

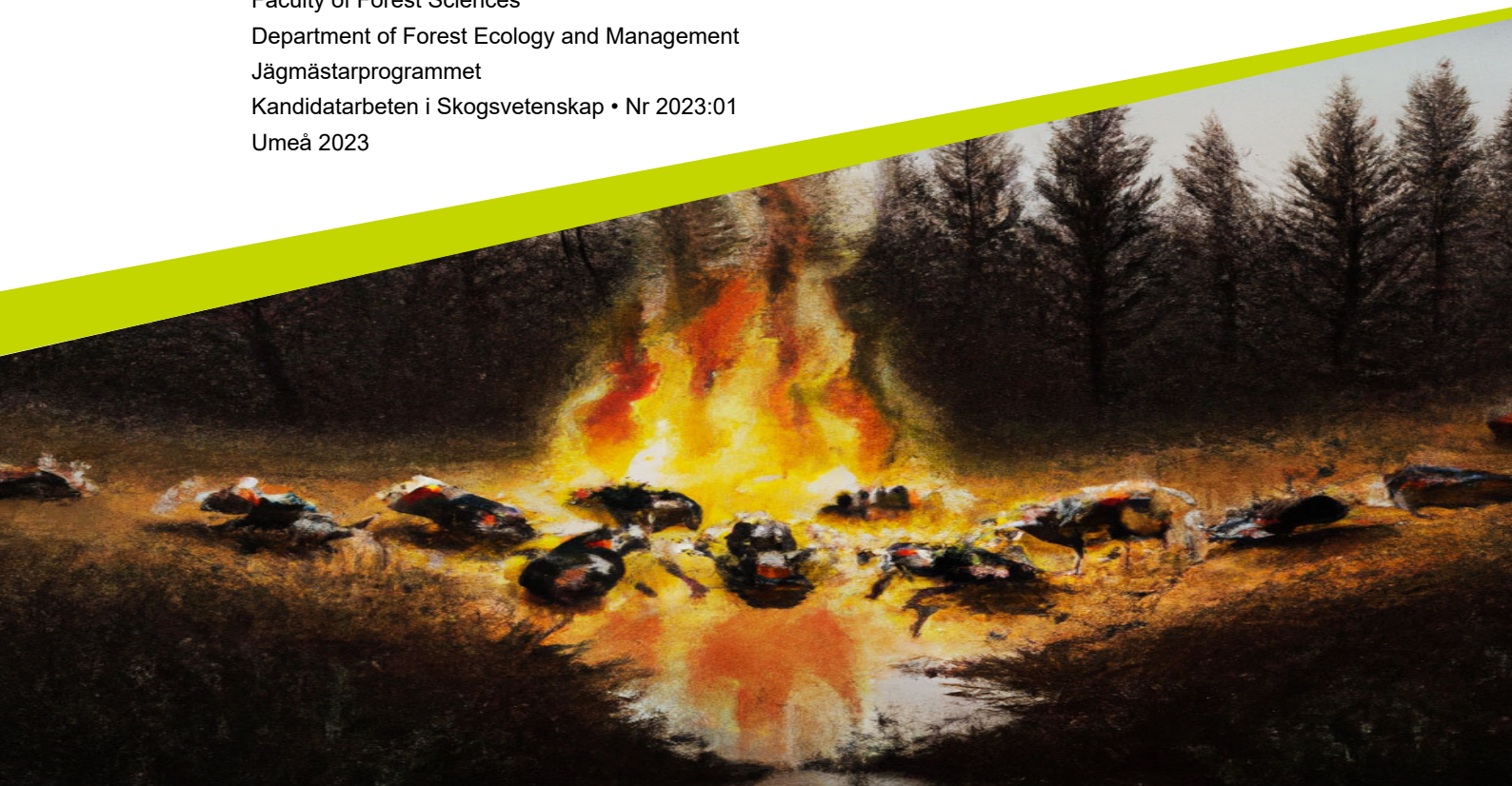


Beetle Diversity – Land Sharing or Land Sparing?

The effects of timber extraction and restoration method on saproxylic beetle assemblages in mature managed pine forests.

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Beetle Diversity – Land Sparing or Land Sharing? *The effects of timber extraction and restoration method on saproxylic beetle assemblages in mature managed pine forests.*

Effekterna av virkesuttag och restaureringsmetod på vedlevande skalbaggar i äldre skötta tallskogar.

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Abstract

The impoverishment of saproxylic beetle communities is a growing concern for management of boreal forest biodiversity. Past research has found active restoration methods, such as creating deadwood and conducting prescribed burnings, to have a short-term positive effect on the species richness and compositional diversity of saproxylic beetle assemblages. However, comparatively little work has been done on the effect of combining these with timber harvests. To efficiently allocate conservation efforts, the relative merits of combining or separating management for these two goals must be understood. Efficiently combining the two could help offset opportunity costs, make restoration efforts self-financing, or reduce goal conflicts between landowners and regulatory agencies. This is conceptualised according to a land-sparing/land-sharing model; wherein land-sparing entails management for biodiversity and timber production on separate lands, and land-sharing combines management for these goals across forest lands. The aim of this study is to examine how the diversity and composition of post-restoration saproxylic beetle assemblages is affected by retention level and choice of restoration method. Twelve stands were examined, each exposed to one of four treatments: prescribed burning with 100% or 50% retention level, and deadwood creation with 100% or 50% retention level. Trunk emergence traps were placed on deadwood in every stand. Treatment, i.e. restoration method and retention level, was found to have a significant effect on both saproxylic beetle abundance ($p = 0.003$) and species richness ($p = 0.03$). However, the direct effect of treatment on the underlying population could not always be separated from the effect of sampling intensity and no effect exclusively dependent on restoration method or retention level could be isolated. Treatment was found to have a significant effect on the composition of saproxylic assemblages ($p = 0.03$), albeit with low explanatory power ($R^2 = 0.35$). Although treatments that included burning and/or partial retention tended to have similar assemblage composition, prescribed burning with 100% retention level maintained higher variation between replicates and more unique species than any other treatment. This study concludes that, although land-sharing strategies might be situationally advantageous, large-scale implementation is unlikely to act as an effective substitute for the complex and highly variable ecological legacies of mimicking natural disturbance regimes and burning untouched stands.

Keywords: Saproxylic Beetles, Ecological Restoration, Deadwood, Biodiversity, Boreal Forests, Fire Ecology, Land-sparing, Land-sharing, Conservation Management

Sammanfattning

Utarmandet av biodiversitet bland vedlevande skalbaggar är ett växande problem för hållbar förvaltning av boreal skog. Tidigare forskning har kommit fram till att aktiva restaureringsmetoder, som att skapa död ved samt naturvårdsbränning, har kortsiktiga positiva effekter på vedlevande skalbaggars artrikedom och artsammansättning. Jämförelsevis få studier har gjorts på effekten av att kombinera dessa med virkesuttag. För att effektivt kunna designa bevarandeinsatser är det viktigt att förstå konsekvenserna av att kombinera respektive separera förvaltning för dessa två skogsbruksmål. Att kombinera naturvård med virkesuttag kan bidra till att minimera alternativkostnader i naturvårdsförvaltning, göra restaureringsinsatser självfinansierande, eller minska målkonflikter i skogsbruket mellan markägare och myndigheter. Detta conceptualiseras enligt en 'land-sparing/land-sharing' modell; där 'land-sparing' förvaltar för biodiversitet och virkesuttag på separata marker medan 'land-sharing' tillämpar kombinerad förvaltning över hela innehavet. Syftet med denna studie är att undersöka hur mångfalden av vedlevande skalbaggar påverkas av hänsynsnivå samt val av restaureringsmetod. Tolv bestånd studerades, var och en utsatt för en av fyra behandlingar; naturvårdsbränning med 100% respektive 50% hänsyn, samt skapande av död ved med 100% respektive 50% hänsyn. Kläckfällor placerades på död ved i varje bestånd. Behandling, dvs. restaureringsmetod och hänsynsnivå, visade sig ha en signifikant effekt både på vedlevande skalbaggars abundans ($p = 0.003$) samt artrikedom ($p = 0.03$). Det gick dock inte alltid att urskilja om detta var en effekt av behandlingen eller stickprovsstorlek. Ingen effekt specifikt mellan restaureringsmetoder eller hänsynsnivå kunde heller identifieras. Val av behandling visade sig ha en signifikant effekt på skalbaggsamhällets artsammansättning ($p = 0.03$), dock med låg förklaringsgrad ($R^2 = 0.35$). Även om behandlingar med naturvårdsbränning och/eller låg hänsynsnivå tenderade ha väldigt lika artsammansättningar, hade bestånd behandlade med naturvårdsbränning med 100% hänsynsnivå högre variation mellan upprepningar och fler unika arter än någon annan behandling. Denna studie drar slutsatsen att även om 'land-sharing' kan vara fördelaktigt i specifika situationer är det osannolikt att storskalig implementering praktiskt kan ersätta efterliknande av naturliga störningsregimer och de komplexa och varierade effekterna av att bränna orörda skogar.

Nyckelord: Vedlevande skalbaggar, Restaureringsekologi, Död ved, Biodiversitet, Boreal skog, Brandekologi, Land-sparing, Land-sharing, Naturvårdsförvaltning

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1. Introduction

1.1 Background

1.1.1 Biodiversity in the Boreal Forest

The global biosphere, across spatial scales and geographic regions, is currently undergoing rates of change and biodiversity loss unprecedented in the human era (Diaz et al. 2019). This global biodiversity crisis extends to boreal forest ecosystems and saproxylic organisms are among those most threatened (Fridman & Walheim 2000; Similä et al. 2003; Hyvärinen et al. 2005; Johansson 2006). Several practices and developments contribute to the loss of biological diversity in boreal forests: most notably intensive industrialised forest management making heavy use of clearcutting and soil scarification, the active and passive suppression of natural disturbance regimes, especially of fire, the historical loss of truly large trees to early commercial exploitation, and the impoverishment of deadwood stocks (Linder & Östlund 1998; Granström 2001; Hyvärinen et al. 2005; Johansson 2006; Kärvelo et al. 2017). Boreal forests are estimated to have historically maintained a fire interval of approximately 60-100 years which, although infrequent by global standards, is far more frequent than at present (Linder & Östlund 1998; Krawchuk et al. 2009). In effect, annual burned area has fallen from approximately 1% in the early modern period to less than 0.01% today (Zackrisson 1997; Granström 2001). Furthermore, average deadwood stocks have fallen from 30-90 m³/ha in old growth forests to an average 10.2 m³/ha in managed forests, although in some areas average losses of upwards of 90% have been recorded (Fridman & Walheim 2000; Siitonen 2001; Hyvärinen et al. 2005; Riksskogstaxeringen 2019). Moreover, there is substantial evidence of extinction debt in boreal forests, i.e. a time lag between extensive habitat destruction and as of yet unrealised biodiversity loss, indicating that the true scale of damage done may still be unknown (Tilman et al. 1987; Johansson 2006).

1.1.2 Land Sharing or Land Sparing in Swedish Conservation?

In response to the impoverishment of biodiversity in boreal forest ecosystems two options have continually been highlighted; adopting sustainable management preventing such loss or completely setting aside substantial land areas as forest reserves (Edwards et al. 2014). These suggestions are often made with reference to the land-sharing/land-sparing model (Parisi et al. 2018). In forestry, land-sharing refers to combining timber extraction with biodiversity conservation across managed forest lands, whereas land-sparing refers to high intensity logging across all productively managed lands whilst managing reserves of intact valuable forests solely for their ecological values (Edwards et al. 2014).

The Swedish conservation model, as enshrined in both forest legislation and certification schemes, is based on a multi-scaled conservation approach which partially integrates both land-sharing and land-sparing (Gustafsson & Perhans 2010). Land-sparing is practiced both in the maintenance of large-scale forest reserves and through voluntary or contracted setting aside of individual stands. Land-sharing occurs on a smaller spatial scale with deadwood creation and green-tree retention, i.e. leaving living trees on harvested sites, in timber harvests. Two separate tendencies indicate that land-sharing may become more prevalent in the future. For one, there is mounting evidence to suggest that the levels of retention currently maintained in harvest operations are too low to effectively maintain species diversity and that these should be increased (Toivanen & Kotiaho 2007; Söderström 2009). Some researchers have even suggested abrogating current legal limits on deadwood volumes left on harvest sites (Johansson et al. 2006). For another, there is some concern that, as formally protected areas grow older and continue to lack natural disturbance regimes, they will increasingly fail to adequately protect and maintain early successional structures and species (Linder & Östlund 1992; Gustafsson & Perhans 2010; Claesson et al. 2015). Partial harvests and prescribed burning have been suggested as countermeasures (Gustafsson & Perhans 2010). In management contexts defined by land-sharing strategies it is especially important to understand species' ecological habitat demands and their reactions to various management regimes (Johansson 2006).

1.1.3 Saproxylic Beetle Ecology and Biodiversity

Speight (1989) defines a saproxylic organism as one which at some point is dependent on dead or decaying wood for the completion of its life cycle. It is estimated that saproxylic organisms make up approximately 30% of biodiversity in European forests, 20-30% of all forest insects in Europe, and approximately 50% of European beetle diversity (Stokland et al. 2012; Parisi et al. 2018). Saproxylic beetles also tend to occupy niches crucial to forest ecosystem functioning by acting as keystone species determining later saproxylic succession and transporting

decomposer communities central to nutrient cycling (Mattson 1977; Paine et al. 1997; Murphy & Lehnhausen 1998).

Saproxyllic Beetles and Fire

Saproxyllic beetles are especially sensitive to disruption of natural fire regimes (Hyvärinen et al. 2005; Hjältén et al. 2018). Fire creates large amounts of deadwood for saproxyllic species and, as fire intensity tends to naturally vary within a stand, this deadwood also tends towards substantial heterogeneity in the microhabitats it supports (Wikars 1997; Esseen et al. 1997; Hyvärinen et al. 2005; Stokland et al. 2012; Hjältén et al. 2018). Fire also produces unique substrate qualities, reduces stand albedo, increases light exposure, and provides habitat for crucial pyrophilous fungal associates, etc. (Wikars 1997; Kouki et al. 2001; Siitonen 2001; Wikars 2002; Stokland et al. 2012; Hjältén et al. 2018). However, fire-adapted saproxyllic beetle species vary in their degree of dependence upon fire. Pyrophilous species are those specifically adapted to and dependent upon structures unique to fire (Wikars 1997; Hjältén et al. 2018). Fire-favoured describes those species which often are present in post-fire environments but do not depend upon them exclusively and do utilise other disturbed microhabitats (Wikars 1997; Hjältén et al. 2018).

1.1.4 Ecological Restoration for Saproxyllic Beetle Diversity

A number of restoration methods for maintaining the diversity of saproxyllic beetles have been suggested. These range from conventional methods, such as multi-scale green-tree retention, to more active management techniques seeking to mimic natural disturbance regimes, such as prescribed burning or manually creating dead wood (Gustafsson & Perhans 2010; Kärvelo et al. 2017).

Diversity, however, is a multifaceted concept, the various aspects of which ought to be outlined. In the context of this thesis diversity is defined as species diversity, which in turn is composed of abundance and species richness. Species richness refers to the number of unique species in a community or assemblage and the abundance of a species is the number of individuals of that species (Bowman & Hacker 2021). The species composition of an assemblage combines species' abundancies and species richness with the identities of the species. Biodiversity, on the other hand, is an often-ambiguous concept describing variation in a number of ecological entities at different scales ranging from genetic to ecosystem diversity (Begon et al. 2006; Bowman & Hacker 2021). As such, biodiversity is the subject of this study only indirectly; in that the species diversity of a stand and the variety of assemblage compositions between stands are aspects of biodiversity.

Judging from previous inquiries into the subject; choice of restoration method has a significant effect on species composition but a minimal effect on species richness.

Hyvärinen et al. (2005), in comparing prescribed burning and green-tree retention, found significant differences in assemblage composition. This is in line with plentiful research showing prescribed burns to support highly distinct saproxylic beetle assemblages (Hjältén et al. 2018). Kärverno et al. (2017) also found significant compositional differences between beetle assemblages after gap-cutting and prescribed burning. These differences, however, were primarily driven by an increased abundance of primary cambivores in burnt areas as a result of fire producing a plentiful supply of weakened, dying trees. It is then doubtful whether such patterns would remain when comparing prescribed burning to deadwood creation.

Many studies have found prescribed burning to have a weak or non-existent effect on species richness (Hyvärinen et al. 2005; Hjältén et al. 2018). Kärverno et al. (2017) found no significant difference in species richness between burnt and gap-cut areas. However, one study on saproxylic beetle assemblages in spruce deadwood found burnt substrates to have significantly lower species richness than unburnt substrates (Johansson 2006). Theoretically, this was due to degraded cambium food quality from burning. That said, it was noted that the manually burnt substrates used in the study only reflect a fraction of the diverse dead wood actually created by prescribed burning. Therefore, this substrate-level reduction in species richness might not be generalisable to a stand-level effect.

Similarly to restoration method, retention level, i.e. the proportion of standing volume left in a stand either as deadwood or living trees after restoration, seems to exert significant influence on assemblage composition, but not species richness. Hyvärinen et al. (2005) found harvest level prior to implementing restoration methods to influence subsequent beetle assemblages. Assemblages exposed to the same retention level were found to have very similar species composition. The same study also found a negative effect of retention level on species richness. However, they acknowledge that this difference was primarily driven by very low species richness found in stands with 100% retention level. As the study compared prescribed burning to green-tree retention their '100%' level did not wholly represent ecological restoration with full retention, but rather the lack of restoration in an already depauperate ecosystem.

Suitable retention levels have also been noted as important ahead of prescribed burning; both for producing important burned substrates and for regulating fire intensity (Johansson 2006; Hjältén et al. 2018). Partially harvested sites, for example, tend to burn with higher intensity by virtue of being drier and laden with logging residue (Hyvärinen et al. 2005). This may significantly impact beetle assemblages as species are adapted to specific pyromes of varying fire size and

intensity which restoration measures will then be more or less successful at replicating (Linder & Östlund 1998; Archibald et al. 2013; Hjältén et al. 2018).

1.2 Problem Specification

Taking the results of the studies above into consideration a problem can be formulated. It is clear, in light of the negative effects exerted by traditional forestry on beetle biodiversity, that some restorative countermeasures have to be undertaken. Theoretically, biodiversity can be effectively promoted by mimicking natural disturbances (Kärvemo et al. 2017; Parisi et al. 2018). For example, the reintroduction of disturbances like pasturing or prescribed burning has been highly beneficial in forest reserves and national parks (Jaworski et al. 2019). Thus, the importance of restoring fire regimes through active management and/or implementing strategies such as dead wood creation has been repeatedly emphasised (Hjältén et al. 2018; Parisi et al. 2018). However, whether these measures ought to be undertaken in complete isolation or in a mixed-use land-sharing context is unknown. In effect, it is of utmost importance to understand how beetle diversity is affected by different restoration methods and how those effects are shaped by integrating partial timber extraction. This thesis is limited to active restoration methods and will specifically consider the creation of deadwood and prescribed burning.

Implications

A satisfactory answer to the problem stated above should be of interest on at least three societal levels. Firstly, understanding exactly what trade-offs there are between different management goals is crucial to policy considerations. Secondly, knowing whether harvests and ecological restoration can be combined in regard to the diversity of certain groups of species would be of interest to large-scale institutional forest actors formulating their ecological landscape plans; potentially highlighting more cost-effective solutions. Finally, results affirming the viability of land-sharing might help mitigate conflicts between government actors concerned with conservation and private landowners, by allowing landowners to retain substantial harvesting rights.

1.3 Aim and Research Question

The aim of this thesis is to investigate how varying levels of retention in final felling ahead of ecological restoration, specifically controlled burning and deadwood creation, affects the diversity, i.e. abundance and species richness, as well as composition, of saproxylic beetle communities. From a larger perspective, these

results might have bearing on the extent to which restoration and conservation efforts can share land with conventional harvest regimes, highlighting opportunities for cost-saving in ecological landscape planning or providing guidance in negotiation between government actors and private landowners.

The proposed research question looks at how the diversity and composition of saproxylic beetle assemblages differs between restoration methods, controlled burning and creation of deadwood, with different levels of retention (50 and 100%).

Research Question: *How is the diversity and composition of a post-restoration saproxylic beetle assemblage affected by choice of restoration method and retention level?*

1.3.1 Hypothesis

Extrapolating the results of previous studies into the matter, the expectation is that both retention level and choice of restoration method will have minimal effect on the abundance and species richness of saproxylic beetles. However, both factors are expected to exert substantial influence on assemblage composition with ordination showing species composition in stands closely grouped according to both retention level and restoration method.

2. Materials and Methods

2.1 Study Area

The Effaråsen field experiment in the county of Dalarna, Sweden, was established in 2012 (Djupström & Weslien 2019). It is a long-term collaborative study between Skogforsk, the Swedish Forest Agency (Skogsstyrelsen) and Stora Enso Skog AB, the current landowner. Effaråsen is a southern boreal landscape located near Mora, Dalarna (see figure 1). The aim of the Effaråsen field experiments is to study and evaluate trade-offs between biodiversity conservation and forest production in old pine forests. The total study area of the experiment is comprised of approximately 140 hectares of an old, relatively homogenous Scots pine (*Pinus sylvestris*) forest with an age range of 120 – 140 years old, but far older trees can be found throughout the site. Density ranges from approximately 350-800 stems/ha. Other plant and tree species found in the area include lingonberry and bilberry shrubs, lichens and mosses, Norway spruce, and birch trees.

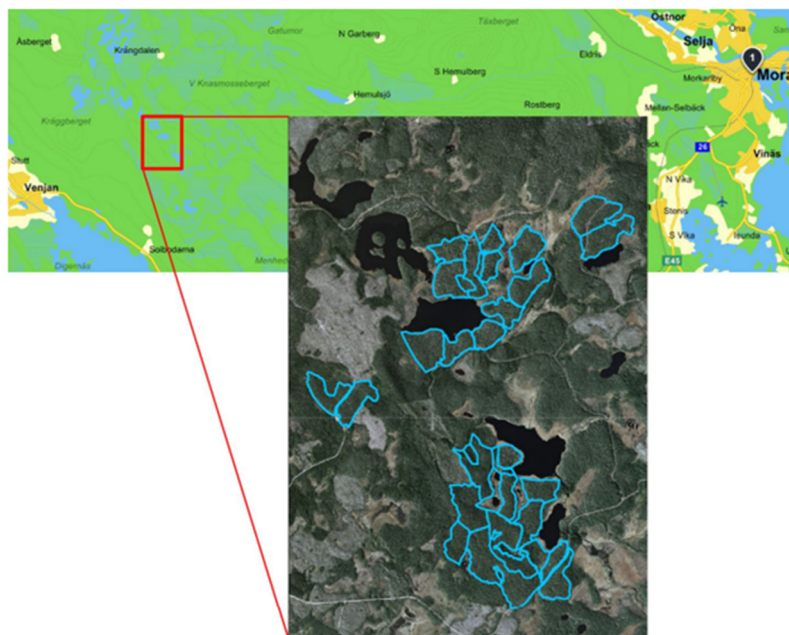


Figure 1: Map of the Effaråsen trial area. Centre coordinate is 6759826,447575 (SWEREF 99 TM) (Djupström & Weslien 2019).

The stands in the study area were naturally regenerated after a large forest fire in 1888 and have been subjected to forest management methods, such as thinning and fertilisation, during the second half of the 20th century. Although few signs of active management can be seen today, the forests, despite their age, lack old growth structures and characteristics such as high volumes of coarse woody debris.

To collect the data analysed in this thesis twelve stands of ~ 5 hectares in size were randomly selected and subjected to four different restoration treatments: deadwood creation with two retention levels (50 and 100%) and prescribed burning with two retention levels (50 and 100%). These will henceforth be referred to as C50, C100, B50, and B100 respectively. There were three stand replications for each treatment. All management practices were carried out within a period of two years (2012-2014), around nine years before beetle collection. Retained trees in the six stands with deadwood creation were divided on a substrate level into four equal parts; living trees, creation of logs, creation of high-stumps (~3 metres in height) and creation of bark-peeled snags. The prescribed fire intensity in the six burned stands was severe enough to cause extensive tree death to the retained trees, resulting in the creation of deadwood. The fire created logs, which are standing trees that were burned and fell, snags, which are standing trees that were burned and killed, and high-stumps, which are standing burned trees that then broke off at the top (varying heights of 2 – 12 metres).

2.2 Data Collection

Trunk emergence traps were used to collect beetles. They provide a measurement of insect production in deadwood subjected to the various treatments. Emergence traps collect all insects emerging from an enclosed section of the deadwood. A section of deadwood is wrapped in a polypropylene weed barrier cloth. The cloth allows water and oxygen to pass through, but not light. The traps are sealed with wires at the ends of the cloth and a container is attached to the top of the trap (see figure 2). Strips of foam carpet underlay were also placed under the wires to further ensure the sides of the trap are fully sealed. The 250 mL translucent container attached to the top of the trap was partly filled with 70% propylene glycol and dish soap to break the surface tension. Insects emerging from the substrate moved towards the light, were caught in the container and preserved in the solution.

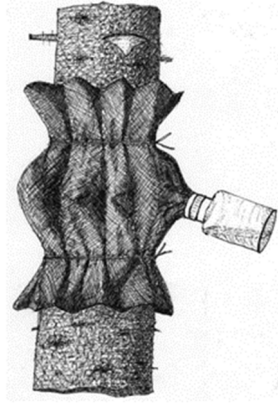


Figure 2: Illustration of an emergence trap (Johansson et al. 2006).

The emergence traps were attached to five of each substrate type (logs, snags and high stumps) in every stand, fifteen traps per stand in total. The collection period occurred during the vegetation season of 2022, specifically between April and October. After collection, all insects underwent species-level identification by Dr. Hans-Erik Wanntorp, a taxonomic expert.

2.3 Data Analysis and Statistics

First, the data was filtered to only contain saproxylic beetles and no other insects, as emergence traps often captured other types of insects, and in some cases even small lizards. Data irrelevant to the analyses was also removed, such as species conservation status. All statistical analyses of the dataset were done using the computer program R-Studio (version 4.2.1). A significance level of 95% was used for all statistical tests ($\alpha > 0.05$).

Secondly, to test for significant differences in species richness and abundance between treatments a one-way analysis of variance (ANOVA) was utilised. Total capture frequency and the number of unique species names were summed over treatment, stand, and trap number. This effectively combined one log, one bark-peeled snag, and one high stump into a single measurement plot theoretically abstracting from the influence of deadwood type on abundance and species richness. Two one-way ANOVA models were then fitted with treatment as the independent variable, one for abundance and one for species richness. Both models were checked against the assumptions necessary for an ANOVA. The abundance model did have a noticeable outlier, so a separate ANOVA was run without this data point, the results of which were compared with the original. ANOVA was conducted on each of the models and p-values were recorded. Where significant effects were found post-hoc examination using Tukey's HSD -test was carried out and significance levels recorded.

Thirdly, to compare the differences in species richness on a stand level and examine the effects of sample size, rarefaction curves were used. Rarefaction curves plot the number of individuals sampled on the x-axis against the measured species richness on the y-axis. This is done by taking a number of observation knots from the actually measured reference sample and plotting their cumulative species richness. This process is then carried through to double the size of the reference sample extrapolating the hypothetical richness of a larger sample size. Observed frequencies were summed over species and treatment and rarefaction curves were created from this data.

Lastly, non-metric multidimensional scaling (NMDS) was used to visualise the distribution of saproxylic beetle compositions through ordination, and permutational analysis of variance (PERMANOVA) was used to test for significant differences in assemblage composition. The number of observations for each species in each stand was extracted, reformatted into a list, and visualised in an NMDS. This data was then inserted into a PERMANOVA with treatment as the explanatory variable and significance levels recorded. Post-hoc examination using a pairwise PERMANOVA with correction for cumulative risk of type-I error was carried out. For further visualisation of data, a Venn diagram was created showing how many unique species were found in each treatment as well as which species were identified in multiple treatments.

3. Results

For complete tables of statistical tests, see appendix.

3.1 Abundance and Species Richness

In total 714 individual beetles of 76 species were caught. A significant effect of treatment on abundance was found (p -value = 0.003046). Saproxyllic beetle abundance showed a general tendency to increase with treatment intensity; being lowest in deadwood creation with 100% retention level and then increasing with reduced retention levels and with burning (see figure 3). Burnt stands were found to have higher abundance than unburnt stands. Post-hoc examination found a pairwise significant difference only between the least intense treatment (C100) and the most (B50) (p -value = 0.0013579). No significant pair-wise differences were found between stands with the same retention level or restoration method. Lower retention level resulted in higher abundance for both restoration methods. When examining assumptions for the abundance ANOVA model a substantial outlier was found. Removing this entry from the dataset resulted in a far better fit against the assumptions. With this outlier included there was a low but non-significant p -value between treatments B100 and C100, but this effect disappeared when the outlier was removed. All results are displayed with the outlier removed.

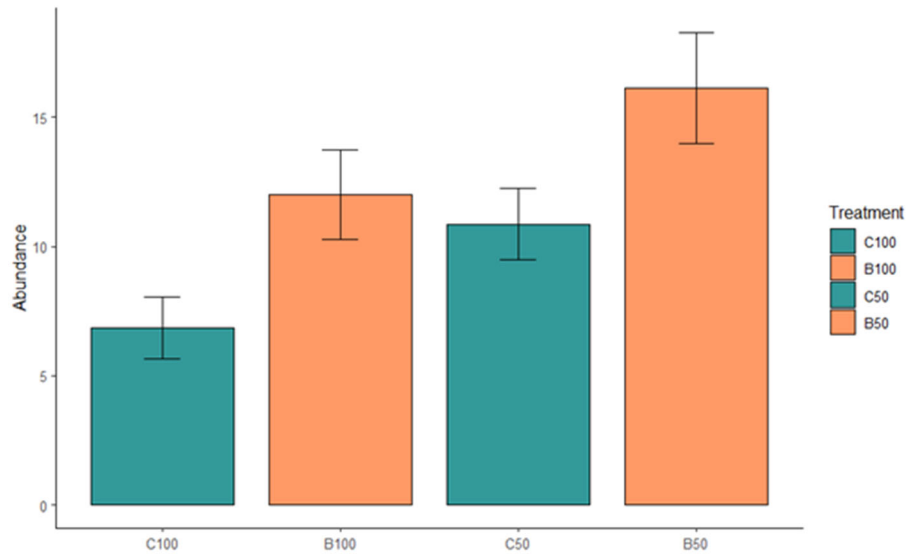


Figure 3: Bar graph of average abundance for a group of three traps (log, snag, and high stump) over stand treatment.

There was a significant effect (p -value = 0.0311) of stand treatment on species richness of saproxylic beetles. Much like abundance, species richness showed a general tendency to increase with treatment intensity; richness being lowest in deadwood creation with 100% retention level and then increasing with lower retention levels and burning (see figure 4). Higher species richness was observed in burnt stands than unburnt stands. A lower retention level resulted in higher average species richness for deadwood creation. However, when comparing the species richness of burnt stands a higher richness was observed in stands with 100% retention level. Post-hoc examination showed a significant difference in species richness between treatments B100 and C100 (p -value = 0.0337468). There was also a low but non-significant p -value between treatments B50 and C100 (p -value = 0.0635689). No significant pair-wise differences were found between stands of the same restoration method.

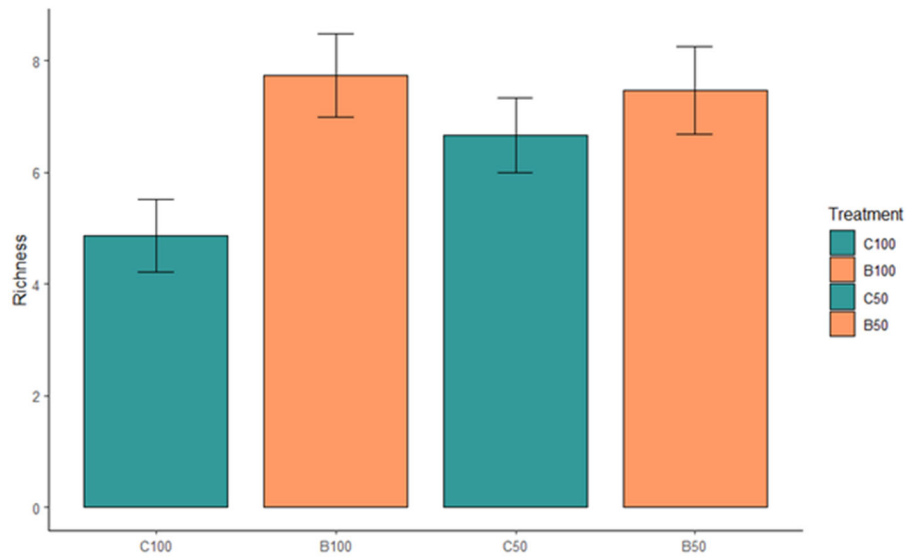


Figure 4: Bar graph of average species richness for a group of three traps (log, snag, and high stump) over stand treatment.

Juxtaposing the rarefaction curves of the two treatments, B100 and C100, for which a significant difference in richness was found, it can be seen that they have highly similar diversity trajectories (see figure 5). This might indicate that the observed differences in richness are an effect of sample size and not a reflection of the underlying population. Furthermore, comparing the curves of treatments B50 and C100, between which a low but non-significant p-value was found in ANOVA, it seems likely that this difference would shrink given increased C100 sample size. Interestingly, while no significant differences were found between B100 and C50 in the ANOVA, a significant treatment-level difference is indicated by their rarefaction curves. On the other hand, the insignificant differences between treatments C100 and C50, B100 and B50, as well as B50 and C50, found in ANOVA, are supported by their rarefaction curves.

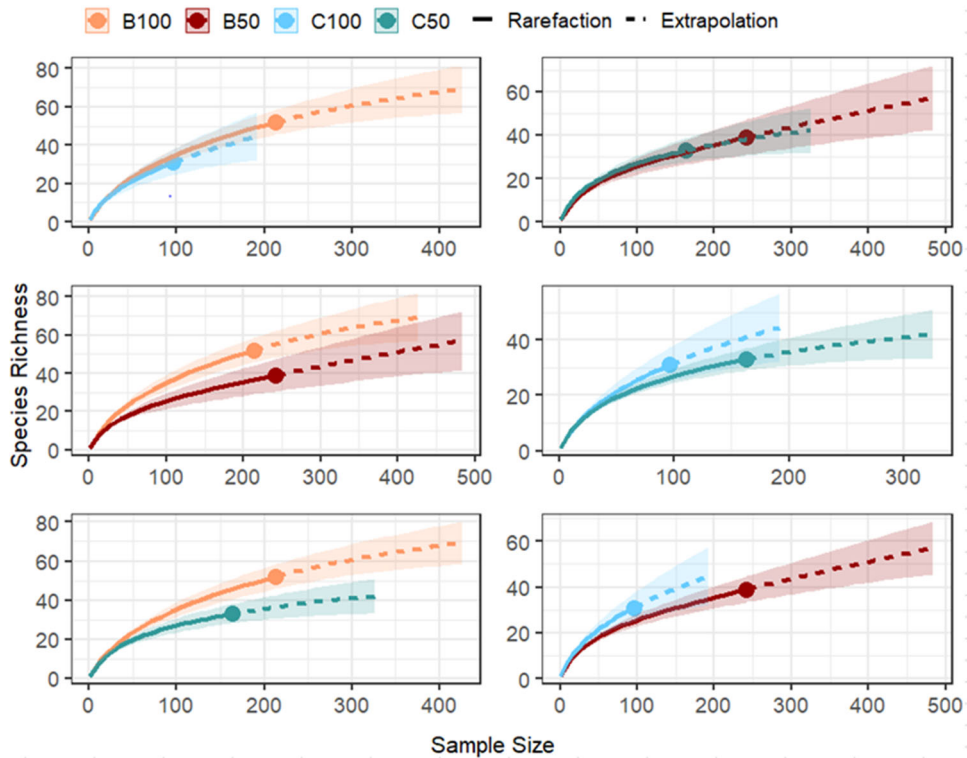


Figure 5: Rarefaction curves of species richness ($q=0$) over sample size for treatments (left to right, top to bottom) (1) B100-C100, (2) B50-C50, (3) B100-B50, (4) C50-C100 (5) B100-C50, and (6) C100-B50.

3.2 Species Assemblage Composition

The PERMANOVA test showed a significant overall effect of stand treatment on assemblage composition (p -value = 0.032), but with quite a low R-squared value ($R^2 = 0.35402$), indicating that a large proportion of unexplained variance remains.

However, the data proved insufficient for identifying any significant pairwise compositional differences. The post-hoc pair-wise comparisons showed low but non-significant p -values for comparisons between B50 vs C100, B100 vs C100, C50 vs C100, and C50 vs B50. This might indicate that C100 stands tended to be distinct compared to the other three treatments, and that intensively managed stands, C50 and B50, tended to be distinct from each other. An NMDS ordination plot allows for visual representation of saproxylic beetle compositions in the four different treatments (see figure 6). The composition distribution of saproxylic beetle assemblages in stands with retention levels of 50% is noticeably narrower than that in stands with retention levels of 100%. From the NMDS, compositions in B100 stands were highly inconsistent and seemed generally intermediate between those in B50 and C50 stands. C100 stands also showed high internal variation in assemblage composition.

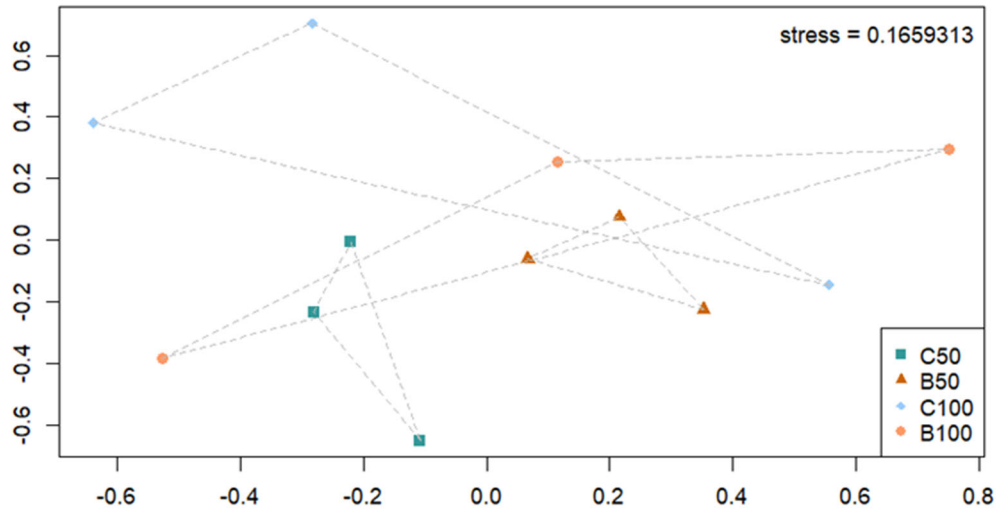


Figure 6: Non-metric multidimensional scaling (NMDS) ordination of observed stand-level assemblage compositions for different stand treatments.

The Venn diagram further expands upon the results of the PERMANOVA and the NMDS ordination plot. Treatments B100 had many unique species, 18 (see figure 7). 4 species were only present in treatment C100, 5 in treatment C50, and 8 in treatment B50. A substantial core of 15 species was present in all four treatments. 13 out of the total 76 species collected were only found in treatments with creation of deadwood, whereas 31 were only found in burnt stands.

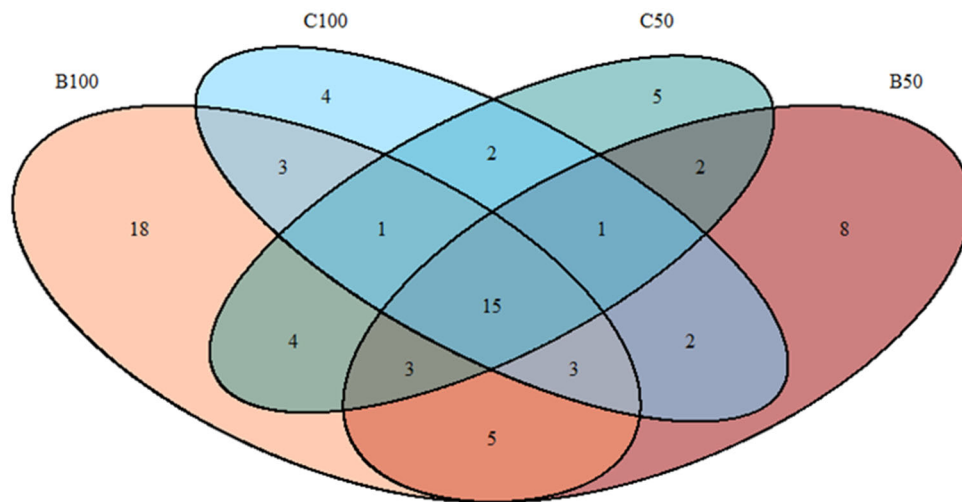


Figure 7: Venn diagram of the number of saproxylic beetle species found in each treatment and their respective unions.

4. Discussion

4.1 Abundance and Species Richness

As stated, the only significant difference in abundance was found between treatments C100 (creation of deadwood with 100% retention level) and B50 (burning with 50% retention level). As such, it is difficult to conclusively demonstrate any clear difference in abundance between restoration methods and between retention levels. It was hypothesised that retention level and choice of restoration method would have a minimal effect on the abundance of saproxylic beetles, which aligns with the results.

However, the results do suggest a general positive effect of disturbance intensity on abundance; with a visually higher abundance of saproxylic beetles in burned stands and stands with partial retention (50%) (see figure 3). One potential reason for this result is insect activity. Insects often display greater flight activity after burning as a result of a warmer microclimate, as well as in stands with lower retention levels as insects have to travel more to find viable substrates (Wikars 1997; Henderson & Southwood 2016; Hjältén et al. 2018). These apparent differences in abundance might then be less a result of genuine differences in the underlying populations and more a result of uneven sampling efficiency between treatments.

Choice of restoration method and retention level had little effect on the richness of saproxylic beetles. The only significant difference in species richness was found between burnt and unburnt stands with a 100% retention level. However, the rarefaction curve between treatments C100 and B100 shows that the number of individuals collected in treatment C100 was around 100, and the number of individuals collected in treatment B100 was over 200 (see figure 5). As discussed, insect activity tends to be higher in burnt stands, which could explain why the number of individuals collected in the C100 stands was half of that in the B100 stands. The extrapolated line of the rarefaction curve hints that if more individuals were to have been collected for treatment C100 the difference in species richness would have been smaller.

As with abundance, it was hypothesised that choice of restoration method and retention level would have minimal effect on the richness of saproxylic beetles; once again aligning with the results. No significant effect of retention level and only a very doubtful effect of restoration method was found. Nevertheless, visual interpretation might suggest retention level to exert a weak positive effect in prescribed burns and a weak negative effect in deadwood creation (see figure 4).

There are several possible explanations for high retention level being associated with low species richness in deadwood creation. As discussed, low species richness might very well be due to low insect activity in sampling. Nevertheless, there are alternative explanations. For one, the effect does parallel similar negative effects of retention level in studies focusing on green-tree retention (Hyvärinen et al. 2005). It was thought that this effect reflected a lack of restoration in an already depauperate ecosystem and was not an effect of retention level as such, and that it was likely to disappear in an investigation focused on deadwood creation. This was not the case. Thus, deadwood creation with full retention (100%) might be too mild a disturbance to provide appropriate levels of exposure for beetles associated with this stage of saproxylic succession. For another, one-time creation of fresh deadwood might not support the niches traditionally exploited by saproxylic beetles in old pine forests. Old-growth coniferous forests usually support heavily fungivorous assemblages, a functional group traditionally associated with deadwood undergoing late-stage decay (Johansson 2006).

If retention level has a minor positive effect on species richness in burnt stands, this is likely an effect of higher deadwood quality as reduced fire intensity caused less extensive degradation of cambium food quality (Johansson 2006). If so, it would support a theory laid out by other similar studies, that the main beneficial effects of burning are the creation of deadwood and signalling for fire-adapted species whilst the deadwood actually created is of poor quality and maintains depauperate assemblages (Hyvärinen et al. 2005; Hjältén 2018).

4.2 Species Assemblage Composition

The results regarding saproxylic beetle assemblage composition show a significant overall effect of stand treatment, but the data proved insufficient for identifying significant pairwise differences. However, visual interpretation using an NMDS ordination allowed for some tendencies to be discerned (see figure 6). Species assemblage composition seems not to differ substantially between restoration methods, as C50 stands had similar composition to B100 stands. Similarly, no great effect of retention levels was observed for prescribed burning; burned stands regardless of retention level seem to yield similar compositions. Interestingly,

however, retention level had a more substantial, but nevertheless insignificant, effect on unburnt stands. To answer the research question, assemblage composition might be driven by retention level, but only in unburnt stands. This would partially support and partially contradict the hypothesis stating that retention level and choice of restoration method should exert a substantial influence on assemblage composition.

The NMDS ordination plot shows a narrower composition distribution for treatments with partial retention (50%) than stands with full retention (100%). One explanation might be that exposure to more intense disturbance, such as partial retention, produces more extreme environments with tapered resource and niche availability. Another might be that timber extraction results in reduced diversity of ecological outcomes between stand repetitions. For example, both land-sharing arrangements (C50 and B50) might narrow the highly variable effects of fire disturbance naturally produced by inter-stand differences in topography, moisture, and forest structure; resembling two fractional subsets of the wide variety of potential legacies produced by fire (Kuuluvainen 2009). On one hand, harvesting before fire ensures high fire intensity, intense scorching, and extensive tree mortality (Hyvärinen et al. 2005). Deadwood creation, on the other hand, only creates unscorched, warm, and sun-exposed deadwood with intact cambium; substrates commonly associated with low-intensity fires (Johansson 2006; Kuuluvainen 2009). Burning after harvest would support truly ‘pyrophilous’ assemblages reliant on large volumes of chemical signals, fire-specific fungal associations, or unique substrate qualities only created by high-intensity fires (Wikars 1997; Hyvärinen et al. 2005; Hjältén et al. 2018). Deadwood creation might then support so-called ‘fire-favoured’ assemblages associated with fire only as far as it is a generic disturbance producing deadwood (Hjältén et al. 2018).

Interestingly, the B100 stands also yielded a composition distribution intermediate between the clustered compositions of B50 and C50. This too could be explained by B50 and C50 treatments representing two potential ecological legacies of more complex disturbances like B100. A connection between these three treatments is supported by the Venn diagram, as B50 and C50 stands had a substantial overlap with B100 (see figure 7). Moreover, B100 stands maintained far more unique species than those treated with partial retention despite similar average plot-level richness (see figure 4). This might indicate that prescribed burning with full retention supports higher variation between stand replicates than treatments with partial retention and that there may be more potential legacies to burning untouched forests beyond those emulated by C50 and B50 treatments. Thus, whilst these three treatments result in similar species richness, burning with full retention might support greater landscape-level diversity. However, it should be noted that C50 and

B50 treatments did support some unique species, perhaps indicating that their successional dynamics may not be entirely reducible to fractional wildfire legacies.

4.3 Land Sharing or Land Sparing?

It is important to keep in mind that this study can draw no definitive conclusions concerning land-sharing and land-sparing, as it only indirectly considered the question through use of retention level as a proxy and only studied its effects on a single group of species using a single trap type. However, some tendencies might still be discerned. On one hand, the results seem somewhat favourable to land-sharing. High retention levels when creating deadwood seems to only support depauperate saproxylic beetle assemblages. Species richness might be lower than that produced by other treatments and assemblage composition is seemingly very different from that created by burning (see figure 4 and 6). Notably, stands treated with C100 maintained few unique species and those species it did maintain were predominantly shared with all other treatments, which could indicate support mainly for deadwood generalists with dubious conservation value (see figure 7). Additionally, deadwood creation with low retention levels supports similar assemblages and levels of richness to prescribed burning. Further, harvest preceding prescribed burning seems to have a minimal effect on species richness and assemblage composition compared to unharvested prescribed burns (see figure 4 and 6). However, some note should be made of the large compositional variation between stand replicates of prescribed burning with full retention as compared to C50 and B50 treatments (see figure 7). As previously mentioned, despite their similar species richness, a land-sparing approach might maintain larger landscape-level diversity. The concern is then that large-scale application of land-sharing arrangements might fail to capture the natural complexity of fire's multiple successional legacies.

The results of this study do correspond with much of conservation land management's received wisdom. Created deadwood in otherwise undisturbed and closed canopy forests seems unable to maintain those saproxylic beetle assemblages found in stands subjected to greater degrees of disturbance. This would support findings that forest reserves lacking natural disturbance regimes require active management to maintain species diversity (Jaworski et al. 2019). Furthermore, the fact that deadwood creation combined with partial harvest only seems able to partially replicate certain aspects of fire does validate the theoretical primacy of emulating natural fire regimes through prescribed burning (Hjältén et al. 2018). This is further supported by 31 species only being found in burnt stands, compared to 13 in stands with deadwood creation. Higher compositional diversity following unharvested prescribed burns also supports certain conservation policies, such as

the Forest Stewardship Council (FSC) rewarding burning with higher retention levels by allowing them to count double or even triple towards minimum annual area burned (Anonymous 2020).

However, it should be noted that, in conservation, matrix quality, i.e. the conservation value of the general managed forest landscape, is often conceptualised as being in a trade-off relationship with the proportion of forests held in reserve (Gustafsson & Perhans 2010). For example, they both represent a draw on institutional tolerance for opportunity costs and contribute to a minimum degree of landscape quality (Gustafsson & Perhans 2010). Extrapolating from current forest developments suggests a continued deterioration of matrix quality as increasing demand for biofuels and other sustainable forest resources drives further intensification of management and extraction (Hunter 1999; Bergh et al. 2005; Andersson et al. 2015; Claesson et al. 2015; Parisi et al. 2018). If land-sharing approaches, as this study suggests, are unable to bring about an opposite development or, as others have suggested, their ability to do so actually further diminishes in a more intensively managed landscape, it stands to reason that the importance of land-sparing approaches to conservation would increase (Gustafsson & Perhans 2010). As such, the proportion of forest lands allocated to reserves might need to increase in the future.

Nevertheless, this study indicates a number of situations where land-sharing approaches may be appropriate. For one, deadwood creation with preceding harvest may be an eminently suitable substitute in situations where and when prescribed burning is inappropriate for reasons of safety, aesthetics, or recreation. For another, the close compositional grouping of treatments with partial retention does confer a predictability which may be a boon when restoration is implemented to maintain one or a few uniquely threatened species. Finally, land-sharing arrangements may still be crucial for maintaining matrix permeability for meta-population concerns and reducing dispersal barriers for migratory and/or environmentally displaced species (Gustafsson & Perhans 2010).

4.4 Strengths and Weaknesses

The novelty of this investigation is largely grounded in a number of methodological advantages over past similar studies. For one, captured beetles were recorded 8-10 years after restoration. Due to restoration ecology being a relatively new field lacking long-term field trials, many previous studies examined beetle diversity immediately following logging/burning (Hyvärinen et al. 2005). As such, these were only able to analyse the effects of attracting beetle species; failing to measure the ability of restored areas to maintain and reproduce saproxylic beetles. This bias

has been suspected of suppressing the importance of retention levels in designing ecological restoration (Hyvärinen et al. 2005). The composition of saproxylic beetle communities is also known to change significantly over time meaning that this study highlights a previously scarcely studied successional phase (Parisi et al. 2018). For another, comparing controlled burning to manual deadwood creation, rather than for example green-tree retention, removes a suite of factors that otherwise obscure the specific impact of the burning itself. These include deadwood volume, light exposure, and availability of weakened, slowly dying trees. Finally, creating several types of deadwood enhanced comparability with the diversity of deadwood produced by controlled burning. Otherwise, the effect of restoration method could be confounded with that of different substrate types supporting compositionally divergent saproxylic beetle assemblages (Similä et al. 2003; Andersson et al. 2015).

On the other hand, this study also had a number of weaknesses constraining the interpretative space afforded its results. One of these is aptly demonstrated by the rarefaction curve of treatment C100, which shows sampling to have ended long before species observations had reached an acceptable level of saturation (see figure 5). As previously discussed, this calls into question some of the study's results regarding the effect of treatment on species richness. Results regarding abundance might have similarly been affected and, should activity biases be inconsistent across species, assemblage composition measurements may have been impacted. Secondly, use of pairwise PERMANOVA for post-hoc examination of restoration treatment's effect on assemblage composition failed to find any significant differences despite a significant effect being identified in the global PERMANOVA (table 5; see appendix). This problem might have been avoided if larger samples were collected; either by using more traps per plot which would enable use of plot-level PERMANOVA, or by having more replicate stands for each treatment.

Thirdly, the sampling utilised only one trap type. Trunk emergence traps are excellent for targeting the ability of restored stands to support beetle reproduction, for measuring substrate-level preferences, and for ensuring captured beetles originate in the stands measured (Andersson et al. 2015). Some studies, however, have utilised a combination of window and emergence traps to analyse differences in the assemblages attracted to a site and the assemblages actually reproduced there (Johansson 2006; Johansson et al. 2006). This additional dimension of interpretation might have helped explain some of the compositional differences between assemblages in treatments B50, C50, and B100. Specifically, it might have helped explain why both B50 and C50 both supported different narrow slices out of the larger compositional range spanned by B100. Did all three treatments attract similar compositions with subsequent reproductive homogeneity in harvested stands being a result of having more consistent deadwood quality? Or do they differ

in the species they attract, with C50 treatment, for example, failing to attract species it could otherwise support as a result of its lack of crucial chemical smoke signals?

The study also suffered from the absence of ‘control’ measurements. However, this was unavoidable due to the deadwood stocks of unrestored sites being insufficient for detailed measurements. That said, similar studies have been performed on sites richer in deadwood (Hyvärinen et al. 2005). This afforded increased interpretative latitude with regards to the relation between beetle communities on restored sites and those that preceded them. In this study such an analysis could have helped determine the nature of the distinctive assemblage composition of C100 treatments. Do C100 stands represent a unique and highly valuable niche community adapted to fresh deadwood from small-scale disturbances that retain shading and moisture from near-full canopy closure? Or do they, as has been suggested in other studies, represent only a motley meeting of highly tolerant late and early successional generalists of dubious value to conservation efforts (Hyvärinen et al. 2005; Johansson 2006; Matveinen-Huju et al. 2006; Perhans et al. 2009)? Further, the utility of the results achieved are somewhat limited by only testing two levels of retention, implying an unrealistically binary choice between land-sparing or land-sharing.

Lastly, this study measures beetle diversity at a single point in time and similarly carries out restoration methods only once. Saproxyllic beetle communities pass through distinct successional patterns with assemblage composition changing alongside with the structural and nutritional conditions of the deadwood substrate (Speight 1989; Saint-Germain et al. 2007; Stokland et al. 2012; Parisi et al. 2018). The diversity of sub-cortical phloem feeders, for example, tends to peak soon after deadwood recruitment, whereas fungivores only come to dominate following bark detachment (Stokland et al. 2012; Parisi et al. 2018). Additionally, deadwood creation predominantly occurs as a result of disturbance which links deadwood’s internal succession to ecosystem-wide successional dynamics (Johansson 2006). It would then stand to reason that the effects of restoration method and retention level on beetle diversity would change over time and that one-time measurements only capture snapshots of far more dynamic ecological legacies. A longer study horizon would also allow for investigation into the effects of recurrent restoration efforts and timber harvests. Recurrent restoration efforts, for example, are probably necessary to maintain the diversity of deadwood size and decay stage that is crucial to saproxyllic beetle diversity (Similä et al. 2003).

4.5 Future Studies

Further studies seem necessary to comprehensively outline the effects of land-sharing and land-sparing in restoration for saproxylic beetle diversity. First and foremost, a general dearth of long-term studies on saproxylic beetles has been repeatedly noted and extends to investigations into their potential restoration (Johansson 2006; Gustafsson & Perhans 2010; Hjältén et al. 2018). To understand the effects of restoration and land-sharing across successional phases as well as the interactions and interferences inherent to recurrent application, long-term observations with repeated resampling seems necessary. Further, modelling multi-scale beetle diversity from stand characteristics could allow for studies into how land-sharing and land-sparing allocation might be optimised across a landscape and for quantification of restoration's opportunity cost trade-off. Moreover, a natural next step would be replicating the analyses of this study on a substrate level to investigate the interaction of restoration method and retention level with various deadwood classes. Finally, similar studies might be attempted across other species groups, restoration and conservation methods, forest types, and historical succession dynamics.

4.6 Conclusion

In conclusion, the abundance and richness of saproxylic beetles is unlikely to differ between restoration methods and retention levels. However, prescribed burning seemingly remains indispensable to restoration for landscape-scale saproxylic beetle diversity, regardless of whether land-sharing or land-sparing is applied. Furthermore, in some situations prescribed burning is out of the question and manually created deadwood must instead be used. As far as economics and mid-successional saproxylic beetles are concerned, this ought to be done in conjunction with timber extraction as part of a land-sharing arrangement. However, it seems unlikely that extensive land-sharing arrangements can act as an effective landscape-level substitute for the complex and highly variable ecological legacies of emulating natural disturbance regimes and burning untouched stands. Nevertheless, land-sharing might still be a useful strategy if and when it would allow larger areas to be restored than otherwise possible, for example by offsetting costs or reducing trade-offs with other ecosystem services such as carbon sequestration or recreation.

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Appendix

Table 1: Statistical table from the one-way ANOVA test on the effect of stand treatment on saproxylic beetle abundance *significant results (p -value < 0.05)

| One-way ANOVA | | | | |
|----------------------|---------|----|---------|-----------|
| Response: Abundance | | | | |
| | Sum Sq | Df | F value | Pr(>F) |
| Treatment | 633.25 | 3 | 5.2306 | 0.003046* |
| Residuals | 2179.18 | 54 | | |

Table 2: Statistical table from the post-hoc Tukey's HSD-tests for the effect of stand treatment on saproxylic beetle abundance *significant results (p -value < 0.05)

| Tukey multiple comparisons of means (Abundance) | | | | |
|--|-----------|------------|-----------|------------|
| Treatment | diff | lwr | upr | p-adj |
| B100-C100 | 5.142857 | -1.2220206 | 11.507735 | 0.1530526 |
| C50-C100 | 4.009524 | -2.2483736 | 10.267421 | 0.3344933 |
| B50-C100 | 9.276190 | 3.0182931 | 15.534088 | 0.0013579* |
| C50-B100 | -1.133333 | -7.3912307 | 5.124564 | 0.9631820 |
| B50-B100 | 4.133333 | -2.1245640 | 10.391231 | 0.3081044 |
| B50-C50 | 5.266667 | -0.8823894 | 11.415723 | 0.1178174 |

Table 3: Statistical table from the one-way ANOVA test on the effect of stand treatment on saproxylic beetle richness *significant results (p -value < 0.05)

| One-way ANOVA | | | | |
|----------------------|--------|----|---------|---------|
| Response: Richness | | | | |
| | Sum Sq | Df | F value | Pr(>F) |
| Treatment | 72.39 | 3 | 3.1771 | 0.0311* |
| Residuals | 417.71 | 55 | | |

Table 4: Statistical table from the post-hoc Tukey's HSD-tests for the effect of stand treatment on saproxylic beetle richness *significant results (p -value < 0.05)

| Tukey multiple comparisons of means (Richness) | | | | |
|---|------------|------------|-----------|------------|
| Treatment | diff | lwr | upr | p-adj |
| C100-C50 | -1.8095238 | -4.5227600 | 0.9037124 | 0.3001028 |
| B50-C50 | 0.8000000 | -1.8660458 | 3.4660458 | 0.8564084 |
| B100-C50 | 1.0666667 | -1.5993792 | 3.7327125 | 0.7150294 |
| B50-C100 | 2.6095238 | -0.1037124 | 5.3227600 | 0.0635689 |
| B100-C100 | 2.8761905 | 0.1629543 | 5.5894266 | 0.0337468* |
| B100-B50 | 0.2666667 | -2.3993792 | 2.9327125 | 0.9934104 |

Table 5: Statistical table from the PERMANOVA test (999 permutations) on the effect of stand treatment on saproxylic beetle composition *significant results (p -value < 0.05)

| PERMANOVA | | | | | |
|------------------|----|---------|----------------|---------|--------|
| | Df | Sum Sq | R ² | F value | Pr(>F) |
| Treatment | 3 | 0.66738 | 0.35402 | 1.4614 | 0.032* |
| Residuals | 8 | 1.21776 | 0.64598 | | |
| Total | 11 | 1.88514 | 1 | | |

Table 6: Statistical table from the post-hoc pair-wise PERMANOVA-tests on the effect of stand treatment on saproxylic beetle composition *significant results (p -value < 0.05)

| Pair-wise PERMANOVA | | | | | | |
|----------------------------|----|-----------|----------|----------------|---------|-------|
| Treatment | Df | Sum Sq | F-Model | R ² | p-value | p-adj |
| C50-B100 | 1 | 0.1814950 | 1.229713 | 0.2351396 | 0.4 | 1.0 |
| C50-B50 | 1 | 0.2406747 | 2.257976 | 0.3608157 | 0.1 | 0.6 |
| C50-C100 | 1 | 0.2252774 | 1.331342 | 0.2497198 | 0.2 | 1.0 |
| B100-B50 | 1 | 0.1182243 | 0.874251 | 0.1793611 | 0.6 | 1.0 |
| B100-C100 | 1 | 0.2585027 | 1.306550 | 0.2462146 | 0.2 | 1.0 |
| B50-C100 | 1 | 0.3105813 | 1.980133 | 0.3311186 | 0.2 | 1.0 |

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