	11.6±1.7	**0.047**
Deadwood diversity	7±0.3	9.5±0.5	**0.02**	7.6±0.5	12.2±0,8	**0.004**
Gap fraction	27±0.01	37±0.02	**0.001**	40±0.02	38±0.01	0.5

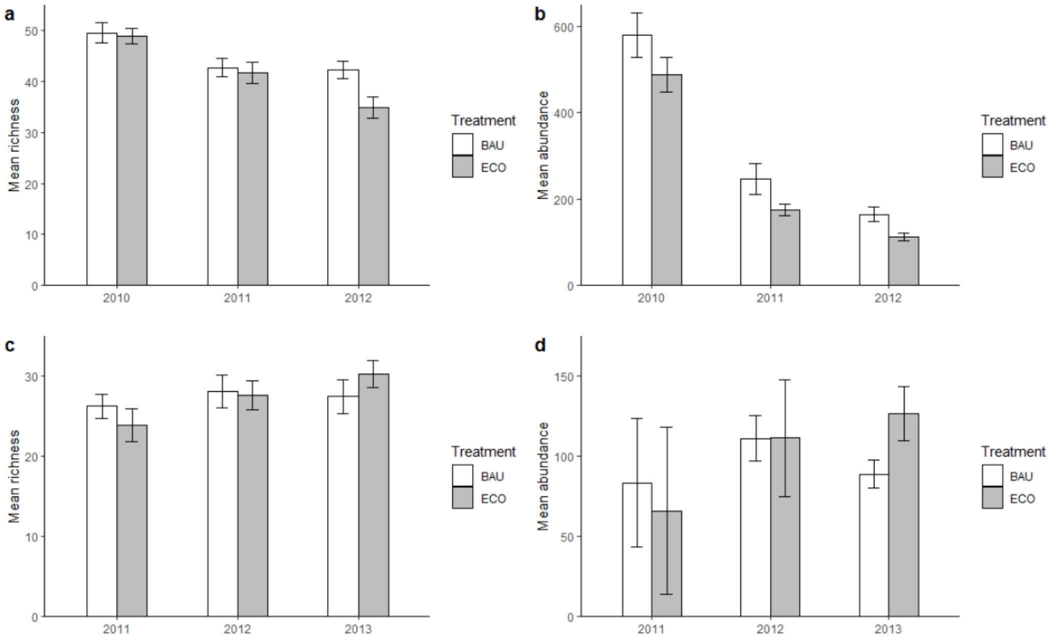

Figure 7. Mean richness and abundance of saproxylic beetles per treatment between different years. a = Mean richness in northern Sweden. b = Mean abundance in northern Sweden. c = Mean richness in southern Sweden. d = Mean abundance in southern Sweden. Whiskers show ±SE.

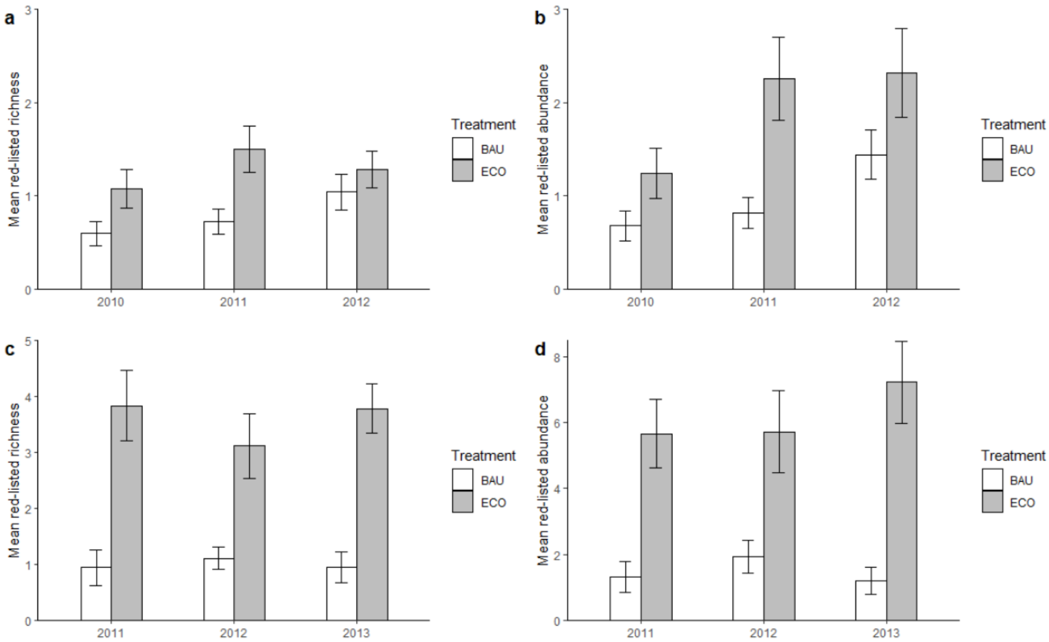

Figure 8. Mean richness and abundance of red-listed beetles per treatment between years. a = Mean richness in northern Sweden. b = Mean abundance in northern Sweden. c = Mean richness in southern Sweden. d = Mean abundance in southern Sweden. Whiskers show ±SE.

3.1. Hypothesis

In northern Sweden, both richness and abundance of all saproxylic beetles were lower in the Ecopark in comparison to BAU (Figure 9 a). In southern Sweden, richness of facultative beetles was higher in the Ecopark, while richness and abundance of obligates was lower (Figure 9 b). Richness and abundance of red-listed beetles was generally higher in the Ecopark in northern Sweden (Figure 10 a). Southern Sweden Ecopark also held higher richness and abundance of red-listed species (Figure 10 b).

3.2. Hypothesis II (HHH)

The abundance of obligate saproxylics was positively related to deadwood diversity within the north Sweden Ecopark (Figure 9 a). Deadwood diversity had low or no relationship with beetle communities in the northern Swedish landscape, BAU and ECO combined (Figure 9 a). Deadwood diversity had negative relationships with richness and abundance of red-listed beetles during the first year of trappings in northern Sweden (Figure 10 a). Within the northern Sweden Ecopark, deadwood diversity had a negative relationship to abundance of red-listed species only in the last year of trappings (Figure 10 a).

3.3. Hypothesis III (HAH)

The abundance of facultative saproxylics was negatively related to deadwood volume in the north Sweden Ecopark (Figure 9 a).
Facultative species richness and obligate richness and abundance had a positive relationship to deadwood volume in the southern Swedish landscape, BAU and ECO combined (Figure 9 b).
In the southern Swedish Ecopark, richness in year one and abundance in years one and two had negative relationships with deadwood volume (Figure 10 b). Deadwood volume show positive relationship with richness in year one, and abundance all years in the southern Swedish landscape, ECO and BAU combined (Figure 10 b). More model results can be found in Appendix 4, tables 3 and 4.

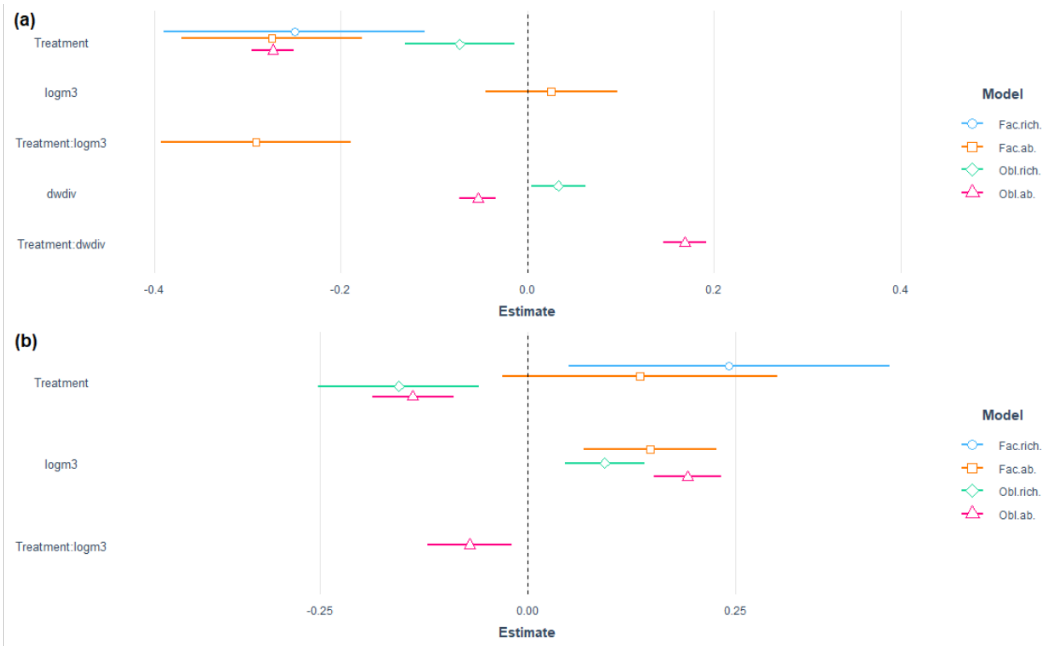

*Figure 9. GLMER results for saproxylic beetles. For significance, estimate+SE bar must not cross the 0.0 line. The further away from 0, the larger effect. Model formulas: x=y~(Treatment*logm3/dwdiv, Treatment+logm3/dwdiv, Treatment+(1|Year), Poisson. Only the best performing model results for each response variable are shown (see Supplementary table 4 in Appendix 3 for all models). (a) = northern Sweden. (b) = southern Sweden. Mind the different axis scales.*

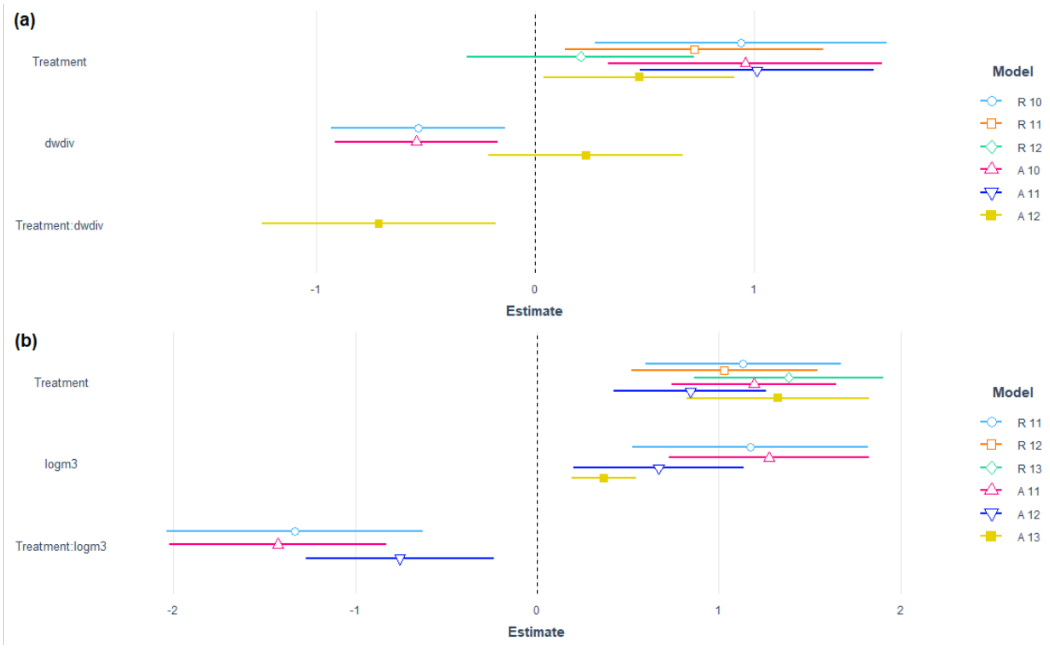

*Figure 10. GLM results for red-listed beetles separate for each year of beetle trappings. For significance, estimate+SE bar must be higher or lower than 0.0. The further away from 0, the larger effect. GLM = x=y~(Treatment*logm3/dwdiv, Treatment+logm3/dwdiv, Treatment), Poisson. (a) = northern Sweden. (b) = southern Sweden. R = richness. A = abundance. Mind the different axis scales.*

3.4. Hypothesis IV

The beetle assemblages differed between Eco and BAU both in the northern Sweden, (Adonis: F=3.09, p=0.001, Figure 11 a), and southern Sweden (Adonis: F = 7.4, p=0.001, Figure 11 b). Community assemblages differed between all years in northern Sweden (Figure 11 a). In southern Sweden, assemblages differed most during the first year, then becoming more similar in the following 2 years, 2012, 2013, although maintaining differences between Ecopark and BAU (Figure 11 b). Deadwood volume (p=0.03, R=0.478), deadwood diversity (p=0.005, R=0.0707) and year (p=<0.001) had significant linear correlation with beetle assemblages in southern Sweden. Deadwood had no correlation with assemblages in northern Sweden.

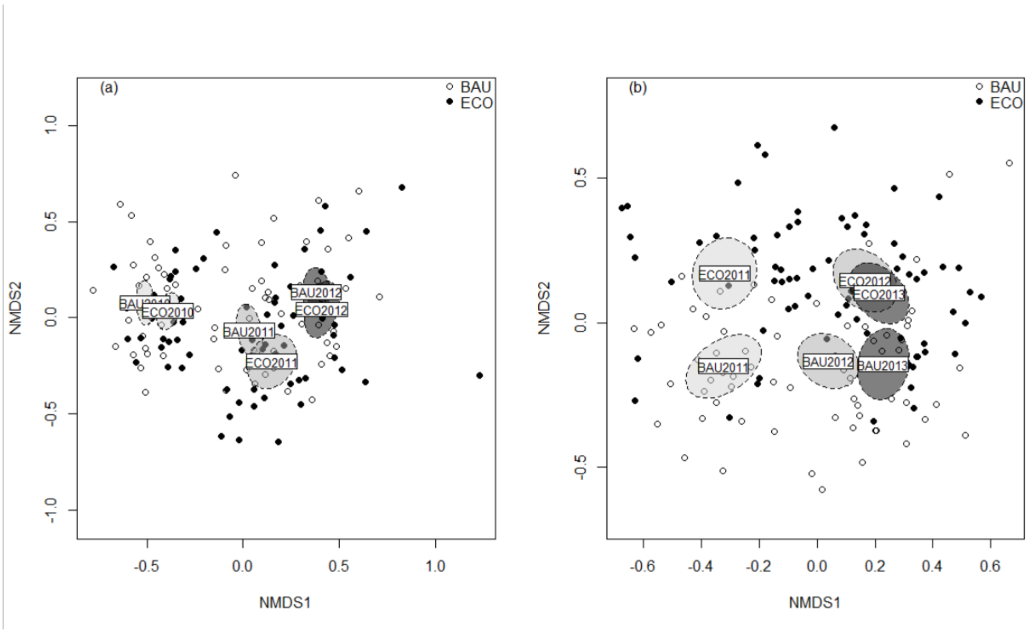

Figure 11. NMDS plot visualizing differences in beetle community assemblages between treatments and years in (a) northern Sweden, stress = 0.19 and (b) southern Sweden, stress = 0.20. Ellipsoids visualize the centroids of treatments and years with standard error, conf = 0.95. Mind differences in axis numbers.

4. Discussion

4.1. General findings

The key finding of this study were that Ecoparks held higher richness and abundance of red-listed beetles, but no conclusive differences in saproxylic beetles. This study did not find results neither supporting nor rejecting that deadwood diversity would increase species richness. Ecoparks, in some cases, presented negative relations to deadwood, compared to BAU-sites.
Deadwood amount had a positive effect on both saproxylic and red-listed beetles, mainly abundances.
Ecoparks contained different assemblages than BAU, most evident in southern Sweden.

4.2. Ecoparks importance for beetles

Both Ecoparks and reference sites (BAU) showed variations in both local stand structures as well as in species richness and abundance. Both Ecoparks held higher richness and abundance of red-listed beetles. However, the southern Swedish Ecopark held only higher richness of facultative saproxylics, while northern Swedish Ecopark being lower on all saproxylics. This could be due to the large proportion of restoration sites (Table 1), and that not enough time has passed since restoration measures to really see the effects, since there can be a time-lag between restoration measures and noticeable effects, a so called colonization credit (Watts 2020). It could also be the case, that restoration measures being carried out do not achieve the goal of increasing general diversity of saproxylic beetles, but only favours red-listed beetles.
Both Ecoparks does, however, hold differing assemblages of saproxylic beetles from their respective BAU-site, which indicate that Ecoparks might house species assemblages that are not found to the same extent in the managed landscape. Although forestry activities are being performed within the Ecoparks, there are still large areas that are exempted from forestry.

The results showing that Ecoparks, in this regard representing larger, landscape conservation areas, house more red-listed species and greater abundance, goes in line with other studies showing that the landscape composition is important for threatened species and the general species richness (Ranius & Fahrig 2006, Hallinger et al 2018, Ranius et al 2019). In our measurements, Ecoparks contained larger amount and diversity of deadwood than reference BAU-sites, as well as more forests of conservation concern, and older forests. This in combination with the differing saproxylic communities and higher red-listed beetle abundance and richness, shows the importance of large, landscape-scale conservation measures, and the maintenance of more natural structures in the landscape.

In some cases, relationships between beetle species richness or abundance and deadwood amount or diversity showed either no effect or slightly negative effects. The intermediate landscape-complexity hypothesis, mainly with support from agricultural landscapes (Tscharnke et al 2012) suggests that the complexity of the landscape dictates the effectiveness of conservation and restoration work. In complex landscapes with more than 20% non-crop areas, local conservation work would have a lower effect due to the overall high biodiversity in the landscape. In intermediate complex landscapes however (1-20% non-crop), local conservation work would have a large effect, due to the overall lack of complexity or biodiversity.

If Ecoparks represent the complex landscape, with at least 50% forests exempt from forestry, in this example, equivalent of non-crop, then reference (BAU) sites represent intermediate complexity, with their 5-6% forests exempted from forestry. This could explain why we may see negative (or no) relationships between local deadwood and richness and abundances in Ecoparks, and why there are some positive relationships in the reference (BAU) sites. This would be in line with the intermediate landscape-complexity hypothesis which, although originating from agricultural systems, have had some support in forest system (Pardini et al 2010, Mori et al 2017). Rubene et al 2017 also highlights that the landscape composition affects outcome of conservation. However, in contrast to this study's results, Rubene's study indicates that increased deadwood amount increases richness in landscapes already rich on deadwood. Landscape complexity could also explain why differences in community assemblages and red-listed species richness and abundance between Ecoparks and BAU is greater in southern Sweden than in northern Sweden, and why deadwood have shown relationships to the community assemblages there and not in northern Sweden. Northern Sweden generally have larger amounts of deadwood in the landscape (Fridman & Walheim 2000). The reason that measured structural differences between Ecoparks and BAU are lesser in northern Sweden, could be that, although the northern Sweden Ecopark does

differ from BAU and other surrounding landscapes, it does not differ as drastically as in southern Sweden.
Southern and central Sweden have a long history of extensive land-use and change, where natural forests containing broadleaves, large and old trees have been converted into dense, coniferous forests of young ages and short rotations (Esseen et al 1997, Björse & Bradshaw 1998, Linder & Östlund 1998, Axelsson & Östlund 2001, Lindbladh et al 2014) This conversion from natural to managed systems is true for other systems than forests as well (Cousins et al 2007). This has led to fragmented remnants of species confined to small unmanaged patches, indicating extinction debts (Dahlström et al 2006, Nilsson & Franzén 2006, Bommarco et al 2014). Although there are indications of extinction debts in northern Sweden as well (Berglund & Jonsson 2005, 2008), this might not have taken as much of an effect yet as in southern Sweden, thus explaining the differences in results in southern and northern Sweden. E.g. the larger contrast in red-listed beetles in southern Sweden between Ecopark and BAU, also indicating an extinction debt in the southern Swedish Ecopark.
As discussed further down, these Ecopark landscapes have not been Ecoparks for very long. And enough time might not have gone by to develop more natural or semi-natural structures. The effects of landscape might increase over time (Jonsell et al 2019, Gran & Götmark 2019), which might very well be the case with these Ecoparks as well.

4.3. Deadwood diversity

The hypothesis that the abundance and richness of beetles increases with increasing deadwood diversity was only partially supported by this study. The abundance of obligate saproxylics was positively affected by deadwood diversity. Richness and abundance of red-listed beetles in northern Sweden had a negative relationship with deadwood diversity during the first year, and the abundance in Ecopark in the third year. As these results differ quite a bit between obligatory, facultative and red-listed species, no general conclusion can be drawn on deadwood diversity and its impact on saproxylic beetles in this study. One explanation to these inconclusive results could be that because the sites history of forestry, which is still carried out at different intensities, not enough deadwood diversity has developed, to impact beetle communities.
There are several studies that have shown the relationship between heterogeneity of both deadwood (Similä et al 2003, Bouget 2013, Seibold 2017) and habitat (Mcgeoch 2007, Joelsson et al 2018) and that of diversity and richness of beetle species. As deadwood volume and diversity can be strongly correlated (Kunttu et al 2015), it is possible that we fail to uncover the true diversity in deadwood.

It could also be that we do not pay enough attention to the amount of different deadwood characteristics, as this has proved to be influential on beetle richness and species assemblages (Økland et al 1996, Brin et al 2011, Ranius et al 2015, Procházka & Schlaghamerský 2019). It could be that, by for example using 10 cm diameter classes, and each diameter class getting 1 individual score to deadwood diversity, deadwood diversity could be misleading. Perhaps more attention should have been paid to amounts of different decay stages and especially large diameter deadwood.

Perhaps it is not either amount or diversity of deadwood, but the amount of certain qualities that is important. Deadwood diversity can still be influential and important as a complement to deadwood amount (Kraut et al 2016). Future studies should focus more on unravelling the importance of certain decay stages, diameters and types of deadwood. It can of course also be possible that more diversity has developed in the time between insect trappings and measurement of structure data, as will be discussed further down in the discussion, regarding methodology. We have therefore not acquired enough evidence to support the habitat heterogeneity hypothesis.

4.4. Deadwood volume

Results of this study supports the HAH, that increasing habitat (deadwood) amounts increase species abundance. As discussed above, increase in deadwood amount is often correlated with increase in deadwood diversity as well, which can be influential for richness and abundance (Kunttu et al 2015, Seibold et al 2016). However, as deadwood diversity and volume were tested separately, and deadwood volume showed more conclusive results, this study supports deadwood amount as being important. This goes in line with several previous studies of habitat amount, among a range of organism groups (Fahrig 2013, Melo et al 2017, Seibold et al 2017, Percel et al 2018, 2019, Watling et al 2020). It should be noted, however, that there are also studies that contradicts habitat amount (Haddad et al 2017, Bueno & Peres 2019). Several studies also dictate that not only one factor of deadwood or habitat characteristics matter, but rather several, or a combination of several different characteristics (Similä et al 2003, Lassauce et al 2011, Kunttu et al 2015, Martin 2018).

Many studies show that sun-exposed sites hold higher richness (Horák & Rébl 2013, Koch Widerberg et al 2012, Seibold et al 2016). However, the reason behind this could be a rise in temperature (Müller et al 2015) or that there is often more deadwood in naturally open areas (Bouget & Duelli 2004, Müller et al 2010), and that these factors matter more than the open canopy (Vodka, Konvicka & Cizek 2008, Hjältén et al 2012). As the effect of canopy openness was not accounted for, its effect cannot be wholly disregarded. However, all plots were considered open and sun-exposed at the time of insect trappings, and therefore it is not likely a major factor. This study's results indicate that deadwood amount has a positive effect on saproxylic beetles, mainly abundances. It should also be remembered that these sites are not unmanaged, natural forests. They have all been managed at one point, and these Ecoparks have not existed 20 years yet, why natural deadwood dynamics might not have had the time to form yet, and that deadwood diversity has not yet formed in order to impact beetle communities.

4.5. Methodology

Focus of species identification in this study has been on saproxylic species, especially rare and red-listed beetles. This has led to grouping some species to genera level instead of species-level (such as most bark beetles) and there has been inconsistence between the two taxonomic experts how they have identified species. However, the variation in identification precision is only between northern and southern areas, making it impossible to compare them. On the other hand, due to great distance between the two study areas, such a comparison would be invalid due to differences in climate and species pool. However, comparisons between Ecoparks and respective BAU-sites can be done since they have the same identification precision.

In future studies, more detailed species identification would be valuable, allowing for example analyses on species specific interactions in Ecoparks and BAU-landscapes.

Trunk-attached window traps were used, which catches a wider range of insects, from those utilizing the local deadwood to visiting insects without affinity to the surrounding structures (Hyvärinen et al 2006). However, window traps are most efficient in terms of catches, and they do catch many species representative to the local species pools (Alinvi et al 2006, Sverdrup-Thygeson & Birkemoe 2008). For this reason, only saproxylic beetles were identified. To further secure species affinity to specific deadwood however, emergence traps could be used, as in Hjältén et al (2012).

There is also the issue of time, seeing as the structural data was measured in 2019, while insect trappings were done in 2010-2013. This time lag in measurements can of course result in slightly higher basal areas and canopy closure than at the time of insect trappings. However, no measures to create new deadwood have taken place and this time lag is likely not enough to result in any large amounts of newly created natural deadwood other than the occasional tree. In boreal forests the accumulation and decay of deadwood is a very slow process.

One should also consider, when interpreting these results, that local structure data is taken within the proximity of the traps (20 m), and that traps were placed close to roads, resulting that most 20 m radius sampling areas were crossed by roads. The sites for the traps were also selected based on canopy structure and light conditions. Stand structure data therefore only represents the proximity to the traps, and for example deadwood amounts can be influenced by the presence of roads, decreasing the per hectare amounts of deadwood. Stand structure data is therefore not fully representative for the sites, but representative of the surroundings of the traps. The high number of plots however, 22-24 per landscape should be enough to cover variations, and the methodology was similar in all areas, resulting in comparable values between the landscapes.

4.6. Implications for management

Stating that only one factor, such as deadwood amount, being the most important for saproxylic beetle communities is probably a simplification, it is rather a combination of factors of different habitat qualities that matter (Lassauce et al 2011, Kunttu et al 2015). However, the importance of having a landscape view is strongly shown in this study, seeing that communities differ in assemblages and responses to deadwood depending on the surrounding landscape (Ecopark or Business as usual). Local deadwood factors do not seem to have positive relationships with beetles within the Ecoparks, but they do within BAU-areas. The results of this study are in line with the habitat amount hypothesis as well as the intermediate landscape-complexity hypothesis. Although the intermediate landscape-complexity hypothesis was not tested in this study per se and can therefore not be fully answered. The main priority should therefore be, in more complex landscapes, to maintain and enhance the complexity of habitats as well as their cover and the amount of deadwood throughout the landscape, rather than focus on directed local measures, for saproxylic and red-listed beetles. However, some species are likely in need of specific interventions, and this should be regarded as well. In the more conventionally managed landscape, local measures to increase the general amount of deadwood in the landscape could be most efficient. As my results do not provide enough support for the habitat heterogeneity hypothesis, recommendations to increase deadwood diversity based on this study alone cannot be given. However, there are plenty of studies that have shown that deadwood diversity is important as well (Gonzáles-Megías et al 2011, Hamm & Drossel 2017, Seibold et al 2016) and should therefore not be disregarded.

Loss of biodiversity is a pressing matter and it is of great importance. Sweden´s goals for sustainable forests have not been met by 2020 (SEPA 2019), and the state of red-listed species in Swedish forests shows a negative trend (ArtDatabanken 2020). Therefore, the need to study how to hinder and change this trend is vital. It is important to know so that conservation and restoration measures can be done correctly, for the best effect, and at the same time being cost-efficient, as correctly guided measures will give value in terms of effect. This study may be used to help provide some guidance in future conservation work.

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Appendix 1. Maps of each site with plot positions and target class.

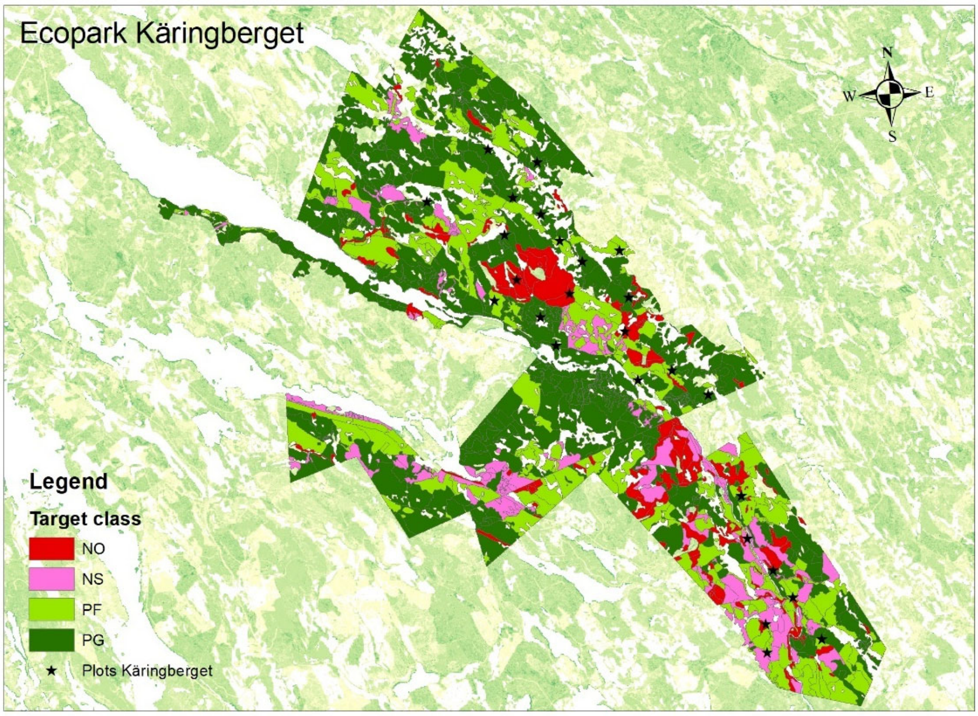

Figure 2. Map of Ecopark Käringberget with plot positions and target classes. Plots marked with stars. NO = Environmental goals with undisturbed forest. NS = Environmental goals with adapted management. PF = Production goals with reinforced considerations. PG = Production goals with general environmental considerations.

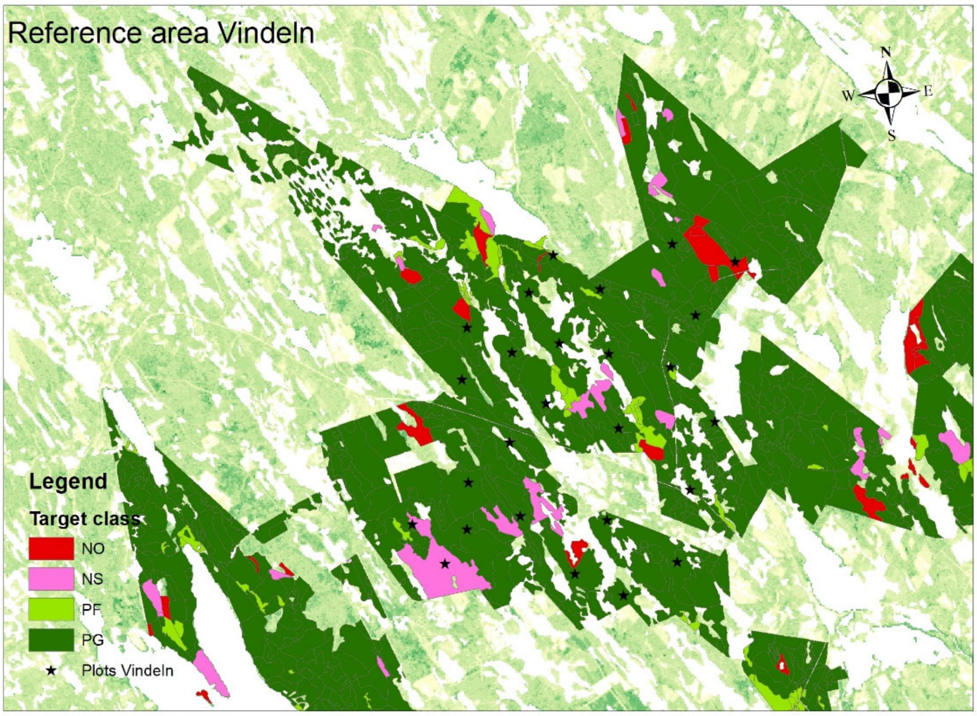

Figure 3. Map of reference site Vindeln with plot positions and target classes. Plots marked with stars. NO = Environmental goals with undisturbed forest. NS = Environmental goals with adapted management. PF = Production goals with reinforced considerations. PG = Production goals with general environmental considerations.

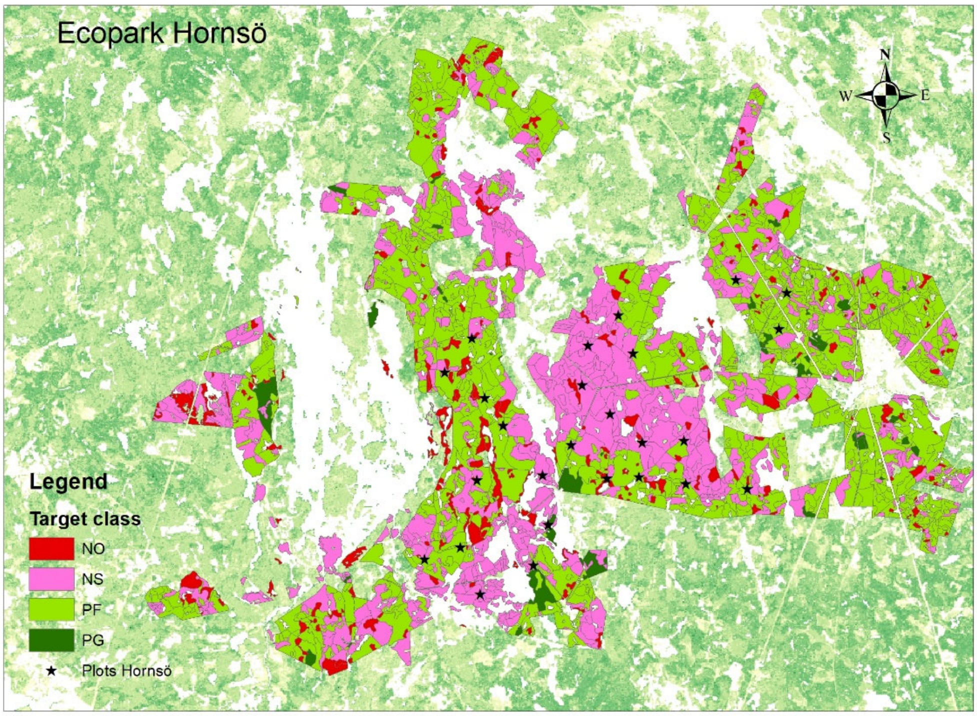

Figure 4. Map of Ecopark Hornsö with plot positions and target classes. Plots marked with stars. NO = Environmental goals with undisturbed forest. NS = Environmental goals with adapted management. PF = Production goals with reinforced considerations. PG = Production goals with general environmental considerations.

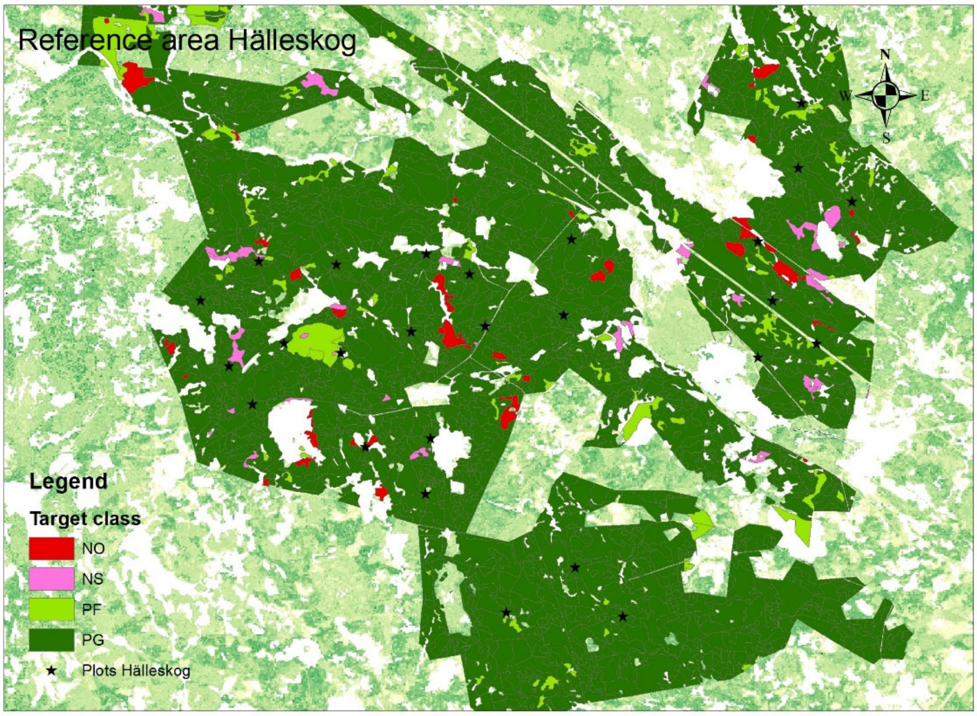

Figure 5. Map of reference site Hälleskog with plot positions and target classes. Plots marked with stars. NO = Environmental goals with undisturbed forest. NS = Environmental goals with adapted management. PF = Production goals with reinforced considerations. PG = Production goals with general environmental considerations.

Appendix 2. Species list

Table 3. Species list. Total abundance of saproxylic and red-listed species for each site. Red-listed species displayed further down separately. Sx category = saproxylic category. SxO = Obligate saproxylic. SxF = Facultative saproxylic. NT = Near threatened. VU = Vulnerable. EN = Endangered.

Saproxylic species	**Hälleskog (BAU)**	**Hornsö (ECO)**	**Vindeln (BAU)**	**Käringberget (ECO)**	**Total**	**Sx category**
Abdera affinis	0	0	2	4	6	SxO
Acanthocinus aedilis	0	0	12	16	28	SxO
Acidota crenata	0	0	22	34	56	SxF
Acmaeops septentrionis	0	0	3	7	10	SxO
Acritus nigricornis	2	0	0	0	2	SxF
Agathidium nigripenne	0	0	0	6	6	SxF
Agathidium seminulum	0	0	14	0	14	SxF
Agrilus viridis	15	6	8	4	33	SxO
Allandrus undulatus	1	1	0	0	2	SxO
Alosterna tabacicolor	2	3	1	0	6	SxO
Ampedus balteatus	589	433	148	142	1312	SxO
Ampedus nigrinus	30	12	571	293	906	SxO
Ampedus nigroflavus	2	2	0	0	4	SxO
Ampedus pomonae	5	8	0	0	13	SxO
Ampedus pomorum	10	16	0	0	26	SxO
Ampedus sanguineus	5	6	0	0	11	SxO
Ampedus tristis	10	5	119	113	247	SxO
Anaspis arctica	0	0	8	27	35	SxO
Anaspis marginicollis	0	0	38	40	78	SxO
Anaspis rufilabris	0	0	41	30	71	SxO
Anastrangalia reyi	19	15	45	22	101	SxO
Anastrangalia sanguinolenta	255	82	21	8	366	SxO
Anidorus nigrinus	17	6	0	0	23	SxO
Anisotoma axillaris	0	0	500	235	735	SxO
Anisotoma castanea	0	0	44	7	51	SxO
Anisotoma glabra	0	0	393	269	662	SxO

Anisotoma humeralis	0	0	41	7	48	SxO
Anthaxia quadripunctata	139	46	150	21	356	SxO
Anthrenus museorum	31	37	27	13	108	SxF
Anthribus nebulosus	56	36	1	1	94	SxF
Aplocnemus nigricornis	12	8	0	0	20	SxO
Aplocnemus tarsalis	0	0	2	0	2	SxO
Arhopalus rusticus	77	133	12	15	237	SxO
Asemum striatum	10	3	89	56	158	SxO
Aspidiphorus orbiculatus	12	11	18	1	42	SxF
Athous subfuscus	142	70	67	58	337	SxF
Atrecus affinis	0	0	0	1	1	SxO
Atrecus longiceps	0	0	5	5	10	SxO
Atrecus pilicornis	0	0	1	2	3	SxO
Bisnius puella	0	0	5	3	8	SxF
Bolitophagus reticulatus	1	1	4	6	12	SxO
Buprestis rustica	8	1	2	0	11	SxO
Callidium coriaceum	0	1	0	0	1	SxO
Calopus serraticornis	0	0	0	1	1	SxO
Cardiophorus ruficollis	140	77	41	17	275	SxO
Carpophilus marginellus	0	0	8	12	20	SxF
Cerylon deplanatum	0	1	0	0	1	SxO
Cerylon ferrugineum	0	0	20	78	98	SxO
Cerylon histeroides	0	0	520	328	848	SxO
Chrysanthia geniculata	0	0	1	0	1	SxO
Chrysanthia viridissima	0	0	0	1	1	SxO
Chrysobothris chrysostigma	5	3	15	5	28	SxO
Cis bidentatus	0	0	4	9	13	SxO
Cis boleti	42	54	428	149	673	SxO
Cis castaneus	0	0	0	1	1	SxO
Cis comptus	0	0	82	114	196	SxO
Cis dentatus	0	0	2	2	4	SxO
Cis glabratus	0	0	10	12	22	SxO
Cis jacquemartii	0	0	9	7	16	SxO
Cis lineatocribratus	0	0	1	2	3	SxO
Cis punctulatus	0	0	19	9	28	SxO
Corticeus linearis	11	2	72	42	127	SxO
Cortinicara gibbosa	13	23	170	202	408	SxF
Cryphalus saltuarius	0	0	0	1	1	SxO
Cryptolestes abietis	0	0	0	3	3	SxO
Crypturgus cinereus	0	0	34	40	74	SxO

Crypturgus hispidulus	0	0	23	21	44	SxO
Crypturgus pusillus	0	0	7	20	27	SxO
Crypturgus subcribrosus	0	0	12	18	30	SxO
Curtimorda maculosa	13	1	16	8	38	SxO
Dacne bipustulata	62	87	139	128	416	SxO
Dasytes niger	148	153	19	31	351	SxO
Dasytes obscurus	15	9	211	82	317	SxO
Dasytes plumbeus	137	318	2	0	457	SxO
Dendroctonus micans	0	0	1	0	1	SxO
Dendrophagus crenatus	1	0	0	4	5	SxO
Dendrophilus pygmaeus	0	0	3	0	3	SxF
Denticollis borealis	4	7	26	53	90	SxO
Denticollis linearis	2	0	6	3	11	SxO
Dictyoptera aurora	0	0	10	13	23	SxO
Dolichosoma lineare	0	0	3	0	3	SxO
Dorcatoma dresdensis	7	10	2	4	23	SxO
Dorcatoma robusta	14	26	17	19	76	SxO
Dromius agilis	0	0	3	5	8	SxF
Dryocoetes autographus	0	0	314	191	505	SxO
Dryocoetes hectographus	0	0	11	6	17	SxO
Dryophilus pusillus	3	0	0	0	3	SxO
Endomychus coccineus	84	105	182	16	387	SxO
Enicmus fungicola	0	0	0	1	1	SxF
Enicmus rugosus	728	1242	791	1054	3815	SxO
Ennearthron cornutum	0	0	1	5	6	SxO
Ernobius explanatus	0	0	0	2	2	SxO
Ernobius nigrinus	0	0	1	0	1	SxO
Euglenes pygmaeus	1	0	21	7	29	SxO
Gaurotes virginea	3	0	1	0	4	SxO
Glischrochilus hortensis	22	64	117	17	220	SxF
Glischrochilus quadripunctatus	18	12	378	668	1076	SxO
Globicornis emarginata	3	8	35	49	95	SxO
Gnathacmaeops pratensis	0	0	1	0	1	SxO
Gnathoncus buyssoni	0	0	38	25	63	SxF
Gnathoncus nannetensis	0	1	13	11	25	SxF
Gonotropis dorsalis	2	0	1	3	6	SxO
Hadreule elongatula	49	14	22	12	97	SxO
Hadrobregmus pertinax	6	16	40	37	99	SxO
Hallomenus binotatus	2	0	1	2	5	SxO

Hylastes brunneus	0	0	4465	3192	7657	SxO
Hylastes cunicularius	0	0	1180	982	2162	SxO
Hylastes opacus	0	0	34	26	60	SxO
Hylobius abietis	340	205	242	244	1031	SxO
Hylobius pinastri	3	2	8	0	13	SxO
Hylurgops glabratus	0	0	4	8	12	SxO
Hylurgops palliatus	0	0	96	88	184	SxO
Ips typographus	3	0	62	51	116	SxO
Judolia sexmaculata	4	2	3	1	10	SxO
Lasconotus jelskii	0	0	0	1	1	SxO
Latridius hirtus	4	36	23	56	119	SxO
Latridius minutus	0	0	17	18	35	SxF
Leptura quadrifasciata	146	89	16	6	257	SxO
Lepturobosca virens	0	0	0	1	1	SxO
Litargus connexus	4	13	12	11	40	SxO
Lordithon lunulatus	0	1	130	71	202	SxF
Lordithon speciosus	0	0	1	0	1	SxO
Lordithon thoracicus	0	0	1	0	1	SxF
Lordithon trimaculatus	0	0	0	7	7	SxO
Lygistopterus sanguineus	25	11	4	5	45	SxO
Magdalis duplicata	0	0	20	5	25	SxO
Magdalis frontalis	0	0	5	1	6	SxO
Magdalis phlegmatica	0	0	2	1	3	SxO
Magdalis ruficornis	0	0	1	1	2	SxO
Magdalis violacea	0	0	50	34	84	SxO
Malthinus biguttatus	0	0	1	0	1	SxO
Malthodes brevicollis	0	0	21	19	40	SxO
Malthodes flavoguttatus	0	0	1	3	4	SxO
Malthodes fuscus	0	0	7	2	9	SxO
Malthodes guttifer	0	0	3	4	7	SxO
Malthodes marginatus	0	0	4	0	4	SxO
Malthodes minimus	0	0	2	1	3	SxO
Megasternum concinnum	0	0	9	2	11	SxF
Megatoma undata	34	98	30	20	182	SxF
Melanotus castanipes	190	44	735	437	1406	SxO
Melanotus villosus	159	100	0	0	259	SxO
Micrambe abietis	0	0	6	0	6	SxF
Microscydmus minimus	0	0	0	1	1	SxO
Molorchus minor	12	26	11	26	75	SxO
Monochamus sutor	2	0	3	0	5	SxO

Mycetina cruciata	3	1	0	0	4	SxO
Mycetochara flavipes	16	26	12	3	57	SxO
Mycetochara obscura	0	0	9	32	41	SxO
Mycetophagus fulvicollis	0	0	0	3	3	SxO
Mycetophagus multipunctatus	0	0	13	44	57	SxO
Mycetophagus populi	1	2	3	2	8	SxO
Nepachys cardiacae	0	0	5	9	14	SxO
Nudobius lentus	0	0	119	135	254	SxO
Orchesia fasciata	0	1	3	0	4	SxO
Orchesia micans	10	5	13	13	41	SxO
Orthocis alni	8	7	43	34	92	SxO
Orthotomicus laricis	0	0	1	1	2	SxO
Orthotomicus proximus	0	0	8	5	13	SxO
Othius subuliformis	0	0	0	1	1	SxF
Oxymirus cursor	4	2	11	7	24	SxO
Pachyta lamed	0	0	7	5	12	SxO
Palorus depressus	1	6	0	0	7	SxF
Pediacus fuscus	0	0	4	8	12	SxO
Philonthus addendus	0	0	1	0	1	SxF
Philonthus marginatus	0	0	4	0	4	SxF
Philonthus politus	0	0	11	0	11	SxF
Phloeotribus spinulosus	0	0	4	0	4	SxO
Phyllodrepa melanocephala	0	0	2	0	2	SxO
Pissodes castaneus	1	0	0	0	1	SxO
Pissodes harcyniae	0	0	2	1	3	SxO
Pissodes pini	137	36	41	28	242	SxO
Pissodes piniphilus	7	6	6	12	31	SxO
Pityogenes bidentatus	0	0	56	31	87	SxO
Pityogenes chalcographus	110	10	571	394	1085	SxO
Pityogenes quadridens	0	0	3	2	5	SxO
Pityophagus ferrugineus	49	18	724	357	1148	SxO
Pityophthorus micrographus	0	0	11	3	14	SxO
Platycerus caprea	0	0	9	2	11	SxO
Platycerus caraboides	0	1	0	0	1	SxO
Platycis minutus	0	0	0	1	1	SxO
Platysoma angustatum	0	0	24	8	32	SxO
Platysoma deplanatum	2	6	0	0	8	SxO
Plegaderus caesus	0	5	0	0	5	SxO

Plegaderus vulneratus	22	50	513	594	1179	SxO
Pocadius ferrugineus	0	0	8	1	9	SxF
Pogonocherus decoratus	0	0	3	2	5	SxO
Pogonocherus fasciculatus	15	4	88	57	164	SxO
Polygraphus poligraphus	0	0	28	13	41	SxO
Polygraphus punctifrons	0	0	5	0	5	SxO
Polygraphus subopacus	0	0	51	45	96	SxO
Pterostichus oblongopunctatus	0	0	0	2	2	SxF
Pyropterus nigroruber	3	2	0	0	5	SxO
Pytho depressus	0	0	17	17	34	SxO
Quedius brevis	0	0	1	0	1	SxF
Quedius maurus	0	0	8	2	10	SxO
Quedius mesomelinus	0	0	4	0	4	SxF
Quedius plagiatus	0	0	50	50	100	SxO
Quedius tenellus	0	0	25	7	32	SxF
Rabocerus gabrieli	0	0	4	7	11	SxO
Rhagium inquisitor	134	121	496	668	1419	SxO
Rhagium mordax	18	46	88	156	308	SxO
Rhizophagus bipustulatus	8	27	17	23	75	SxO
Rhizophagus cribratus	0	0	2	1	3	SxO
Rhizophagus dispar	0	0	58	55	113	SxF
Rhizophagus fenestralis	2	6	0	0	8	SxO
Rhizophagus ferrugineus	122	113	2068	1146	3449	SxO
Rhyncolus ater	1	29	9	9	48	SxO
Rhyncolus sculpturatus	18	85	11	11	125	SxO
Salpingus ruficollis	51	31	52	73	207	SxO
Saperda scalaris	17	24	3	1	45	SxO
Schizotus pectinicornis	4	6	5	14	29	SxO
Selatosomus aeneus	8	20	60	35	123	SxF
Sepedophilus littoreus	0	0	6	0	6	SxF
Serropalpus barbatus	2	1	0	0	3	SxO
Silvanoprus fagi	9	2	6	4	21	SxO
Silvanus bidentatus	0	3	4	1	8	SxO
Soronia grisea	31	35	55	117	238	SxO
Soronia punctatissima	17	10	20	59	106	SxO
Sphaeriestes bimaculatus	0	0	0	1	1	SxO
Sphaeriestes stockmanni	1	0	0	0	1	SxO
Sphaerites glabratus	0	0	5	1	6	SxF
Sphindus dubius	99	145	29	23	296	SxF

Stagetus borealis	0	1	1	0	2	SxO
Stenichnus bicolor	0	0	2	0	2	SxF
Stenurella melanura	102	81	3	2	188	SxO
Stephanopachys substriatus	0	0	1	1	2	SxO
Stephostethus pandellei	0	0	15	45	60	SxF
Stephostethus rugicollis	0	0	54	69	123	SxF
Stictoleptura maculicornis	20	13	1	1	35	SxO
Stictoleptura rubra	13	5	0	0	18	SxO
Synchita humeralis	13	15	8	3	39	SxO
Tachinus subterraneus	0	0	1	0	1	SxF
Tachyta nana	0	1	2	6	9	SxO
Tetratoma ancora	0	0	8	15	23	SxO
Tetropium castaneum	6	4	58	15	83	SxO
Thanasimus femoralis	20	21	84	79	204	SxO
Thanasimus formicarius	177	264	452	529	1422	SxO
Tomicus minor	0	0	9	4	13	SxO
Tomicus piniperda	0	0	574	473	1047	SxO
Tomoxia bucephala	246	227	0	0	473	SxO
Trichius fasciatus	116	61	0	1	178	SxO
Trichophya pilicornis	0	0	1	0	1	SxF
Triplax aenea	3	0	22	48	73	SxO
Triplax rufipes	0	23	0	0	23	SxO
Triplax russica	28	62	43	149	282	SxO
Triplax scutellaris	0	0	9	15	24	SxO
Trypodendron domesticum	0	0	14	39	53	SxO
Trypodendron laeve	0	0	6	40	46	SxO
Trypodendron lineatum	0	0	3502	2916	6418	SxO
Trypodendron signatum	0	0	13	6	19	SxO
Tyrus mucronatus	0	0	2	3	5	SxF
Xantholinus tricolor	0	0	1	1	2	SxF
Xylechinus pilosus	0	0	0	1	1	SxO
Xylita laevigata	6	3	103	108	220	SxO
Zilora ferruginea	0	0	1	1	2	SxO
Grand Total	5592	5475	24036	19227	54330	
Red-listed Species	**Hälleskog (BAU)**	**Hornsö (ECO)**	**Vindeln (BAU)**	**Käringberget (ECO)**	**Total**	**Red-list**
Acmaeops septentrionis	0	0	3	7	10	NT
Aegomorphus clavipes	32	58	0	0	90	NT
Ampedus cinnabarinus	8	6	0	0	14	NT
Ampedus nigroflavus	2	2	0	0	4	NT

Ampedus sanguinolentus	4	6	0	0	10	NT
Anaesthetis testacea	0	5	0	0	5	VU
Anoplodera sexguttata	0	3	0	0	3	NT
Aplocnemus impressus	0	1	0	0	1	NT
Carphacis striatus	0	22	0	0	22	VU
Cerylon deplanatum	0	1	0	0	1	NT
Cis dentatus	0	0	2	2	4	NT
Colydium elongatum	0	10	0	0	10	EN
Corticeus bicolor	0	0	0	2	2	NT
Cryptocephalus distinguendus	1	0	1	0	2	NT
Denticollis borealis	4	7	26	53	90	NT
Dermestes palmi	0	0	1	1	2	VU
Dicerca furcata	0	0	0	1	1	NT
Dircaea australis	0	11	0	0	11	EN
Drapetes mordelloides	4	1	0	0	5	VU
Enedreytes sepicola	0	1	0	0	1	NT
Ennearthron laricinum	0	0	0	2	2	NT
Exocentrus adspersus	0	1	0	0	1	VU
Glischrochilus quadrisignatus	0	1	0	0	1	NT
Gonotropis dorsalis	2	0	1	3	6	NT
Harminius undulatus	0	0	2	4	6	NT
Ipidia binotata	1	3	0	0	4	NT
Lacon conspersus	0	0	4	2	6	NT
Lacon fasciatus	0	0	8	12	20	NT
Lasconotus jelskii	0	0	0	1	1	VU
Microrhagus lepidus	0	1	0	0	1	NT
Monochamus galloprovincialis	1	1	0	0	2	NT
Mordellistena humeralis	0	0	2	0	2	NT
Mycetochara obscura	0	0	9	32	41	NT
Mycetophagus decempunctatus	0	1	0	0	1	VU
Mycetophagus fulvicollis	0	0	0	3	3	NT
Necydalis major	19	15	2	1	37	NT
Orchesia fasciata	0	1	3	0	4	NT
Osphya bipunctata	0	2	0	0	2	VU
Pedostrangalia pubescens	7	33	0	0	40	VU
Phloiotrya rufipes	0	1	0	0	1	NT

Phyllodrepa clavigera	0	0	0	3	3	NT
Phymatodes alni	0	14	0	0	14	NT
Platysoma deplanatum	2	6	0	0	8	NT
Platysoma minus	0	1	3	7	11	NT
Pyrrhidium sanguineum	0	11	0	0	11	NT
Saperda perforata	0	1	0	0	1	NT
Stagetus borealis	0	1	1	0	2	NT
Stenagostus rufus	0	2	0	0	2	VU
Strangalia attenuata	0	13	0	0	13	VU
Tachyta nana	0	1	2	6	9	NT
Tragosoma depsarium	0	20	0	0	20	VU
Triplax rufipes	0	23	0	0	23	NT
Uloma rufa	0	1	0	0	1	NT
Xyleborinus saxesenii	0	2	0	0	2	NT
Xyleborus monographus	0	4	0	0	4	NT
Xylotrechus antilope	1	41	0	0	42	NT
Zilora ferruginea	0	0	1	1	2	NT
Grand Total	88	335	71	143	637	

Appendix 3. Formulas

H = Height of tree from ground surface to the top branch of the crown.
D = Diameter at breast height, 1,3 m (DBH).
L = Length of log.

Volume formula (dm3) for pine in southern Sweden, H>=4 m, D>=4,5cm, south of 60° (Brandel 1990)
$10^{-1,38903} \times D^{1,84493} \times (D+20,0)^{0,06563} \times H^{2,02122} \times (H-1,3)^{-1,01095}$

Volume formula (dm3) for spruce in southern Sweden, H>=4 m, D>=4,5 cm, south of 60° (Brandel 1990)
$10^{-1,02039} \times D^{2,00128} \times (D+20,0)^{-0,47473} \times H^{2,87138} \times (H-1,3)^{-1,61803}$

Volume formula (dm3) for birch in southern Sweden, latitude -56,9º, H>=6 m, D>=4,5 cm (Brandel 1990)
$10^{-0,89363} \times D^{2,23818} \times (D+20,0)^{-1,06930} \times H^{6,02015} \times (H - 1,3)^{-4,51472}$

Volume formula (dm3) for pine in northern Sweden, H>=4 m, D>=4,5cm, north of 60° (Brandel 1990)
$10^{-1,20914} \times D^{1,94740} \times (D+20,0)^{-0,05947} \times H^{1,40958} \times (H-1,3)^{-0,45810}$

Volume formula (dm3) for spruce in northern Sweden, H>=4 m, D>=4,5 cm, north of 60° (Brandel 1990)
$10^{-0,79783} \times D^{2,07157} \times (D+20,0)^{-0,73882} \times H^{3,16332} \times (H-1,3)^{-1,82622}$

Volume formula (dm3) for birch in northern Sweden, latitude 59,0°-, H>=6 m, D>=4,5 cm (Brandel 1990)
$10^{-0,84627} \times D^{2,23818} \times (D+20,0)^{-1,06930} \times H^{6,02015} \times (H - 1,3)^{-4,51472}$

Basal area per tree
pi*(D/200)^2)

Formula to calculate logs
D1/2*D2/2*pi*L

Appendix 4. model results and dAIC

Table 4. GLMER (generalized linear mixed effect model) results of saproxylic (facultative and obligate) in northern and southern Sweden. Log-mean higher than 0 shows positive effects vs intercept, lower than 0 is negative effect. Numbers highlighted as bold hold significance, p <0,05. *GLMER = x=y~(Treatment,Treatment*logm3/dwdiv,Treatment+logm3/dwdiv)+(1|Year), Poisson. Bracketed letters () next to model name shows which models were compared for dAIC, models with the same letters were compared to each other. Lowest dAIC highlighted in yellow, models within 2 dAIC highlighted in orange. Dwdiv =deadwood diversity, logm3 =log-transformed deadwood volume. ECO = Ecopark, compared to BAU.*

Northern Sweden							
Model	Predictors	Log-mean	SE	p	Random effect (year)	dAIC	weight
Facultative richness	Treatment (ECO)	-0.05	0.18	0.802	$\sigma^2 = 0.17$	1.9	0.146
Treatment*logm3 (a)	logm3	0.01	0.07	0.870	$\tau00 = 0.01$ Year		
	Treatment(ECO)*logm3	-0.10	0.09	0.262	ICC = 0.07		
Facultative richness	Treatment (ECO)	-0.14	0.16	0.378	$\sigma^2 = 0.17$	3.0	0.083
Treatment*dwdiv (a)	dwdiv	0.02	0.13	0.898	$\tau00 = 0.01$ Year		
	Treatment(ECO)*dwdiv	-0.10	0.15	0.520	ICC = 0.07		
Facultative richness	Treatment (ECO)	-0.23	0.07	**0.002**	$\sigma^2 = 0.17$	1.2	0.211
Treatment+logm3 (a)	logm3	-0.04	0.05	0.358	$\tau00 = 0.01$ Year		
					ICC = 0.07		
Facultative richness	Treatment (ECO)	-0.22	0.08	**0.005**	$\sigma^2 = 0.17$	1.4	0.184
Treatment+dwdiv (a)	dwdiv	-0.05	0.07	0.454	$\tau00 = 0.01$ Year		
					ICC = 0.07		
Facultative richness	Treatment (ECO)	-0.25	0.07	**<0.001**	$\sigma^2 = 0.17$	0.0	0.376
Treatment (a)					$\tau00 = 0.01$ Year		
					ICC = 0.07		
Facultative abundance	Treatment (ECO)	0.37	0.12	**0.002**	$\sigma^2 = 0.08$	0.0	1
Treatment*logm3 (b)	logm3	0.03	0.04	0.479	$\tau00 = 0.07$ Year		
	Treatment(ECO)*logm3	-0.35	0.06	**<0.001**	ICC = 0.45		
Facultative abundance	Treatment (ECO)	0.02	0.11	0.842	$\sigma^2 = 0.08$	31.9	<0.001
Treatment*dwdiv (b)	dwdiv	0.02	0.08	0.845	$\tau00 = 0.07$ Year		
	Treatment (ECO*dwdiv	-0.28	0.10	**0.007**	ICC = 0.45		
Facultative abundance	Treatment (ECO)	-0.31	0.05	**<0.001**	$\sigma^2 = 0.08$	47.9	<0.001

Treatment (b)					τ00 = 0.07 Year ICC = 0.45		
Obligate richness Treatment*logm3 (c)	Treatment (ECO) logm3 Treatment(ECO)*logm3	-0.07 -0.02 0.02	0.07 0.03 0.03	0.271 0.531 0.594	σ^2 = 0.03 τ00 = 0.01 Year ICC = 0.25	6.6	0.019
Obligate richness Treatment*dwdiv (c)	Treatment (ECO) dwdiv Treatment(ECO)*dwdiv	-0.12 0.02 0.05	0.06 0.05 0.06	**0.040** 0.728 0.343	σ^2 = 0.03 τ00 = 0.01 Year ICC = 0.25	1.1	0.300
Obligate richness Treatment+logm3 (c)	Treatment (ECO) logm3	-0.04 -0.01	0.03 0.02	0.135 0.731	σ^2 = 0.03 τ00 = 0.01 Year ICC = 0.25	4.9	0.045
Obligate richness Treatment+dwdiv (c)	Treatment (ECO) dwdiv	-0.07 0.06	0.03 0.02	**0.015** **0.024**	σ^2 = 0.03 τ00 = 0.01 Year ICC = 0.25	0.0	0.520
Obligate richness Treatment (c)	Treatment (ECO)	-0.04	0.03	0.097	σ^2 = 0.03 τ00 = 0.01 Year ICC = 0.25	3.0	0.115
Obligate abundance Treatment*logm3 (d)	Treatment (ECO) logm3 Treatment(ECO)*logm3	-0.33 0.03 0.04	0.03 0.01 0.01	**<0.001** **0.004** **0.002**	σ^2 = 0.00 τ00 = 0.33 Year ICC = 0.99	279.2	<0.001
Obligate abundance Treatment*dwdiv (d)	Treatment (ECO) dwdiv Treatment(ECO)*dwdiv	-0.56 -0.09 0.28	0.02 0.02 0.02	**<0.001** **<0.001** **<0.001**	σ^2 = 0.00 τ00 = 0.33 Year ICC = 0.99	0.0	1
Obligate abundance Treatment (d)	Treatment (ECO)	-0.24	0.01	**<0.001**	σ^2 = 0.00 τ00 = 0.33 Year ICC = 0.99	337.2	<0.001
Southern Sweden							
Model	Predictors	Log-mean	SE	p	Random effect (year)	dAIC	weight
Facultative richness Treatment*logm3 (e)	Treatment (ECO) logm3 Treatment(ECO)*logm3	0.28 0.26 -0.11	0.37 0.18 0.22	0.446 0.134 0.608	σ^2 = 0.23 τ00 = 0.02 Year ICC = 0.07	1.7	0.183
Facultative richness Treatment*dwdiv (e)	Treatment (ECO) dwdiv Treatment(ECO)*dwdiv	0.28 0.20 -0.08	0.26 0.25 0.29	0.279 0.432 0.780	σ^2 = 0.23 τ00 = 0.02 Year ICC = 0.07	4.4	0.049
Facultative richness Treatment+logm3 (e)	Treatment (ECO) logm3	0.10 0.19	0.12 0.10	0.399 0.059	σ^2 = 0.23 τ00 = 0.02 Year ICC = 0.07	0.0	0.437
Facultative richness	Treatment (ECO)	0.21	0.10	**0.039**	σ^2 = 0.23	2.5	0.128

Treatment+dwdiv (e)	dwdiv	0.14	0.13	0.295	τ00 = 0.02 Year ICC = 0.07		
Facultative richness Treatment (e)	Treatment (ECO)	0.24	0.10	**0.014**	σ^2 = 0.23 τ00 = 0.02 Year ICC = 0.07	1.5	0.203
Facultative abundance Treatment*logm3 (f)	Treatment (ECO) logm3 Treatment(ECO)*logm3	0.40 0.36 -0.16	0.26 0.12 0.15	0.122 **0.003** 0.280	σ^2 = 0.12 τ00 = 0.10 Year ICC = 0.45	0.8	0.3952
Facultative abundance Treatment*dwdiv (f)	Treatment (ECO) dwdiv Treatment(ECO)*dwdiv	0.16 -0.03 0.17	0.18 0.18 0.21	0.364 0.865 0.412	σ^2 = 0.12 τ00 = 0.10 Year ICC = 0.45	13.2	<0.001
Facultative abundance Treatment+logm3 (f)	Treatment (ECO) logm3	0.14 0.25	0.08 0.07	0.110 **<0.001**	σ^2 = 0.12 τ00 = 0.10 Year ICC = 0.45	0.0	0.6001
Facultative abundance Treatment+dwdiv (f)	Treatment (ECO) dwdiv	0.30 0.10	0.07 0.09	**<0.001** 0.276	σ^2 = 0.12 τ00 = 0.10 Year ICC = 0.45	11.9	0.0016
Facultative abundance Treatment (f)	Treatment (ECO)	0.32	0.07	**<0.001**	σ^2 = 0.12 τ00 = 0.10 Year ICC = 0.45	11.1	0.0024
Obligate richness Treatment*logm3 (g)	Treatment (ECO) logm3 Treatment(ECO)*logm3	-0.07 0.19 -0.05	0.15 0.07 0.08	0.625 **0.005** 0.566	σ^2 = 0.04 τ00 = 0.00 Year ICC = 0.01	1.7	0.2319
Obligate richness Treatment*dwdiv (g)	Treatment (ECO) dwdiv Treatment(ECO)*dwdiv	-0.08 0.19 -0.01	0.10 0.09 0.11	0.455 **0.039** 0.935	σ^2 = 0.04 τ00 = 0.00 Year ICC = 0.01	4.3	0.0627
Obligate richness Treatment+logm3 (g)	Treatment (ECO) logm3	-0.16 0.16	0.05 0.04	**0.002** **<0.001**	σ^2 = 0.04 τ00 = 0.00 Year ICC = 0.01	0.0	0.5345
Obligate richness Treatment+dwdiv (g)	Treatment (ECO) dwdiv	-0.08 0.19	0.04 0.05	**0.042** **0.001**	σ^2 = 0.04 τ00 = 0.00 Year ICC = 0.01	2.3	0.1697
Obligate richness Treatment (g)	Treatment (ECO)	-0.04	0.04	0.286	σ^2 = 0.04 τ00 = 0.00 Year ICC = 0.01	12.2	0.0012
Obligate abundance Treatment*logm3 (h)	Treatment (ECO) logm3 Treatment(ECO)*logm3	0.06 0.32 -0.12	0.08 0.03 0.04	0.419 **<0.001** **0.007**	σ^2 = 0.01 τ00 = 0.03 Year ICC = 0.71	0.0	1
Obligate abundance	Treatment (ECO)	-0.15	0.05	**0.005**	σ^2 = 0.01	40.0	<0.001

Treatment*dwdiv (h)	dwdiv	0.16	0.05	**0.001**	τ_{00} = 0.03 Year		
	Treatment(ECO)*dwdiv	0.16	0.06	**0.006**	ICC = 0.71		
Obligate abundance Treatment (h)	Treatment (ECO)	0.05	0.02	**0.017**	σ^2 = 0.01	144.7	<0.001
					τ_{00} = 0.03 Year		
					ICC = 0.71		

Table 5. GLM (generalized linear model) model results of red-listed beetles in northern and southern Sweden separated for each year. Log-mean higher than 0 shows positive effects vs intercept, lower than 0 is negative effect. Numbers highlighted as bold hold significance, p <0,05. *GLM = x=y~(Treatment,Treatment*logm3/dwdiv,Treatment+logm3/dwdiv), Poisson. Bracketed letters () next to model name shows which models were compared for dAIC, models with the same letters were compared to each other. Lowest dAIC highlighted in yellow, models within 2 dAIC highlighted in orange. Dwdiv =deadwood diversity, logm3 =log-transformed deadwood volume. ECO = Ecopark, compared to BAU.*

Northern Sweden						
Model	Predictors	Log-mean	SE	p	dAIC	weight
Richness '10 Treatment*logm3 (a)	Treatment (ECO)	0.89	0.78	0.255	8.9	0.0078
	logm3	-0.11	0.35	0.740		
	Treatment (ECO)*logm3	-0.13	0.42	0.764		
Richness '10 Treatment*dwdiv (a)	Treatment (ECO)	1.04	0.69	0.131	2.0	0.2551
	dwdiv	-0.78	0.74	0.290		
	Treatment (ECO)*dwdiv	-0.13	0.83	0.871		
Richness '10 Treatment+logm3 (a)	Treatment (ECO)	0.68	0.33	**0.042**	7.0	0.0203
	logm3	-0.20	0.19	0.301		
Richness '10 Treatment+dwdiv (a)	Treatment (ECO)	0.94	0.34	**0.006**	0.0	0.6846
	dwdiv	-0.89	0.34	**0.008**		
Richness '10 Treatment (a)	Treatment (ECO)	0.59	0.32	0.068	6.1	0.0321
Abundance '10 Treatment*logm3 (b)	Treatment (ECO)	0.93	0.75	0.214	10.9	0.0030
	logm3	-0.02	0.32	0.948		
	Treatment (ECO)*logm3	-0.16	0.39	0.690		
Abundance '10 Treatment*dwdiv (b)	Treatment (ECO)	0.93	0.64	0.149	2.0	0.2620
	dwdiv	-0.94	0.71	0.188		
	Treatment (ECO)*dwdiv	0.04	0.79	0.956		
Abundance '10 Treatment+logm3 (b)	Treatment (ECO)	0.66	0.31	**0.035**	9.1	0.0076
	logm3	-0.13	0.18	0.476		

Abundance '10 Treatment+dwdiv (b)	Treatment (ECO)	0.96	0.32	**0.003**	0.0	0.7112
	dwdiv	-0.90	0.31	**0.004**		
Abundance '10 Treatment (b)	Treatment (ECO)	0.60	0.30	**0.047**	7.6	0.0160
Richness '11 Treatment*logm3 (c)	Treatment (ECO)	0.87	0.72	0.232	3.3	0.065
	logm3	-0.11	0.35	0.753		
	Treatment (ECO)*logm3	-0.04	0.40	0.912		
Richness '11 Treatment*dwdiv (c)	Treatment (ECO)	0.48	0.68	0.483	1.9	0.133
	dwdiv	-0.81	0.81	0.314		
	Treatment (ECO)*dwdiv	0.54	0.85	0.525		
Richness '11 Treatment+logm3 (c)	Treatment (ECO)	0.79	0.31	**0.011**	1.3	0.175
	logm3	-0.14	0.17	0.406		
Richness '11 Treatment+dwdiv (c)	Treatment (ECO)	0.88	0.32	**0.006**	0.3	0.292
	dwdiv	-0.33	0.26	0.203		
Richness '11 Treatment (c)	Treatment (ECO)	0.72	0.30	**0.016**	0.0	0.335
Abundance '11 Treatment*logm3 (d)	Treatment (ECO)	0.89	0.66	0.176	3.9	0.048
	logm3	-0.12	0.33	0.711		
	Treatment (ECO)*logm3	0.09	0.37	0.803		
Abundance '11 Treatment*dwdiv (d)	Treatment (ECO)	0.78	0.62	0.208	1.6	0.156
	dwdiv	-0.76	0.76	0.313		
	Treatment (ECO)*dwdiv	0.51	0.79	0.520		
Abundance '11 Treatment+logm3 (d)	Treatment (ECO)	1.04	0.28	**<0.001**	2.0	0.127
	logm3	-0.05	0.14	0.739		
Abundance '11 Treatment+dwdiv (d)	Treatment (ECO)	1.15	0.29	**<0.001**	0.0	0.341
	dwdiv	-0.30	0.21	0.161		
Abundance '11 Treatment (d)	Treatment (ECO)	1.01	0.27	**<0.001**	0.1	0.328
Richness '12 Treatment*logm3 (e)	Treatment (ECO)	1.05	0.70	0.137	1.7	0.16
	logm3	0.38	0.26	0.145		
	Treatment (ECO)*logm3	-0.47	0.34	0.169		

Richness '12	Treatment (ECO)	0.98	0.57	0.087	1.7	0.16
Treatment*dwdiv (e)	dwdiv	0.52	0.43	0.228		
	Treatment (ECO)*dwdiv	-0.80	0.52	0.124		
Richness '12	Treatment (ECO)	0.16	0.27	0.556	1.6	0.17
Treatment+logm3 (e)	logm3	0.10	0.16	0.540		
Richness '12	Treatment (ECO)	0.24	0.29	0.413	1.9	0.14
Treatment+dwdiv (e)	dwdiv	-0.06	0.24	0.809		
Richness '12	Treatment (ECO)	0.21	0.26	0.432	0.0	0.37
Treatment (e)						
Abundance '12	Treatment (ECO)	1.82	0.55	**0.001**	4.7	0.085
Treatment*logm3 (f)	logm3	0.33	0.22	0.136		
	Treatment (ECO)*logm3	-0.72	0.28	**0.009**		
Abundance '12	Treatment (ECO)	1.68	0.46	**<0.001**	0.0	0.904
Treatment*dwdiv (f)	dwdiv	0.38	0.38	0.308		
	Treatment (ECO)*dwdiv	-1.18	0.45	**0.009**		
Abundance '12	Treatment (ECO)	0.48	0.21	**0.025**	8.8	0.011
Treatment (f)						
Southern Sweden						
Model	Predictors	Log-mean	SE	p	dAIC	weight
Richness '11	Treatment (ECO)	4.94	1.09	**<0.001**	0.0	0.9259
Treatment*logm3 (g)	logm3	1.96	0.55	**<0.001**		
	Treatment (ECO)*logm3	-2.23	0.60	**<0.001**		
Richness '11	Treatment (ECO)	2.67	0.72	**<0.001**	5.3	0.0666
Treatment*dwdiv (g)	dwdiv	1.92	0.67	**0.004**		
	Treatment (ECO)*dwdiv	-1.63	0.72	**0.025**		
Richness '11	Treatment (ECO)	1.40	0.26	**<0.001**	9.6	0.0075
Treatment (g)						
Abundance '11	Treatment (ECO)	5.27	0.93	**<0.001**	0.0	0.954
Treatment*logm3 (h)	logm3	2.13	0.47	**<0.001**		
	Treatment (ECO)*logm3	-2.38	0.51	**<0.001**		
Abundance '11	Treatment (ECO)	2.56	0.61	**<0.001**	6.1	0.046
Treatment*dwdiv (h)	dwdiv	1.98	0.57	**<0.001**		
	Treatment (ECO)*dwdiv	-1.46	0.61	**0.016**		

Abundance '11 Treatment (h)	Treatment (ECO)	1.46	0.22	**<0.001**	18.0	<0.001
Richness '12 Treatment*logm3 (i)	Treatment (ECO)	1.60	0.97	0.098	3.5	0.068
	logm3	0.55	0.53	0.300		
	Treatment (ECO)*logm3	-0.45	0.59	0.439		
Richness '12 Treatment*dwdiv (i)	Treatment (ECO)	0.94	0.70	0.178	2.0	0.141
	dwdiv	0.48	0.73	0.510		
	Treatment (ECO)*dwdiv	-0.02	0.79	0.980		
Richness '12 Treatment+logm3 (i)	Treatment (ECO)	0.90	0.31	**0.003**	2.1	0.136
	logm3	0.18	0.23	0.433		
Richness '12 Treatment+dwdiv (i)	Treatment (ECO)	0.92	0.27	**0.001**	0.0	0.382
	dwdiv	0.47	0.28	0.098		
Richness '12 Treatment (i)	Treatment (ECO)	1.03	0.26	**<0.001**	0.7	0.273
Abundance '12 Treatment*logm3 (j)	Treatment (ECO)	2.21	0.88	**0.012**	0.0	0.442
	logm3	1.12	0.50	**0.023**		
	Treatment (ECO)*logm3	-0.56	0.52	0.282		
Abundance '12 Treatment*dwdiv (j)	Treatment (ECO)	1.66	0.52	**0.002**	1.2	0.248
	dwdiv	1.17	0.51	**0.022**		
	Treatment (ECO)*dwdiv	-0.82	0.56	0.140		
Abundance '12 Treatment+logm3 (j)	Treatment (ECO)	1.02	0.23	**<0.001**	6.1	0.021
	logm3	0.08	0.17	0.628		
Abundance '12 Treatment+dwdiv (j)	Treatment (ECO)	0.97	0.20	**<0.001**	1.2	0.237
	dwdiv	0.47	0.21	**0.023**		
Abundance '12 Treatment (j)	Treatment (ECO)	1.08	0.20	**<0.001**	4.3	0.052
Richness '13 Treatment*logm3 (k)	Treatment (ECO)	2.59	1.02	**0.011**	1.1	0.19
	logm3	0.95	0.56	0.091		
	Treatment (ECO)*logm3	-0.87	0.61	0.150		
Richness '13 Treatment*dwdiv (k)	Treatment (ECO)	2.36	0.71	**0.001**	1.6	0.15
	dwdiv	1.15	0.72	0.109		
	Treatment (ECO)*dwdiv	-1.25	0.78	0.108		
Richness '13 Treatment+logm3 (k)	Treatment (ECO)	1.24	0.31	**<0.001**	1.1	0.19
	logm3	0.20	0.21	0.352		

Richness '13	Treatment (ECO)	1.37	0.27	**<0.001**	2.0	0.13
Treatment+dwdiv (k)	dwdiv	0.06	0.27	0.833		
Richness '13	Treatment (ECO)	1.38	0.27	**<0.001**	0.0	0.34
Treatment (k)						
Abundance '13	Treatment (ECO)	2.21	0.88	**0.012**	0.9	0.3933
Treatment*logm3 (l)	logm3	1.12	0.50	**0.023**		
	Treatment(ECO)*logm3	-0.56	0.52	0.282		
Abundance '13	Treatment (ECO)	2.72	0.61	**<0.001**	11.3	0.0021
Treatment*dwdiv (l)	dwdiv	1.49	0.61	**0.015**		
	Treatment (ECO)*dwdiv	-1.24	0.65	0.055		
Abundance '13	Treatment (ECO)	1.32	0.26	**<0.001**	0.0	0.6030
Treatment+logm3 (l)	logm3	0.61	0.15	**<0.001**		
Abundance '13	Treatment (ECO)	1.70	0.23	**<0.001**	12.7	0.0011
Treatment+dwdiv (l)	dwdiv	0.36	0.19	0.065		
Abundance '13	Treatment (ECO)	1.79	0.23	**<0.001**	14.0	<0.001
Treatment (l)						

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