Ecological Restoration of Natural Disturbances in Boreal Forests

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Restoring Natural Disturbances in Boreal Forests

Abstract

Worldwide declines in biodiversity have accentuated the need for conservation actions. Unfortunately, the decline is unlikely to be reversed by traditional conservation alone. Instead the practice of ecological restoration has come to play an ever increasing role. It is therefore important to develop methods that are beneficial for biodiversity, cost efficient and applicable on larger scales. By using a before-after control-impact experiment in boreal forest voluntary set-asides, I evaluated the response of forest-dwelling beetles and flat bugs to two cost neutral ecological restoration methods. The two restoration treatments, restoration burning and artificial gap creation were aimed at emulating natural disturbance processes, at the same time as they were expected to improve conditions for biodiversity. I compared the results from the two treatments with that of unmanaged reference stands.

I found that beetles showed strongest response to restoration burning by increasing in abundance and species richness directly, as well as one year after restoration. In addition the composition of species communities differed significantly between beetles collected in burned stands compared to those collected in gap-cut and reference stands immediately after restoration. One year after restoration the composition of species communities differed significantly between all three treatment groups. Flat bugs also responded strongest to restoration burning by displaying higher abundance and species richness in burned stands compared to gap-cut- and reference stands. I also found that dead wood substrate type mattered for beetles. Tree species and tree posture, i.e. if the trees were standing up or lying down, had the strongest effect on the composition of species communities emerging from the dead wood. In addition, tree species was of importance for abundance and species richness in gap-cut stands, where spruce trees generally had higher counts that birch- and pine trees.

As the voluntary set-asides already were established and the restoration costs were fully covered by revenues from the extracted timber, the restoration methods applied in this study may prove particularly useful. Not only because of the positive effects on forest biodiversity, but also due to their high level of applicability and cost effectiveness.

Keywords: boreal forests, ecological restoration, natural disturbances, forest fire, artificial gap creation, biodiversity, saproxylic beetles, flat bugs

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Dedication

To Trillian and Thor, my everlasting sources of inspiration and joy.

Det glittrar så gnistrande vackert i ån
Det kvittrar så lustigt i furen
Här ligger jag lat som en bortskämd son
I knät på min moder naturen

Gustaf Fröding

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Hjältén, J. Hägglund, R. Johansson, T., Roberge, J.-M., Dynesius, M. & Olsson, J. Forest restoration by burning and gap cutting of voluntary set-asides yield distinct immediate effects on saproxylic beetles. (in review).

II Hägglund, R., Dynesius, M., Johansson, T., Olsson, J., Roberge, J.-M. & Hjältén, J. Restoration measures emulating natural disturbances can have positive effects on saproxylic beetle assemblages. (manuscript).

III Hägglund, R. & Hjältén, J. Substrate specific restoration promotes saproxylic diversity in boreal forest set-asides. (manuscript).

IV Hägglund, R., Hekkala, A.M., Hjältén, J. & Tolvanen, A. (2015). Positive effects of ecological restoration on rare and threatened flat bugs (Heteroptera: Aradidae). *Journal of Insect Conservation* 19(6), 1089-1099.

Paper IV is reproduced with the permission of the publishers.

The contribution of Ruaridh Hägglund to the papers included in this thesis was as follows:

I Hägglund main responsible for data analyses, contributed to the interpretation of the results and writing. Hägglund also contributed to data collection in the field.

II Hägglund main responsible for data analyses, interpreting the results and writing. Hägglund also contributed to data collection in the field.

III Hägglund full responsibility for the sampling design, planning and conduction of field work all and data analysis, main responsible for writing.

IV Hägglund main responsible for species identification, data analyses, interpretation of results and writing. Hägglund also contributed to data collection in the field.

1 Background

1.1 Disturbance history of boreal Fennoscandia

1.1.1 Natural disturbances

During the millennia that have passed since the last glaciation the forests of Fennoscandia have been under the influence of natural disturbances, e.g. forest fires, wind storms and insect outbreaks, thereby contributing to, and changing the structure and composition of what today is known as boreal forests (Clear *et al.*, 2015; Clear *et al.*, 2014; Esseen *et al.*, 1997; Östlund *et al.*, 1997).

During intensive fires most trees in entire forests stands were killed and replaced with entirely new generations of trees, often light demanding pioneer species such as birch (*Betula pubescence* and *B. pendula*) and aspen (*Populus tremula*), but also pine (*Pinus sylvestris*). Over time the broad leaved trees died and were replaced with more long lived species such as pine or spruce (*Picea abies*), depending upon site conditions and surrounding seed sources (Brumelis *et al.*, 2011; Kuuluvainen & Aakala, 2011; Shorohova *et al.*, 2009). Other times fires were less intensive and would only kill small trees or those species that do not withstand fire as well as pine, e.g. spruce. The resulting forest would then often comprise multiple cohorts of pines (Kuuluvainen & Aakala, 2011; Shorohova *et al.*, 2009; Angelstam & Kuuluvainen, 2004). In forests where fire occurred less frequently, spruce trees would often dominate the stands. Unlike large scale disturbances small scale disturbances such as senescence, snow loads, insect attacks and fungal infections resulted in that the death of single trees or small groups of trees, drove changes in structure and composition of these forest (Kuuluvainen & Aakala, 2011; Shorohova *et al.*, 2009; Angelstam & Kuuluvainen, 2004).

1.1.2 Anthropogenic disturbances

Even though humans have inhabited the northern parts of Fennoscandia for many millennia, their influence on the structure and composition of surrounding forests has been of moderate intensity and restricted to local scales during most of the this period (Östlund *et al.*, 1997). Apart from slash and burn agricultural activities in limited geographical areas during the 17th and 18th centuries (Niklasson & Granström, 2000), it was not until the middle of the 19th century that forests began to be intensively utilized for human use with consequences on structure and composition (Rautio *et al.*, 2016; Esseen *et al.*, 1997; Östlund *et al.*, 1997). It was the economic value of the largest pine trees, tar and char coal that were the initial reasons behind the industrial exploitation (Östlund *et al.*, 1997; Tirén, 1937). As the largest pine trees dwindled in numbers, dimension criteria were lowered and the harvest continued. With the introduction of pulp production, dimension criteria were further reduced and spruce also became a species of interest (Tenow, 1974). Even though the forests were under some pressure at the beginning of the 20th century, high grading was the most common forestry practice, leaving a constant forest cover (Axelsson & Östlund, 2001; Esseen *et al.*, 1997). With the introduction of rotation forestry, i.e. clear felling with subsequent reforestation of monocultures, in the middle of the 20th century a large transformation in structure and composition of boreal Sweden was initiated. Deciduous trees, such as birch and aspen, were not as economically important, and much effort was spent on reducing the proportion of deciduous trees in the forests (Axelsson & Östlund, 2001). Infrastructure to supress forest fires was built up, and very efficient in reducing the area of forests burning each year (Niklasson & Granström, 2000; Esseen *et al.*, 1997). Formerly heterogeneous forest stands in matter of vertical structure and tree species composition were transformed into even aged monocultures of either pine or spruce (Linder & Östlund, 1998). In addition to the effect that two centuries of industrialized forestry has had on the age and species distribution of living trees, there has occurred a dramatic reduction in the availability and variability of dead wood (Siitonen *et al.*, 2001). The main reason behind the reduction of dead wood is that trees are removed from forests before they die from the natural causes mentioned in the previous paragraph. Another reason, although not as influential, is that dead wood has been viewed as possible source for forest pests, e.g. bark beetles (Wermelinger, 2004), and also used as an energy source for heating houses and therefore actively removed (Ehnström, 2001).

1.2 Biodiversity and dead wood in boreal forests

A great proportion of the biodiversity present in boreal ecosystems is associated with the natural disturbances shaping the forests and the structures within. Even though the boreal forests of Fennoscandia are a rather young, at least in an evolutionary perspective, the boreal biome is not. A multitude of species have therefore had time to evolve and adapt to make use of the resources available within boreal forests. One of the most important structural features for many of the forest dwelling species is dead wood (Dahlberg & Stockland, 2004; Siitonen, 2001) created either by senescence or natural disturbances. Approximately 6000-7000 of all forest dwelling species in Sweden depend on dead wood during some part of their life cycle (Dahlberg & Stockland, 2004), they are often referred to as saproxylic species (Stokland *et al.*, 2012). Many of these species do not only depend on dead wood per se, they have also evolved to make use of certain types of dead wood, e.g. tree species, tree posture, moisture level, sun exposure, mortality factor, i.e. the way the tree died also influences dead wood quality (Andersson *et al.*, 2015; Stokland *et al.*, 2012; Lindhe *et al.*, 2005; Stokland *et al.*, 2005).

At present, the amount of dead wood in boreal Fennoscandia is but a fraction (2-10 m^3/ha) of what it was before the introduction of industrialized forestry (40-170 m^3/ha) (Aakala, 2010; Siitonen, 2001). In addition, the variability of dead wood structures is low compared to more natural conditions. As a consequence the longevity of more than a thousand saproxylic species is in danger and they are therefore included in the Swedish red-list of threatened species (Gärdenfors, 2015). It is therefore vital to increase the amount and variation of dead wood in boreal Fennoscandia

1.3 Forest management implications and ecological restoration

In response to the growing evidence on the negative impacts of modern forestry on biodiversity, questions about the sustainability of these forestry practises have been raised (Simonsson *et al.*, 2015). As a result, forest certification schemes such as the Forest Stewardship Council (FSC) and the Programme for the Endorsement of Forest Certification (PEFC) have come to play an important role in the conservation of forest biodiversity in boreal forests. On the national scale, certifications schemes demand that certified partners conduct certain conservation efforts, e.g. setting forest stands aside from ordinary forestry, leaving buffer zones of trees alongside wetlands and water bodies, leaving snags and logs on clear cuts, and also actively creating dead wood in connection to final harvesting (Johansson *et al.*, 2013; Gustafsson *et al.*, 2012). Prescribed burning of clear-cuts and to some extent standing forests are also included in the FSC-standards for boreal Fennoscandia (Johansson *et al.*, 2013; Anonymous, 2010). In addition to voluntary certification schemes the Swedish forest legislation (SFS, 1993) clearly states that environmental protection and forestry production should be prioritised equally in forest management.

Even though the conservation measures mentioned above have been incorporated and implemented for more than two decades the red-list of threatened species associated to forest habitats has not shrank during the same period. In contrary there has been an increase in the number of red-listed species. In the Swedish red-list of year 2000, 2101 species associated to forests were red-listed, and in red-list of 2015, the number was 2246. A part of this increase is due to the fact that more species were evaluated in 2015 compared to 2000. However, the proportion of all red-listed species has been more or less constant during the same period, 21% of all evaluated species were categorized as red-listed in the year 2000, and 19.8% in 2015 (Gärdenfors, 2015; Gärdenfors, 2000).

1.3.1 Ecological restoration

It has been pointed out that it may take considerable time before changes in forestry practises result in increased population sizes of the species negatively affected by former practices. Furthermore, it has been questioned if the current measures are sufficient to mitigate the negative effects on forest biodiversity (Johansson et al. 2013). As a consequence, there is still a need for further actions than those implemented by legislation and certification schemes, to restore the forest associated biodiversity in Fennoscandia. Kuuluvainen (2002) suggests that an appropriate way of promoting biodiversity is to move away from the one solution practice, i.e. rotation forestry, and instead consider local site conditions and natural disturbance dynamics when planning forestry actions. In addition, there is also a need for more active measures aiming at improving conditions for biodiversity. Lindenmayer *et al.* (2006) proposes that ecological restoration should be guided by the natural disturbances originally creating the habitat sought for. In boreal Eurasia it would be reasonable to conduct restoration burnings of standing forests and also mimicking small scale gap dynamics by creating canopy gaps and a variation in dead wood substrates within the gaps (Shorohova *et al.*, 2011; Kuuluvainen, 2009; Esseen *et al.*, 1997) to improve the conditions for many of the species that have suffered from modern forest practises.

2 Objectives

The large scale experiment described in this thesis sets out to evaluate the response of saproxylic invertebrate communities to two restoration treatments aimed at mimicking natural disturbance processes, restoration burning and artificial gap creation. The design of the experiment also allows me to evaluate the importance of dead wood diversity for saproxylic beetles.

Recent research has been conducted on the effects of mimicking natural disturbances as a means of promoting biodiversity (Hekkala *et al.*, 2014; Toivanen & Kotiaho, 2007; Hyvärinen *et al.*, 2005). However, few studies have been as geographically spread out as the experiment evaluated in this thesis, created such a variation in mortality factors and maybe most importantly for future implementation in forest management, been designed to be easily applied, i.e. the stands were already set-aside from ordinary forestry production as a means FSC certification fulfilment and that revenues from the harvested timber fully covered the costs of restoration.

Through studying patterns of abundance, species richness and species composition of forest dwelling invertebrates, the aim of this thesis is to evaluate short-term effects of ecological restoration mimicking natural disturbances.

In this thesis I address the following questions:

1. How do forest dwelling beetle communities respond to the two ecological restoration methods, restoration burning and artificial gap creation? (Papers I & II)

2. Does the creation of a diverse set of dead wood substrate types, i.e. tree species and mortality factor, increase saproxylic beetle diversity? (Paper III)

3. How do flat bugs respond to the two ecological restoration methods restoration burning and gap creation? (Paper IV)

4. Is the flat bug response to restoration burning valid for a greater geographical region, i.e. boreal Fennoscandia? (Paper IV)

3 Materials and methods

3.1 Study areas

3.1.1 Sweden (Papers I, II, III & IV)

The study was conducted in the middle and northern boreal zones (Ahti *et al.*, 1968) of Sweden (Fig. 1). Initially 30 forest stands that were similar in terms of tree age, tree species composition, field layer vegetation and productivity, were selected to be included in the experiment (Table 1 in Paper II). Information on stand characteristics was provided by the land owner, but the final stand selection was done after field visits. The selected stands varied from 3.5 to 21 ha in size and were dominated by Scots pine (*Pinus sylvestris*) and/or Norway spruce (*Picea abies*). Downy birch (*Betula pubescens*), silver birch (*B. pendula*), aspen (*Populus tremula*) and goat willow (*Salix caprea*) occurred scattered throughout the stands. The dominant forest type in all stands was mesic dwarf-shrub (Arnborg, 1990) with *Vaccinium myrtillus* as the dominant species in the field layer (Table 1 in Paper II). All stands were part of the land owner's system of voluntary set-asides established according to FSC certification requirements (Anonymous, 2010).

3.1.2 Finland (Paper IV)

The study was conducted in two separate nature protection areas of the inland region of eastern Finland (Fig. 1). The northern area, Pahamaailma, is situated in the northern boreal zone , and the southern area, Elimyssalo, is situated in the middle boreal zone (Ahti *et al.*, 1968). Both of the Finish study areas were dominated by Scots pine, but also contained scattered occurrences of Norway spruce, silver birch, downy birch and aspen (Table 1 in Paper IV). The forest floor vegetation was dominated by the ericaceous dwarf shrubs *Vaccinium vitis-idea*, *V. myrtillus* and mosses, primarily *Pleurozium schreberi*.

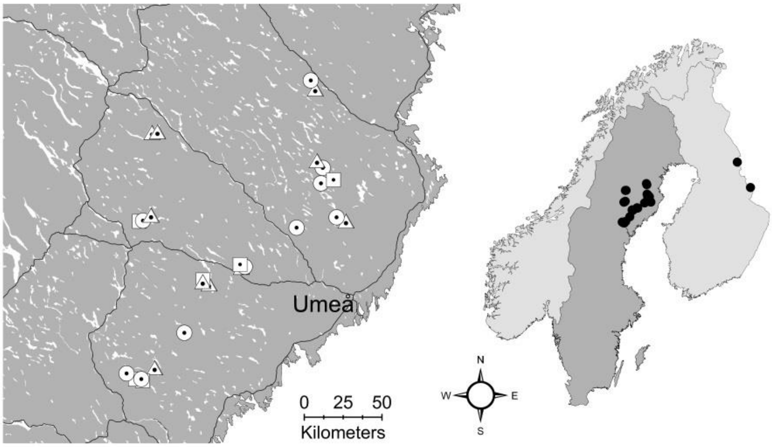

Figure 1: Overview of the forest areas included in the two study systems of the thesis. Left hand picture depicts a zoomed in view of the Swedish study. Circle = references, triangles = artificial gap cuttings, and squares = restoration burnings.

3.2 Experimental design

3.2.1 Sweden (Papers I, II, III & IV)

During the fall of 2009 and early spring of 2010 two restoration treatments were assigned to ten forest stands each. The treatments were aimed at mimicking natural disturbances. An additional ten forest stands were chosen as untreated references. The two treatments were, restoration burning and artificial gap creation including the creation of coarse woody debris (CWD). In the ten stands assigned for restoration burning, up to 35% of the tree volume was harvested during the early spring of 2011. The harvest covered the cost of restoration, at the same time as it facilitated faster dehydration of the field- and humus layer before burning. Six stands were burned during the summer of 2011, whereas four stands could not be burned due to unfavourable local weather conditions. Those four stands were therefore excluded from experiment. In the ten stands assigned for artificial gap creation, standard harvesters were used to create gaps with a diameter of 20 m covering approximately 19% of each stand's total area. Cut trees were removed from every second gap to cover the cost of restoration and to reduce the risk of creating more fresh CWD than is prescribed by Swedish forestry legislation i.e.

$5 m^3 ha^{-1}$. In the remaining gaps CWD substrates were created in four separate ways: i) trees were cut at the base and left as logs, ii) trees were cut approximately three meters above ground creating high stumps, iii) trees were pushed over and left as simulated wind breaks, and iv) trees were girdled at approximately three meters above ground and left to die standing.

3.2.2 Finland (Paper IV)

Three restoration treatments were applied: prescribed burning with lower fuel load (BurnLow), prescribed burning with higher fuel load (BurnHigh) and untreated controls (Control). The treatments were replicated three times in each forest stand as a randomized complete block design where each experimental block ranged between 2 and 10 ha in size. Within each block, three experimental stands (75 m x 100 m) were established. The blocks were nested within larger areas where restoration treatments were applied (Fig. 1 in Paper IV). For the treatments BurnLow and BurnHigh trees were randomly selected to be cut at the base and left on the ground as fuel; no trees were removed from experimental stands. The total volume of trees cut at each experimental stand was based on the initial volume of the growing stock at the block level. In the BurnLow treatment, 20 % of the volume of living trees was cut and in BurnHigh 40 % of the volume was cut. Trees were cut during the winter of 2005–2006, and prescribed burnings were carried out in June and early July during the summer of 2006.

3.3 Sampling and data analyses

3.3.1 Direct effects of ecological restoration (Paper I)

Due to the fact that one of the six stands that were burned, was burned more than one month later than the other five, this stand was not included in the study of direct effects. In order to achieve a balanced design five stands each of the gap cuttings and references were included in the study. The five gap-cuttings and references included were the ones that were geographically closest to the burned stands. In each of the 15 study stands, three flight intercept traps (Fig. 2) were placed at a distance of 30 m from the centre of each forest stand with a between-trap angle of 120^0 (Fig. 1 in Paper IV). The year before treatment (2010), beetles were trapped between the 1st of June and the end of September. During the treatment year (2011), traps were placed on the burned stands and on the corresponding gap-cut and reference stands 1-2 days after the fires. Four stands were burned between the 13^{th} and 14^{th} of June and the remaining stand was burned on the 15^{th} of July. The traps were emptied at the end of September. Beetles were counted and identified to species level by experts. Beetles were classified as saproxylic according to the definition of Stokland *et al.* (2012) and nutritional preference was classified in accordance to the database for saproxylic beetles (Anonymous 2007), with the addition of species confined to the northern part of Sweden (Hilszczański, J., Pettersson, R. and Lundberg, S. pers. comm.). Red-list status was based on the Swedish red-list (Gärdenfors 2015). The classification of fire favoured and fire dependent species follows Wikars (2006).

Two statistical analysis methods were used to investigate direct effects of ecological restoration on saproxylic beetle communities. Analyses were conducted for all saproxylic beetles as well as for six subgroups of beetles. The subgroups were based on each beetle species nutritional preferences, known relation to forest fire and red-list category. Generalized linear mixed effects models (GLMM) were used to analyse differences in abundance and species richness of beetles between years within the same treatment, and between treatments within the same year. When significant differences were detected pairwise comparisons with Tukey tests were applied. Differences in species composition were analysed with ManyGLM, which is a model based analysis of multivariate abundance data. As it is not possible to include random effects in this analysis method, differences in species composition between treatments were analysed separately for the two years. When significant differences were detected, pairwise analyses were conducted to investigate between which treatments the differences lay, and at the same time which species significantly contributed to the differences. All analyses were carried out in R (R Core Team, 2016)

3.3.2 Short term effects of ecological restoration (Paper II)

Similar to the case in Paper I, three flight intercept traps per stand were used to collect beetles. Sampling was conducted one year before restoration (2010) and one year after restoration (2012). Traps were placed in the same way as in paper I. The trapping period was equally long for both sampling periods, lasting from the first week of June to the last week of September. Traps were emptied at the end of each trapping period. All traps were intact throughout the first year of sampling, but during 2012 three traps broke, one each in three of the burned stands. Data from these three traps were excluded from the analyses.

The data analysis studying effects on beetle communities one year after restoration was conducted in much the same way as in paper one. However, in this study non-saproxylic beetles were also included. Therefore analyses of effects of restoration were conducted for all beetles collected and eight subgroups of beetles. Just as in Paper I, GLMM:s were used to investigate

Figure 2: Left hand picture: flight intercept traps used for collecting beetles in Papers I & II, and flat bugs in Paper IV (Swedish part). Right hand picture: eclector traps used for collecting beetles in Paper III. Photo: R. Hägglund

differences in abundance and species richness, and ManyGLM to investigate differences in species composition. All data analysis were carried out in R (R Core Team, 2016).

3.3.3 Substrate specific restoration (Paper III)

Beetles were sampled using eclector traps attached to dead wood substrates of different types (Fig. 2). Sampling was conducted on a total of 12 different substrate types (Table 1 in Paper III). In each stand the aim was to sample five trees of each tree species and mortality factor, i.e. the way the tree died and species. In stands containing less than five trees of a certain substrate type, as many substrates of that certain type as possible were sampled. In the burned stands traps were attached to standing spruce-, pine-, and birch trees that were killed during restoration fire. In gap-cut stands traps were attached to cut logs, tipped over logs, high stumps and girdled trees, of spruce and pine. Due to the scarcity of birch, traps were only attached to birch trees that were cut at the base and left as logs.

Similar to the cases in Papers I & II, the data analyses of beetle response to different dead wood substrates created during restoration were carried out using two separate analysis methods. Abundance and species richness were analysed by fitting generalized mixed-effect models (GLMM) to investigate if there were any differences between the dead wood substrates created during restoration. Tree species, mortality factor and the interaction between these two factors were set as fixed effects in the models. Species composition was analysed by using permutational multivariate analyses of variance (PERMANOVA). Due to the design of the study all analyses on differences between substrate types were analysed separately for burned and gap-cut stands. Data analyses on abundance and species richness were carried out in R (R Core Team, 2016). Analyses of species composition were carried out in PRIMER-E v7 (Clarke & Gorley, 2015) with the add-on package PERMANOVA+ (Anderson *et al.*, 2008).

3.3.4 Flat bug response to ecological restoration (Paper IV)

Sweden

In each of the 18 studied forest stands, three flight intercept traps and 10 pitfall traps were used to collect flat bugs. The traps used for collecting flat bugs were the same as used for collecting beetles in paper II. In addition to the flight intercept traps ten pitfall traps were placed at a distance of ten meters from each other along three straight lines origin at the centre of each forest stand, orientated in such directions that the trapping lines also were separated by an angle of 120^0, with the end of each line ending up in between two intercept traps (Fig. 1 in Paper IV). Collection of flat bugs was carried out between the 1st of June and 30th of September (intercept traps) and 1st of June to 15th of July (pitfall traps) one year after restoration (2012). Traps were emptied once at the end of the sampling period. Collected flat bugs were counted and identified to species level by me.

Pitfall and flight intercept catches were pooled within each experimental forest stand, and the nonparametric Kruskal–Wallis rank sum test was used to compare the total number of individuals and the number of flat bug species collected in the different treatments. The same test was also used to investigate if individual species differed in the number of collected flat bugs between treatments. When significant differences were found, the Mann–Whitney U test was used to conduct pairwise post hoc comparisons, revealing between which treatments the differences lay. In order for the robustness in the statistical analysis to be adequate during the analyses of single species, analyses were only carried out when there were at least five individuals in total and when the individuals were collected from at least four sites (Johansson et al. 2010) All analyses were carried out in R (R Core Team, 2016)

Finland

In each experimental stand six flight intercept traps were attached to trunks of living pine trees. Flatbugs were collected one year before restoration (2005), and the same year as restoration treatments were carried out (2006). Sampling was conducted between the 15th of May and 15th of September for both sampling years. Collected flat bugs were counted and identified to species level by Anne-Maarit Hekkala.

The flat bugs collected in the six traps placed within each experimental stand were pooled. Post-treatment differences in the total number of flat bugs collected, number of individuals collected of each species, as well as total number of flat bug species collected were conducted by fitting generalized linear mixed effects models (GLMM) to the data. The numbers of individuals/species collected per experimental stand were set as response variables, respectively. Experimental treatment was set as a fixed factor and block nested within study area as random factors. Model assumptions were reviewed visually with no apparent violations of model assumptions observed. All analyses were carried out in R (R Core Team, 2016)

4 Results

4.1 Direct effects of ecological restoration (Paper I)

In total, 15100 saproxylic beetles, belonging to 328 species were collected during the two sampling years. The year before treatment 7534 individuals of 253 species were collected and directly after restoration 7566 individuals of 252 species were collected. Before restoration the catches were distributed accordingly: 2413 (N=5), 2106 (N=5) & 3015 (N=5) individuals in reference stands, stands that were about to be burned and stands that were about to be gap-cut, respectively, and after restoration the catches were distributed accordingly: 1083 (N=5), 4999 (N=5) & 1484 (N=5) individuals in reference stands, burned stands and gap-cut stands, respectively.

Overall abundance, overall species richness and species composition did not differ between any of the treatment groups before restoration (Fig. 3).

After restoration, burned stands differed in species composition from gap-cut stands and references. Even though the nMDS visualisation suggests that there might be some separation in species composition between gap-cut and reference stands (Fig. 3 in Paper I), there was no significant difference between the two treatments after restoration (Table 3 in Paper I). Of the total 328 species collected, 50 species contributed significantly to the differences between treatments. Thirty-seven of them were more common in burned stands than in gap-cut and/or reference stands, and 15 of the 37 are known to be favoured by forest fires (Wikars, 2006).

After restoration the overall abundance of saproxylic beetles was higher in burned stands than both gap-cut stands and references (Fig. 3), functional groups contributing most to these differences were: cambium consumers, fungivores and predators (Fig 1 in Paper I). There was however no difference in abundance between gap-cut stands and references. The patterns for species richness were similar to those of abundance; nevertheless, there was no difference in species richness between burned and gap-cut stands. Cambium consumers were the nutritional subgroup contributing most to the higher species richness in burned stands compared to references. Overall abundance and species richness was lower the year after restoration in references and gap-cut stands. In contrast to this, burned stands showed higher abundance after- compared to before restoration. Species richness, on the other hand, did not differ between years for the burned stands. (Fig. 1 & 2 in Paper I).

The subgroup showing the strongest response to restoration were, not surprisingly, the subgroup of fire favoured beetles. Fire favoured beetles displayed a 30-fold increase in abundance and four fold increase in the number of species collected (Fig. 1 in Paper I)

4.2 Short term effects of ecological restoration (Paper II)

In total, 30207 beetles, belonging to 541 species were collected during the two sampling years. The year before treatment 13050 individuals belonging to 366 species were collected, and the year after treatment 17157 beetles belonging to 448 species were collected. Before restoration the catches were distributed accordingly: 5127 (N=10), 2340 (N=6) & 5583 (N=10) individuals in reference stands, stands that were about to be burned and stands that were about to be gap-cut, respectively. After restoration the catches were distributed accordingly: 5205 (N=10), 5044 (N=6) & 6908 (N=10) individuals in reference stands, burned stands and gap-cut stands, respectively.

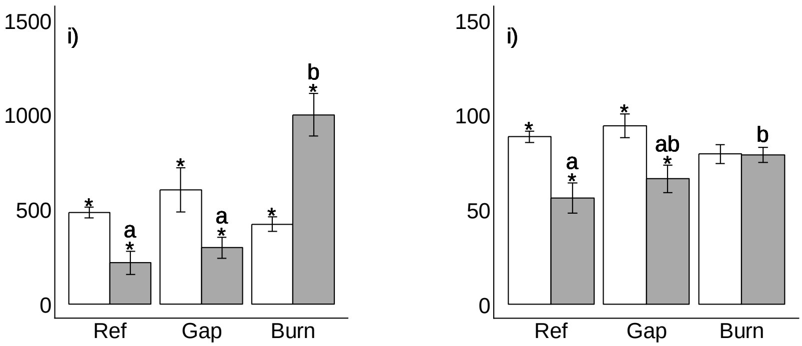

Figure 3: Abundance (left) and species richness (right) of all beetles collected before restoration (white) and directly following restoration (grey). Differing letters indicate differences between treatments within sampling years, and stars indicate differences between years within treatment.

Similar to that of the case in Paper I there was no difference in overall abundance, overall species richness or species composition between any of the treatments groups before restoration (Fig. 4).

After restoration, all three treatments differed in overall species composition (Table 3 in Paper II). In addition, most of the studied subgroups also differed in species composition between treatments. However, non-saproxylic beetles, predatory beetles and wood borers did not differ in species composition between gap-cut stands and references, and cambium consumers did not differ in species composition between burned and gap-cut stands. Red-listed species did not display any differences in species composition between treatments before or after restoration. Of the 448 species collected after restoration, 96 species contributed significantly to the differences in species composition of all species collected. Fifty-eight species were more common in burned stands than in gap-cut stands and/or references, including 17 species that are considered fire favoured and one red-listed species. Thirty-four species were more common in gap-cut stands than in references and/or burns. Fourteen species were more abundant in references than in gap-cut or burned stands and two species were more common in references than in both burned and gap-cut stands.

Overall abundance and overall species richness was higher in burned stands compared to reference stands after restoration (Fig. 4). In addition, the overall species richness was higher in burned stands compared to gap cut-stands after restoration (Fig. 4). The nutritional subgroups explaining the largest part of these differences were the cambium consumers and predators. However, the overall abundance of beetles did not differ between gap-cut stands and references or between gap-cut stands and burned stands. Furthermore, we found no differences in overall species richness between gap-cut stands and reference stands. Overall abundance and species richness was higher the year after restoration in burned stands compared to the year before restoration. This was however, not the case for gap-cut stands and references, in these two treatments there was no difference in overall abundance and species richness between the two sampling years (Fig. 2 & 3 in Paper II).

Just as in Paper I, fire favoured beetles showed the strongest response to restoration burning by almost displaying a 20-fold increase in abundance and a tenfold increase in the number of species collected (Fig. 2 & 3 in Paper II).

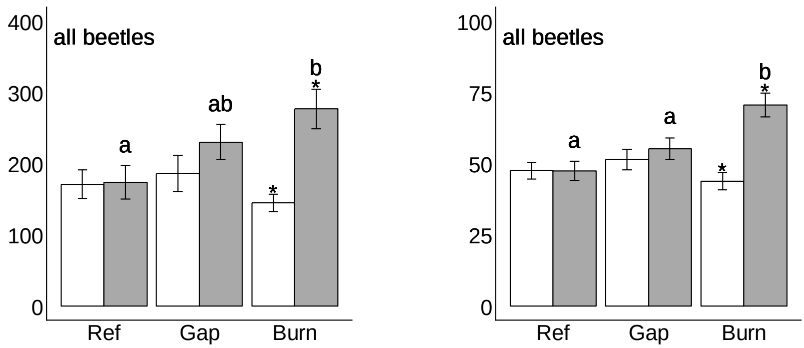

Figure 4: Abundance (left) and species richness (right) of all beetles collected before restoration (white) and one year after restoration (grey). Differing letters indicate differences between treatments within sampling years, and stars indicate differences between years within treatment.

4.3 Substrate specific restoration (Paper III)

In total, 12498 beetles, belonging to 193 species were collected. In the burned stands 2211 beetles were collected in the 76 traps used and in the gap-cut stands 10287 beetles were collected in the 307 traps used.

In the burned stands there was no difference in abundance or species richness between any of the substrate types, regardless of tree species or mortality factor. In contrast to this, there were differences in species composition between tree species. Birch trees had significantly different species compositions of beetles than both spruce- and pine trees. Although not significant (p=0.06), the results from the pairwise comparisons between spruce- and pine trees (Table 2 in Paper III) together with the nMDS visualisation (Fig. 3 in Paper III) and the fact that both species harboured unique species suggests that there is a trend indicating differences in species composition between these two tree species.

In the gap cut stands tree species significantly affected both abundance and species richness of beetles. Spruce trees had higher abundances of beetles compared to the other two tree species. Species richness was also higher in spruce trees than in pine- and birch trees. In addition, pine trees harboured more species than birch trees. The analyses of species composition revealed that there were differences in composition between tree species, mortality factor as well as the interaction between the two variables. Pairwise testing revealed significant differences between both tree species and tree posture, i.e. whether the trees were standing up or lying down (Fig. 5 & Table 4 in Paper III).

4.4 Flat bug response to ecological restoration (Paper IV)

In total, 81 flat bugs belonging to 9 species were collected. Sixty-four of the flat bugs were collected in the Swedish part of the study and 23 in the Finnish part. Of the Swedish flat bugs, 42 were collected in the burned stands and 16 were collected in gap-cut stands, no flat bugs were found in the reference stands. All but one of the flat bugs collected in the Finnish part of the study were collected in the burned stands, 14 in the treatment with lower fuel load (BurnLow) and 8 in the treatment with higher fuel load (BurnHigh). The remaining flat bug was collected in a reference stand. No flat bugs were found the year before restoration (Finland only).

In both study areas, i.e. Sweden and Finland, flat bugs were collected in higher abundances in burned stands compared to references. In the Swedish part of the study there was no difference in abundance between gap-cut stands and any of the two other treatments (Table 2 in Paper IV). In the Finnish part of the study there was no difference between the two types of burning treatments evaluated, i.e. BurnLow and BurnHigh (Table 3 in Paper IV). The response in number of species trapped differed between the two study systems. In Sweden the number of species was higher in burned stands compared to both the gap-cut stands and the reference stands. An interesting finding from Sweden; was that two species, *Aradus betulae* and *A. betulinus*, that previously have not been regarded as fire favoured had significantly higher abundances in burned stands than any of the other two treatment types. In the Finnish part of the study there were no differences in the number of species collected in any of the different treatments.

5 Discussion

The aim of this thesis was to generate knowledge on how two cost neutral methods of ecological restoration affect forest dwelling invertebrates, and if ecological restoration mimicking natural disturbances can be used to promote invertebrate biodiversity in boreal forests. We found that restoration burning increased abundance and species richness for most of the beetles groups studied, and that flat bugs also responded with increased abundance in stands subjected to restoration burning. The short-term effects of artificial gap creation were, however, not as clear as for restoration burning. Nevertheless, as the differences between gap-cut stands and the other two treatments were slightly more pronounced one year after restoration compared to the same year as gap-cuttings were carried out it is likely that this trend will continue and that the beetle communities in the three treatments will differentiate more with time. I therefore advise forest managers to include both restoration burning and artificial gap creation, with the extraction of timber financing restoration treatments, as a conservation tool to be commonly used in the management of boreal forest set-asides.

5.1 Papers I & II

5.1.1 Effects of restoration burning

In accordance with previous studies (Hekkala *et al.*, 2014; Boucher *et al.*, 2012; Hjältén *et al.*, 2010; Moretti & Barbalat, 2004) we found strong positive effects of restoration burning on the abundance and species richness of saproxylic beetles. The positive effects were consistent during both years following restoration. Such positive effects are often attributed to a combination of the increase in dead wood created during forest fires (Hekkala *et al.*, 2016; Eriksson *et al.*, 2013; Siitonen, 2001), and that many species are attracted to the smoke and heat produced by the fire itself (Wikars, 1997). This is especially true for fire favoured beetles, which together with cambium consumers displayed the strongest response to restoration burning. The same year as restoration burnings were carried out fire favoured beetles displayed a 30-fold increase in abundance and a fourfold increase in species richness compared to pre-restoration numbers. Cambium consumers displayed a six fold increase in abundance and a twofold increase in species richness. Even though the total number of fire favoured beetles and cambium consumers was lower one year after restoration (mean±se, N=6: 53.4±11.3 resp. 81.1±16.4) compared to the year of restoration (mean±se, N=5: 271.8±42.0 resp. 417.8±124.1) there was still an increase compared to before restoration (mean±se, N=6: 2.7±0.9 resp. 18.9±5.3). This suggests that many of the beetles attracted to the burned stands managed to reproduce in the newly created habitat. However, for individual dead wood substrates, the effects on saproxylic species have been found ephemeral and the positive effects may start decreasing after ca five years (Komonen *et al.*, 2014). On the other hand, burned areas can probably maintain high population of fire favoured species over considerable time as weakened trees will continue to die for many years after a fire, thus creating new fresh dead wood substrates that can be colonized (Boucher *et al.*, 2012). Recent data from our study stands show support for the latter, even five years after burning a significant number of trees are still dying, most likely due to the combined effect of fire and bark beetle attacks (Kärvemo et al. submitted manuscript).

The composition of species was altered in the burned stands compared to the un-treated references directly following restoration burning (Paper I; Fig. 3), confirming the work of Hekkala *et al.* (2014); Johansson *et al.* (2011); Hyvärinen *et al.* (2009) who found similar patterns. Considering that the differences in species composition remained even one year after restoration, this further confirms that restoration burnings have a strong effect on the saproxylic communities even sometime after the actual fire (Paper II; Table 3). Bearing in mind that 14 of the 34 species significantly contributed to the differences in species composition directly after restoration burning, and that 16 of the 55 species one year after restoration burning are considered fire favoured it is reasonable to argue that they had a large part in the shift of species composition witnessed. However, the remaining species that contributed significantly to the differences in species composition are not known to be especially favoured by forest fire, but all of them are saproxylic. It is therefore likely that the increase in dead wood (Komonen *et al.*, 2014) and the higher amounts of volatiles released in burned stands attracted beetles from afar.

Although the numbers and size of forest fires are far from the pre-fire-suppression era (Niklasson & Granström, 2000; Zackrisson, 1977) the fact that so many fire favoured species and individuals were found in the burned stands suggests that the surrounding landscape still caters the needs for some of the fire favoured species. Nevertheless the occasional forest fire may be of great importance for temporarily increasing the numbers of fire favoured species, increasing their chances to sustain viable population sizes in to the future. Bearing in mind the wide spread use and distribution of voluntary set-asides in boreal Fennoscandia, restoration burning of already established voluntary set-asides should therefore be incorporated, to a greater extent than is practised today, in the forest management of boreal Fennoscandia.

5.1.2 Effects of artificial gap creation

A sudden addition of dead wood often has a positive effect on the abundance and species richness of saproxylic beetles (Komonen *et al.*, 2014; Hyvärinen *et al.*, 2006; Hyvärinen *et al.*, 2005). This was however not confirmed in our study. The lack of response during the first sampling period could possibly be explained by the fact that we sampled beetles the same year as the restoration was conducted and that many saproxylic beetles show a slow to response to increases in dead wood. It is also likely that the shorter time period for sampling in 2011 compared to 2010 affected the number of beetles collected. Especially as the period missing from the sampling conducted in 2011 was the beginning of summer when saproxylic beetles often are most active. It has also been argued that window traps do not necessarily provide a good proxy for beetle production in a stand as this trap type is claimed to collect a high proportion of transient beetles from the landscape that are not necessarily linked to the specific habitat characteristics in the sites of interest (Boucher *et al.*, 2012). However, Sverdrup-Thygeson and Birkemoe (2009) found that window traps in fact do not trap beetles indiscriminately, but rather catch beetles connected to the habitat in which the traps are placed. Considering that gap-cut stands and reference stands were rather similar in structure, except for in the actual canopy gaps, the activity of beetles would not be expected to differ between the treatments, why the trapping in our case actually can be considered a measure of beetles present in the stands.

In contrast to earlier studies (Komonen *et al.*, 2014; Toivanen & Kotiaho, 2007), the overall abundance and species richness of saproxylic species did not increase the year after restoration. Furthermore, as the sampling period was as long as before restoration, which was not the case during the sampling that was conducted the same year as restoration, this suggests that the increase of dead wood was not sufficient (Müller & Bütler, 2010) to attract enough beetles to influence the overall patterns of abundance and species richness. Yet, a few subgroups of saproxylic species did show positive responses to gap-cutting. Fire favoured beetles, cambium consumers and wood borers did increase in abundance one year after restoration. In addition, fire favoured beetles also increased in abundance during the sampling conducted the same year as restoration was carried out. It is therefore likely that these subgroups are better at detecting increases of volatiles released from dead wood than other saproxylic species and by so having lower threshold volumes of dead wood than other functional subgroups.

In line with the lack of response in abundance and species richness there were no significant differences in species composition between gap-cut stands and reference stands directly after restoration. It is therefore reasonable to assume that the same mechanisms behind the lack of response in abundance and richness are adequate for species composition as well. However, the species composition analyses including all species collected in 2012, revealed that there was a difference in species composition between gap-cut stands and references one year after restoration (Table 3 in Paper II) confirming the results of Toivanen and Kotiaho (2007) and also supporting our prediction in Paper I, i.e. the species composition of saproxylic beetles will diverge given time. It is likely that the species present in the surrounding forests have had enough time to respond to the increase of dead wood. It is also likely that the variation of dead wood substrates, i.e. tree species (Toivanen & Kotiaho, 2010; Paper IV) and mortality factor have (Hjältén *et al.,* 2012; Paper IV) have contributed to attract a different set of saproxylic species than the reference stands.

The species groups significantly contributing to differences in species composition between gap-cut- and reference stands one year after restoration were primarily fungivores, cambium consumers and predators (Table 4 in Paper II). Of the 26 species that significantly contributed to differences in species composition, 18 species displayed higher abundances in gap-cut- than reference stands. A majority of these are known to be fungivores, suggesting that initial colonization by wood decaying fungi already had set in one year after restoration. Cambium consumers are known to react rapidly to increases of dead wood enabling them to utilize the resources present in recently dead wood, explaining their affinity to gap-cut stands.

Considering the fact that there was a difference in species composition between gap-cut- and reference stands one year after restoration implies that gap-cut stands contribute to a richer biodiversity in boreal landscapes than if all voluntary set-asides were left unmanaged. This suggests that the creation of artificial gaps in voluntary set-asides is an appropriate and cost efficient way of improving conditions for increased biodiversity and should be implemented at a larger scale.

5.1.3 Restoration burning vs artificial gap creation

As expected, the abundance and species richness of beetles was higher in burned than gap cut-stands and species composition also differed between the two treatments immediately (Boucher *et al.*, 2012) as well as one year after restoration (Toivanen & Kotiaho, 2007). Increases in abundance and species richness are often attributed to increases in the volume of dead wood available for colonisation (Müller *et al.*, 2008; Similä *et al.*, 2002; Martikainen *et al.*, 2000). Even though the difference in dead wood volume was not significant between the two treatments, it is still possible that dead wood volumes influenced the abundance and species richness. Lassauce *et al.* (2011) suggest that differences in dead wood structure also contribute to increases in abundance and species richness. Considering that the dead wood substrates created in our study differ considerably between the two overarching treatments it is likely that this also affected the abundances and species richness of beetles in our study. Another important consideration to be made is the attractive forces of forest fires on many saproxylic beetles (Hekkala *et al.*, 2014; Boucher *et al.*, 2012; Hjältén *et al.*, 2010; Moretti & Barbalat, 2004) already mentioned. Bearing in mind that there were no significant differences in overall abundance and species richness between gap-cut stands and references it is likely that the release of attractive volatiles from the gap-cut stands was not at all in parity with that of the burned stand, and that this contributes to the difference in response displayed between the two treatments.

Differences in species composition are often attributed to differences in dead wood qualities such as, mortality factor and tree species (Boucher *et al.*, 2012; Hjältén *et al.*, 2012; Toivanen & Kotiaho, 2010). This has most likely contributed to the differences in species composition that we have observed. However, given the great difference in overall treatment, i.e. burning vs. gap-cutting and the attractive forces associated to the two treatments that have been discussed in the previous paragraph, it is more likely that the overall treatment has had a greater impact on which species were attracted to the studied forest stands (Toivanen & Kotiaho, 2007; Wikars, 2002). This is supported by the fact that 10 of 23 species significantly contributing to the differences in composition between burned and gap-cut stands directly after restoration are known to be favoured by forest fire. Further supporting this, the same patterns were observed one year after restoration, with 17 of the 43 species known to be favoured by forest fire, and in addition, the results from Paper III also show that fire favoured species prefer the burned stands (Appendix A in Paper III).

5.2 Paper III

5.2.1 Restoration burning

In accordance with Stokland *et al.* (2012) we found that there were differences in species composition between tree species. The main differences in species composition lay between the two conifer species and birch trees. However, the almost significant difference between spruce- and pine trees together with the nMDS visualisation suggests that there is a trend towards differences in species composition between spruce- and pine trees as well. It is interesting that differences in species composition between tree species seem to be present even when the trees had been killed during restoration fires. Our results therefore suggest that differences in nutrients and structures present before fire were not lost, which has been suggested in other studies (Toivanen & Kotiaho, 2010; Wikars, 2002), instead the differences in available resources were sufficiently maintained to support different beetle communities between tree species. It is likely that the low intensity of the restoration fires left the trees intact enough to differentiate in resources present, and by so attracting different saproxylic beetle assemblages (Hjältén *et al.*, 2012; Lassauce *et al.*, 2011).

The lack of differences in abundance and species richness between tree species is interesting in itself. As pine trees were sampled at greater volumes than spruce- and birch trees it would be expected that more beetles would have been collected from pine trees, primarily because there is more resource available in a larger piece of wood (McGeoch *et al.*, 2007). Pine trees were also exposed to higher levels of transmitted solar radiation which would be expected to increase the metabolic rate of beetles (Allen *et al.*, 2002) allowing for more individuals to hatch during a given period of time, such as our sampling period, resulting in higher abundances of saproxylic beetles. This has been showed in other studies (Vodka & Cizek, 2013; Lindhe *et al.*, 2005), but our study and the study by Wu *et al.* (2015) could not confirm such patterns of abundance.

5.2.2 Artificial gap creation

Contrary to that of the restoration burnings, we did find differences in abundance and species richness between the three tree species studied in the gap cut stands. Spruce trees displayed higher abundances and species richness of saproxylic beetles than both birch- and pine trees. In addition, pine trees showed a higher species richness than birch trees, without differing in abundance. Since there was no difference in the amount of potential solar radiation reaching each trapping positions, this cannot explain the differences observed. As the sampled volume was higher for spruce- compared to birch trees, it is likely that this also affected the abundance and species richness of beetles collected. Nevertheless, the sampled volume of pine trees was higher than that of spruce trees without displaying any increase in abundance or species richness for pine trees compared to spruce trees.

A more likely explanation to the differences in abundance and species richness between spruce- and pine trees is that more beetle species are known to be associated with spruce trees compared to pine trees (Stokland *et al.*, 2012; Jonsson *et al.*, 2005). This is however not true for birch trees compared to the other studied tree species. In contrary, more beetle species are known to be associated with birch trees compared to both spruce- and pine trees (Stokland et al. 2012). It is however possible that the lower number of beetles emerging from birch trees is an effect of sampling effort as birch trees were sampled at significantly lower volumes than both spruce- and pine trees in the gap cut stands (Table 6 in Paper III). It is also possible that the general lack of birch trees in the landscape affects local species pools negatively, thereby reducing the number of individuals that are within colonisable distances to the experimental sites.

Just as for the burned stands and as expected from other studies (Toivanen & Kotiaho, 2010; Dahlberg & Stockland, 2004), there were differences in the composition of saproxylic beetles communities between all three tree species sampled. In addition, spruce- and pine trees harboured unique species. This further suggests that the tree species per se is an important factor when it comes to which beetle species are attracted to, and manage to reproduce in the different tree species.

We also found that mortality factor played a significant role in the compositions of beetles emerging from different substrates, especially for spruce trees. Differences in species composition between dead wood substrates standing up and lying down have been reported earlier (Hjältén *et al.*, 2012; Ulyshen & Hanula, 2009; McGeoch *et al.*, 2007), and were further confirmed in our study. Even though the composition of species did not differ between all mortality factors, the general pattern was that dead wood substrates lying down on the forest floor had separate beetle communities than those that were standing up. A possible explanation to the patterns observed can be that the moisture levels in dead wood substrates lying down will differ from those standing up, and thereby attract different species (Boulanger & Sirois, 2007). However, since we did not measure moisture levels within the dead wood substrates we cannot confirm this. It should also be observed that the composition of saproxylic communities emerging from spruce trees cut as high stumps were different from the communities emerging from girdled spruce trees. It is likely that this is an effect of the time it takes for the trees to die and the trees chemical defence mechanisms; girdled trees take some time to die and possibly try and defend themselves by producing more resin, whilst trees cut as high stumps die immediately. Thus, this could affect which species manage to colonize the trees. The patterns concerning pine trees were not as pronounced as for spruce trees, none of the differences fell out significant. Nevertheless the nMDS-visualisation suggests that there is a trend towards the same patterns as for spruce trees.

5.3 Paper IV

Previous studies have showed that many flat bug species respond positively to forest fires (Heikkala, 2016; Johansson *et al.*, 2010; Hjältén *et al.*, 2006). This study, which includes two geographically separated study systems, supports these findings. In Sweden the stands subjected to prescribed burning generally attracted higher numbers of flat bugs than controls and the numbers of species collected were also higher in burned stands compared to both controls and gap-cut stands. Further confirming these conclusions is that all but one specimen of the flat bugs caught in the Finnish part of the study were collected in burned areas.

Other studies, primarily conducted in continental Europe, have showed that an increase in dead wood volume without forest fires also have positive effects on the numbers of flat bugs attracted to a certain forest stand (Seibold *et al.*, 2014; Gossner *et al.*, 2007). This could imply that forest fire per se is of secondary importance compared to the availability of dead wood. However, the volumes of dead wood did not differ significantly between the gap-cut and burned stands in the Swedish part of the study, but the difference in species richness was highly significant. Our study, as well as the ones by (Johansson *et al.*, 2010; Gossner *et al.*, 2007; Hjältén *et al.*, 2006) suggests that burning per se, at least in northern boreal settings, most likely makes stands further attractive to more flat bug species than previously believed, e.g. *Aradus betulae* and *A. betulinus,* which were found in significantly higher numbers in burned stands than gap-cut stands and references.

In the Finnish part of the study, we had the opportunity to evaluate the effect of increased fuel loads, i.e. volume of dead trees left prior to burning, on the number of flat bugs collected. Nevertheless, we found no effect of increasing fuels loads on the numbers of flat bugs attracted to the burned stands. Two likely explanations are: either sufficient amounts of dead wood were created in both treatment types to attract similar amounts of flat bugs (some threshold value was reached), or that there was too little variation in the volume of dead wood between the two treatments to attract different amounts of flat bugs.

Thus, although we are unable to separate the effect of fire and dead wood availability in the two parts of this study, there are strong indications that forest fire per se provides an attractive habitat to flat bugs. Furthermore the geographical range of our study shows that restoration burning is an appropriate restoration measure to promote the presence of flat bugs in boreal landscapes.

6 Conclusions and implications for forest management

It has been showed that forestry practiced in boreal Fennoscandia during the two last centuries has had negative effects on the population sizes of many forest-dwelling species (Siitonen, 2001). Attempts to counteract this have been conducted within the realms of environmentally certified forestry for almost two decades (Johansson *et al.*, 2013; Gustafsson *et al.*, 2012), without reducing the number of forest-dwelling species included in the Swedish red-list (Gärdenfors, 2015). It is therefore evident that, in order to promote biodiversity conservation in the future, restoration of degraded habitat is essential. Within this thesis I have been able to show that restoration burning is a fast and efficient way of improving conditions for many saproxylic beetles and flat bugs. However, one should be aware that many species are disfavoured by burning, which suggests that alternative restoration measures also need to be considered. Although the direct effects of gap-cutting on beetle communities were not significant, I did find support for that, given time, beetle communities in gap-cut stands also differed significantly from the un-treated reference stands as well as from the burned stands. In addition, I also found that the creation of differing substrate types, i.e. tree species and mortality factor had a significant effect on beetle communities hatching from the dead wood substrates created. I therefore conclude that it is important to create as much variety as possible, regarding both forest structure and dead wood substrates, in attempts to improve conditions for biodiversity in boreal forests.

6.1 Implications for management

Restoration measures often need to be repeated at regular intervals in a landscape in order to be efficient (Hekkala et al. 2014). However, restoration of legally protected areas, e.g. nature reserves and national parks, is often controversial due to their already high conservation values as well as aesthetic reasons (Angelstam *et al.*, 2011). In their place, voluntary set-asides could play an important role in the management of boreal forest landscapes. As stipulated in the Swedish FSC-standards, voluntary set-asides cover 5% of the certified productive forest area in Sweden (Anonymous, 2010). In addition, as the revenues from thinning prior to burning and the trees extracted during gap-cutting covered restoration costs, the restorations conducted in this study where cost-neutral (Olov Norgren pers. comm.). We therefore suggest that voluntary set-asides thus provide an excellent opportunity for implementing active and cost-efficient landscape management for biodiversity conservation. Ecological restoration of voluntary set-asides can therefore act as an important complement to the often passive conservation measures provided by formally protected areas such as nature reserves and national parks.

7 Future research

Even though this thesis offers some insights into how ecological restoration mimicking natural disturbances affects some of the forest dwelling species present in boreal Fennoscandia, there are still knowledge gaps to be filled. One of the main shortcomings of this thesis is the limited time span of the study. It would be of great interest and importance to determine long term effects of the restoration methods evaluated within the realms of this thesis. Many of the beetle species collected during the three years following restoration are early successional species that depend on ephemeral components of the dead wood, e.g. easily available sugars of the phloem and fungi that rapidly colonize recently killed trees. It would therefore be of great interest to revisit the experiment in a few years' time to see if the patterns revealed in this study, e.g. the differences in species composition, continue to diverge over time or if the patterns instead start to converge as for Hekkala *et al.* (2014). Even though we found red-listed species, they were collected at rather low abundances and their response could not be evaluated properly. As many red-listed species are known to be late successional species, it is likely that revisiting the experiment in a few years' time would shed more light upon the response of red-listed species.

One rewarding thing about working with invertebrates such as beetles and flat bugs is that it involves working with many species. Despite this, within the scope of this thesis I have only covered a small proportion of all organism groups affected by the applied restoration treatments. It would therefore be of great interest to include more species groups in the evaluation. Fortunately this work has already been initiated to some extent. One of my fellow PhD-students is working on how birds respond to restoration, and I am currently running a small project studying nocturnal moths' response to artificial gap creation. Within the project we have also collected data on vascular plants, bryophytes, lichens and wood decaying fungi to be able to evaluate their response to restoration. One obvious way to gain more knowledge upon the effects of restoration would simply be to dig deeper into this data. Nevertheless, it would also be interesting to include species groups that have not yet been included, e.g. ungulates, small mammals, ground dwelling fungi, spiders, etc.

After spending quite some time in the stands included in this study I have noticed that the production of blue berries seems to be greater in the burned stands compared to the gap-cut stands and references. I would therefore find it interesting to dwell deeper into studying ecosystem services provided by boreal forests and how they are affected by ecological restoration.

Despite that the forest stands evaluated in this study are situated far apart and by that cover a rather large part of boreal Sweden, it is not possible to evaluate landscape effects of restoration. It would therefore be of great importance for science and management if entire landscapes could be used an experimental areas. However, this is unfortunately beyond the scope of most research budgets. A possible way might instead be to involve major forest owners in landscape scale management, implementing different management/restoration scenarios on entire landscapes.

8 Svensk sammanfattning

Global liksom lokal förlust av biologisk mångfald har betonat behovet av bevarandeåtgärder inom många områden, däribland skog. Att den negativa trenden kan vändas endast genom passiva bevarandeåtgärder så som generell och förstärkt naturhänsyn, inrättandet av naturreservat och bildandet av nationalparker är osannolikt. För att stärka den biologiska mångfalden behövs istället aktiva åtgärder som är applicerbara i stor skala, kostnadseffektiva och gagnar så många arter som möjligt. Ett storskaligt försök initierades med syfte att studera hur vedlevande skalbaggar och barkskinnbaggar påverkas av naturvårdsbränning och luckhuggning. I de luckhuggna bestånden skapades dessutom flera olika substrattyper av död ved. Resultat från dessa behandlingar jämfördes med obehandlade referensområden. Restaureringsåtgärderna utfördes i frivilliga avsättningar och finansierades till fullo genom ett visst uttag av timmer före restaureringsåtgärderna utfördes.

Vedlevande skalbaggar och barkskinnbaggar svarade starkast på naturvårdsbränningar, men även luckhuggningar gynnade skalbaggsamhällena. Vedlevande skalbaggar ökade i abundans och artrikedom redan samma år som restaureringsåtgärderna utfördes, ökning höll i sig även året efter restaurering. Första sommaren efter restaurering samt ett år efter restaurering skiljde sig dessutom artsammansättningen i de brända bestånden från både de luckhuggna- som referensbestånden. Ett år efter restaurering skiljde sig även artsammansättningen av skalbaggar åt mellan luckhuggningarna och referenserna. Substrattyp, d.v.s. trädart och på vilket sätt trädet dött, var också av betydelse för artsammansättnigen av de vedlevade skalbaggar som kläckte ut ur den döda veden. Den största skillnaden i artsammansättning var mellan trädart och ifall de döda träden stod upp eller låg ned.

Med tanke på att frivilliga avsättningarna redan är en väl integrerad del av det svenska skogsbruket, behandlingarna var kostnadsneutrala samt att den biologiska mångfalden påverkades positivt av restaureringsåtgärderna rekommenderar jag att frivilliga avsättningar aktivt används till att främja biologisk mångfald. Mina förslag är att man inom skogsbruket utför fler naturvårdbränningar i de frivilliga avsättningarna, samt att man samtidigt kompletterar detta med att i andra frivilliga avsättningar öppnar luckor i krontäckningen och skapar dödvedssubstrat med så stor variation i trädart och dödsorsak som möjligt.

9 References

Aakala, T. (2010). Coarse woody debris in late-successional Picea abies forests in northern Europe: Variability in quantities and models of decay class dynamics. *Forest Ecology and Management,* 260(5), pp. 770-779.

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968). Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici,* 5, pp. 169-211.

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science,* 297(5586), pp. 1545-1548.

Anderson, M.J., Gorley, R.N. & Clarke, K.R. (2008). *PERMANOVA+ for PRIMER: guide to software and statistical methods*: PRIMER.E Ltd.

Andersson, J., Hjältén, J. & Dynesius, M. (2015). Wood-Inhabiting Beetles in Low Stumps, High Stumps and Logs on Boreal Clear-Cuts: Implications for Dead Wood Management. *Plos One,* 10(3).

Angelstam, P., Andersson, K., Axelsson, R., Elbakidze, M., Jonsson, B.G. & Roberge, J.-M. (2011). Protecting Forest Areas for Biodiversity in Sweden 1991-2010: the Policy Implementation Process and Outcomes on the Ground. *Silva Fennica,* 45(5), pp. 1111-1133.

Angelstam, P. & Kuuluvainen, T. (2004). Boreal forest disturbance regimes, successional dynamics and lanscape structures - a European perspective. *Ecological Bulletins,* 51, pp. 117-136.

Anonymous (2010). Svensk skogsbruksstandard enligt FSC. Forest Stewardship Council.

Arnborg, T. (1990). Forest types of northern Sweden: Introduction to and translation of "Det nordsvenska skogstypsschemat". *Vegetatio,* 90(1), pp. 1-13.

Axelsson, A.L. & Östlund, L. (2001). Retrospective gap analysis in a Swedish boreal forest landscape using historical data. *Forest Ecology and Management,* 147(2-3), pp. 109-122.

Boucher, J., Azeria, E.T., Ibarzabal, J. & Hebert, C. (2012). Saproxylic beetles in disturbed boreal forests: Temporal dynamics, habitat associations, and community structure. *Ecoscience,* 19(4), pp. 328-343.

Boulanger, Y. & Sirois, L. (2007). Postfire Succession of Saproxylic Arthropods, with Emphasis on Coleoptera, in the North Boreal Forest of Quebec. *Environmental Entomology,* 36(1), pp. 128-141.

Brumelis, G., Jonsson, B.G., Kouki, J., Kuuluvainen, T. & Shorohova, E. (2011). Forest Naturalness in Northern Europe: Perspectives on Processes, Structures and Species Diversity. *Silva Fennica,* 45(5), pp. 807-821.

Clarke, K.R. & Gorley, R.N. (2015). *PRIMER v7: User Manual/Tutorial*. [Computer Program]. Plymouth, UK: PRIMER E.

Clear, J.L., Molinari, C. & Bradshaw, R.H.W. (2014). Holocene fire in Fennoscandia and Denmark. *International Journal of Wildland Fire,* 23(6), pp. 781-789.

Clear, J.L., Seppa, H., Kuosmanen, N. & Bradshaw, R.H.W. (2015). Holocene stand-scale vegetation dynamics and fire history of an old-growth spruce forest in southern Finland. *Vegetation History and Archaeobotany,* 24(6), pp. 731-741.

Dahlberg, A. & Stockland, J.N. (2004). *Vedlevande arters krav på substrat - sammanställning och analys av 3600 arter*: Skogsstyrelsen.

Ehnström, B. (2001). Leaving dead wood for insects in boreal forests - Suggestions for the future. *Scandinavian Journal of Forest Research*, pp. 91-98.

Eriksson, A.M., Olsson, J., Jonsson, B.G., Toivanen, S. & Edman, M. (2013). Effects of restoration fire on dead wood heterogeneity and availability in three Pinus sylvestris forests in Sweden. *Silva Fennica,* 47(2), p. article id 954.

Esseen, P.-A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997). Boreal forests. *Ecological Bulletins,* 46, pp. 16-47.

Gossner, M., Heinz, E. & Blaschke, M. (2007). Factors determining the occurrence of Flat Bugs (Aradidae) in beech dominated forests. *Waldökologie online,* 4, pp. 59-89.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lohmus, A., Martinez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A. & Franklin, J.F. (2012). Retention Forestry to Maintain Multifunctional Forests: A World Perspective. *Bioscience,* 62(7), pp. 633-645.

Gärdenfors, U. (2000). *Rödlistade arter i Sverige 2000 - The 2000 Red List of Swedish Species*. Uppsala: ArtDatabanken SLU.

Gärdenfors, U. (2015). *Rödlistade arter i Sverige 2015- The 2010 Red List if Swedish Species*. Uppsala: Artdatabanken SLU.

Heikkala, O. (2016). *Emulation of natural disturbances and the maintenance of biodiversity in manged boreal forests: the effects of prescribed fire and retention forestry on insect assemblages.* Diss. Vantaa, Finland: University of Eastern Finland.

Hekkala, A.-M., Paatalo, M.-L., Tarvainen, O. & Tolvanen, A. (2014). Restoration of Young Forests in Eastern Finland: Benefits for Saproxylic Beetles (Coleoptera). *Restoration Ecology*, 22(2), pp. 151-159.

Hekkala, A.M., Ahtikoski, A., Paatalo, M.L., Tarvainen, O., Siipilehto, J. & Tolvanen, A. (2016). Restoring volume, diversity and continuity of deadwood in boreal forests. *Biodiversity and Conservation,* 25(6), pp. 1107-1132.

Hjältén, J., Atlegrim, O., Sandström, F., Pettersson, R. & Rexstad, E., A (2006). Occurence of flat bugs (Heteroptera: Aradidae) in burned and unburned forests. *Entomologica Fennici,* 17, pp. 130-135.

Hjältén, J., Gibb, H. & Ball, J.P. (2010). How will low-intensity burning after clear-felling affect mid-boreal insect assemblages? *Basic and Applied Ecology,* 11(4), pp. 363-372.

Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P. & Hilszczanski, J. (2012). Micro and Macro-Habitat Associations in Saproxylic Beetles: Implications for Biodiversity Management. *Plos One,* 7(7).

Hyvärinen, E., Kouki, J. & Martikainen, P. (2009). Prescribed fires and retention trees help to conserve beetle diversity in managed boreal forests despite their transient negative effects on some beetle groups. *Insect Conservation and Diversity,* 2(2), pp. 93-105.

Hyvärinen, E., Kouki, J., Martikainen, P. & Lappalainen, H. (2005). Short-term effects of controlled burning and green-tree retention on beetle (Coleoptera) assemblages in managed boreal forests. *Forest Ecology and Management,* 212(1-3), pp. 315-332.

Hyvärinen, E., Kouki, J. & Martikninen, P. (2006). Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in Finnish boreal forests. *Conservation Biology,* 20(6), pp. 1711-1719.

Johansson, T., Andersson, J., Hjältén, J., Dynesius, M. & Ecke, F. (2011). Short-term responses of beetle assemblages to wildfire in a region with more than 100 years of fire suppression. *Insect Conservation and Diversity,* 4(2), pp. 142-151.

Johansson, T., Hjältén, J., de Jong, J. & von Stedingk, H. (2013). Environmental considerations from legislation and certification in managed forest stands: A review of their importance for biodiversity. *Forest Ecology and Management,* 303, pp. 98-112.

Johansson, T., Hjältén, J., Stenbacka, F. & Dynesius, M. (2010). Responses of eight boreal flat bug (Heteroptera: Aradidae) species to clear-cutting and forest fire. *Journal of Insect Conservation,* 14(1), pp. 3-9.

Jonsson, B.G., Kruys, N. & Ranius, T. (2005). Ecology of species living on dead wood - Lessons for dead wood management. *Silva Fennica,* 39(2), pp. 289-309.

Komonen, A., Kuntsi, S., Toivanen, T. & Kotiaho, J.S. (2014). Fast but ephemeral effects of ecological restoration on forest beetle community. *Biodiversity and Conservation,* 23(6), pp. 1485-1507.

Kuuluvainen, T. (2002). Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica,* 36(1), pp. 97-125.

Kuuluvainen, T. (2009). Forest Management and Biodiversity Conservation Based on Natural Ecosystem Dynamics in Northern Europe: The Complexity Challenge. *Ambio,* 38(6), pp. 309-315.

Kuuluvainen, T. & Aakala, T. (2011). Natural Forest Dynamics in Boreal Fennoscandia: a Review and Classification. *Silva Fennica,* 45(5), pp. 823-841.

Kärvemo, S., Björkman, K., Johansson, T., Weslien, J. & Hjältén, J. Forest restoration as a double-edged sword: conservation and the risk of bark-beetle damages. (submitted manuscript).

Lassauce, A., Paillet, Y., Jactel, H. & Bouget, C. (2011). Deadwood as a surrogate for forest biodiversity: Meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecological Indicators,* 11(5), pp. 1027-1039.

Lindenmayer, D.B., Franklin, J.F. & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation,* 131(3), pp. 433-445.

Linder, P. & Östlund, L. (1998). Structural changes in three mid-boreal Swedish forest landscapes, 1885-1996. *Biological Conservation,* 85(1-2), pp. 9-19.

Lindhe, A., Lindelöw, A. & Åsenblad, N. (2005). Saproxylic beetles in standing dead wood density in relation to substrate sun-exposure and diameter. *Biodiversity and Conservation,* 14(12), pp. 3033-3053.

Martikainen, P., Siitonen, J., Punttila, P., Kaila, L. & Rauh, J. (2000). Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biological Conservation,* 94(2), pp. 199-209.

McGeoch, M.A., Schroeder, M., Ekbom, B. & Larsson, S. (2007). Saproxylic beetle diversity in a managed boreal forest: importance of stand characteristics and forestry conservation measures. *Diversity and Distributions,* 13(4), pp. 418-429.

Moretti, M. & Barbalat, S. (2004). The effects of wildfires on wood-eating beetles in deciduous forests on the southern slope of the Swiss Alps. *Forest Ecology and Management,* 187(1), pp. 85-103.

Müller, J., Bussler, H. & Kneib, T. (2008). Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. *Journal of Insect Conservation,* 12(2), pp. 107-124.

Müller, J. & Bütler, R. (2010). A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. *European Journal of Forest Research,* 129(6), pp. 981-992.

Niklasson, M. & Granström, A. (2000). Numbers and sizes of fires: Long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology,* 81(6), pp. 1484-1499.

R Core Team (2016). *R: A language and environment for statistical computing*. [Computer Program]. Vienna, Austria: R Foundation for Statistical Computing.

Rautio, A.M., Josefsson, T., Axelsson, A.L. & Östlund, L. (2016). People and pines 1555-1910: integrating ecology, history and archaeology to assess long-term resource use in northern Fennoscandia. *Landscape Ecology,* 31(2), pp. 337-349.

Seibold, S., Bässler, C., Baldrian, P., Thorn, S., Müller, J., Gossner, M.M., R. Leather, S. & Gange, A. (2014). Wood resource and not fungi attract early-successional saproxylic species ofHeteroptera -an experimental approach. *Insect Conservation and Diversity,* 7(6), pp. 533-542.

Svensk författningssamling [SwedishCode of Statutes]. 1993:553 (1993).

Shorohova, E., Kneeshaw, D., Kuuluvainen, T. & Gauthier, S. (2011). Variability and Dynamics of Old-Growth Forests in the Circumboreal Zone: Implications for Conservation, Restoration and Management. *Silva Fennica,* 45(5), pp. 785-806.

Shorohova, E., Kuuluvainen, T., Kangur, A. & Jogiste, K. (2009). Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Annals of Forest Science,* 66(2), p. 20.

Siitonen, J. (2001). Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins,* 49, pp. 11-41.

Siitonen, J., Penttila, R. & Kotiranta, H. (2001). Coarse woody debris, polyporous fungi and saproxylic insects in an old-growth spruce forest in Vodlozero National Park, Russian Karelia. *Ecological Bulletins,* 49, pp. 231-242.

Similä, M., Kouki, J., Mönkkönen, M. & Sippola, A.L. (2002). Beetle species richness along the forest productivity gradient in northern Finland. *Ecography,* 25(1), pp. 42-52.

Simonsson, P., Gustafsson, L. & Östlund, L. (2015). Retention forestry in Sweden: driving forces, debate and implementation 1968-2003. *Scandinavian Journal of Forest Research,* 30(2), pp. 154-173.

Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012). *Biodiversity in dead wood*. Cambridge: Cambridge university press.

Stokland, J.N., Tomter, S.M. & Söderberg, U. (2005). Development of dead wood indicators for biodiversity monitoring: Experiences from Scandinavia. In: Marchetti, M. (ed. *Monitoring and Indicators of Forest Biodiversity in Europe - From Ideas to Operationality*. (European Forest Institute Proceedings. Joensuu: European Forest Institute, pp. 207-226.

Sverdrup-Thygeson, A. & Birkemoe, T. (2009). What window traps can tell us: effect of placement, forest openness and beetle reproduction in retention trees. *Journal of Insect Conservation,* 13(2), pp. 183-191.

Tenow, O. (1974). *Det nordiska skogslandskapets och skogsbrukets utveckling fram till 1900-talet - en kort översikt*. (Swedish Cinoferous Forest Project, Internal Report 2.

Tirén, L. (1937). Skogshistoriska studier i trakten av Degerfors i Västerbotten. . *Meddelanden från statens skogsförsöksanstalt,* 30, pp. 67-322.

Toivanen, T. & Kotiaho, J.S. (2007). Mimicking natural disturbances of boreal forests: the effects of controlled burning and creating dead wood on beetle diversity. *Biodiversity and Conservation,* 16(11), pp. 3193-3211.

Toivanen, T. & Kotiaho, J.S. (2010). The preferences of saproxylic beetle species for different dead wood types created in forest restoration treatments. *Canadian Journal of Forest Research,* 40(3), pp. 445-464.

Ulyshen, M.D. & Hanula, J.L. (2009). Habitat associations of saproxylic beetles in the southeastern United States: A comparison of forest types, tree species and wood postures. *Forest Ecology and Management,* 257(2), pp. 653-664.

Wermelinger, B. (2004). Ecology and management of the spruce bark beetle Ips typographus - a review of recent research. *Forest Ecology and Management,* 202(1-3), pp. 67-82.

Wikars, L.-O. (1997). *Effects of forest fire and the ecology of fire adapted insects.* Diss. Uppsala, Sweden: University of Uppsala.

Wikars, L.-O. (2006). *Åtgärdsprogram för bevarande av brandinsekter i boreal skog. Rapport nr. 5610*: Swedish Environmental Protection Agency.

Wikars, L.O. (2002). Dependence on fire in wood-living insects: An experiment with burned and unburned spruce and birch logs. *Journal of Insect Conservation,* 6(1), pp. 1-12.

Vodka, S. & Cizek, L. (2013). The effects of edge-interior and understorey-canopy gradients on the distribution of saproxylic beetles in a temperate lowland forest. *Forest Ecology and Management,* 304, pp. 33-41.

Wu, J., Pan, H., Zhang, J., Yang, S.Z. & Zhao, M.S. (2015). Effect of sun exposure on saproxylic beetle assemblages may change with topoclimate in a subtropical forest of east China. *Journal of Insect Conservation,* 19(5), pp. 877-889.

Zackrisson, O. (1977). Influence of forest fires on north Swedish boreal forest. *Oikos,* 29(1), pp. 22-32.

Östlund, L., Zackrisson, O. & Axelsson, A.L. (1997). The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere,* 27(8), pp. 1198-1206.

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