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– Prescribed burning and gap cutting effects on plant diversity and community composition

Estrategias de restauración en bosques boreales. Efectos de quema prescrita y claras en la diversidad y composición de comunidades vegetales

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Swedish University of Agricultural Sciences, SLU
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Abstract

The boreal biome is one of the largest in the world and their forests have been widely exploited for centuries. Consequently, it has suffered ecological simplification and loss of biodiversity. Under these circumstances passive conservation is no longer enough and active restoration techniques need to be tested. I evaluated short- and long-term effects of two restoration methods aimed to increase ecosystem structural variability. I focused on the responses of two organism groups: vascular plants in the field layer and bryophytes in the ground layer. A before-after control-impact study design was applied. It consisted of 18 voluntary set-asides in northern Sweden; each assigned to one of three treatments: prescribed restoration burning, gap cutting and untreated stands. Data was collected in three occasions: once prior to restoration (2010) and twice post restoration; one year after (2012) and eight years after (2019). I analysed the differences in two diversity measures (richness and Shannon Diversity) with linear mixed effect models and community composition changes with multivariate methods. My results showed that fire treatment caused an initial decline in diversity for both field and ground layer. However, in the long-term the field layer recovered and surpassed the diversity values present in the area before restoration. Ground layer did not show any sign of recovery. Community composition in burned stands differed significantly between each time point as well as when compared to other treatments, for both layers. By contrast, I found no significant differences in diversity measures or community composition due to gap cutting. The restoration methods tested in this study displayed some divergent results. Prescribed burning generated opposite responses depending on time since restoration for vascular plants in the field layer. However, it was found consistently detrimental in the ground layer and therefore not to recommend when bryophytes are the target species. The absence of effects from gap cutting can be understood as that minor changes in canopy cover does not affect the vegetation structure of forest stands. My study highlights the importance of including more than one organism group, different restoration methodologies and long-term studies in order to properly asses restoration outcomes at landscape level.

Keywords: restoration ecology, boreal forest, fire, gap cutting, biodiversity, voluntary set-asides, vascular plants, bryophytes, forest management.

Preface

Here I present my master thesis, the culmination of all the work I have done during the last year. Working at SLU with the VFM department has been a truly enriching experience.

I am deeply grateful for all the guidance, encouragement and support I have received from my supervisor, Jörgen Sjögren.

I would also like to give an acknowledgment to my assistant supervisor Joakim Hjältén, for helping me develop a more critical and scientific thinking.

To my fellow master students, thank you for being always there and help me throughout this process.

Finally, a special thanks to my sister, Laura, for all the time dedicated.

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Abbreviations

CBD	Convention on Biological Diversity
EU	European Union
ISA	Indicator Species Analyses
SCB	Statistiska Centralbyrån (Sveriges Officiella Statistik)
SD	Shannon Diversity
SLU	Swedish University of Agricultural Sciences

1. Introduction

Over the last century there has been a major shift in forestry practises, from local selective felling to large-scale intensive exploitation (Östlund et al., 1997). Specially in the boreal zone (sensu Ahti et al. (1968)) where modern forestry practices include thinning, clearcutting and even aged monoculture plantations (Esseen et al., 1997, Östlund et al., 1997, Wallenius, 2011). Consequently, the previously highly diverse and heterogeneous ecosystem (Esseen et al., 1997, Östlund et al., 1997) has suffered ecological simplification. Therefore, many species that are highly specialized, dead wood dependent or associated with old growth forest are now threatened with extinction (Kuuluvainen, 2009, Virkkala, 2016, Paillet et al., 2010).

To cope with biodiversity loss, traditional conservation measures have been directed to the establishment of national parks or nature reserves. However, these passive conservation measures are not enough and other active ecological restoration methodologies need to be applied (Kuuluvainen, 2009, Angelstam et al., 2011, Halme et al., 2013, Johansson et al., 2013). During the last decade several international strategies have been established. The commitment is to restore at least 15% of degraded forest ecosystems to halt the loss of biodiversity, specifically in managed forests (Aichi Convention on Biological Diversity (2010) altogether with the EU Biodiversity Strategy (2011)).

In Sweden 75% of the area is covered by forests, of which 77% is considered productive forests which are exploited under high-intensity forestry (Levers et al., 2014) to almost their full extension (Skogsstyrelsen, 2015). The Swedish Forestry Act (1993) established that maintaining biological diversity was equally important as timber production (Johansson et al., 2013), but currently only 6% of productive forest land is formally protected (SCB, 2018) . Nevertheless, more than 60% of productive forest land has FSC (Forest Stewardship Council) and/or PEFC (Programme for the Endorsement of Forest Certification) certification according to Skogsstyrelsen (2015). One of the specific requirements of these certifications is that 5% of the area has to be voluntarily set aside for biodiversity conservation purposes (Anonymus, 2014). The aim is to protect and preserve habitats threatened due to forestry (Gustafsson and Perhans, 2010, Johansson et al., 2013) and facilitate the integration between forest management operations and restoration measures (Lindenmayer et al., 2012).

Biodiversity and vegetation composition are one of the key pieces for ecosystem functioning (Nilsson and Wardle, 2005, Wardle et al., 2012). Particularly, understory vegetation on boreal forests floors strongly affects conifer regeneration (Mallik, 2003), nutrient recycling and microbial activity (Wardle and Zackrisson, 2005). These understory vegetation is composed by mainly ericaceous dwarf shrubs in the field layer together with feather mosses and lichens in the ground layer (Nilsson and Wardle, 2005). Some studies have found fire driven cyclic dynamics, for example *Empetrum nigrum* dominates the understory vegetation in the absence of fire while *Vaccinium spp*. is more common when fire is recurrent (Nilsson and Wardle, 2005). Nevertheless, the current fire suppression policy has decreased wildfires to almost non-existing (Wallenius, 2011). Thus, the change in the disturbance regime can impact the ecosystem functionality (Mallik, 2003, Wardle et al., 2012) through biodiversity and community changes. Several authors argue that recovering disturbance regimes in boreal forest will recreate heterogeneous habitats and succession processes, allowing a higher species diversity (Angelstam, 1998, Lindenmayer et al., 2006).

The methodology applied and analysed in this study aims to mimic boreal forest natural disturbances, specifically fires (prescribed burning) and canopy openings (gap cutting). Boreal wildfires can generate divergent responses, depending on their severity. High intensity fires can drive communities towards earlier successional states (Hekkala et al., 2014a), while low intensity fires allow the expansion of pioneer and opportunistic species (Schimmel and Granström, 1996, Wang and Kemball, 2005) by removing dwarf shrubs and feather mosses (Nilsson and Wardle, 2005). Other small-scale forest's dynamics like canopy openings are particularly important in undisturbed boreal forest (Esseen et al., 1997). Canopy gaps allow more light to reach the ground which boost the diversity and abundance of certain vegetation species (Thomas et al., 1999). Applying gap cutting methodology is expected to create small scale disturbances. The method aims to mimic windblown tree dynamics (Kuuluvainen and Aakala, 2011) and allow multiple successional stages (Hekkala et al. (2014b). Several studies have shown differential effects of gap cutting and prescribed burning depending on the target group (Versluijs et al., 2017, Hjältén et al., 2017, Hekkala et al., 2014a).

Boreal forest vegetation is considered extremely resilient to disturbances (Rydgren et al., 2004) but field and ground layer are adapted to distinct ecological requirements (Esseen et al., 1997). Therefore they might react differently to specific methodologies. Studies about forest restoration would be more complete if more than one organism groups were included. Here I present a study that analyses the effects of two restoration methods on two of the main organism groups present in the boreal understory vegetation (Nilsson and Wardle, 2005):

(1) vascular plants mainly dominated by ericaceous dwarf shrubs in the field layer and (2) bryophytes, with feather mosses preponderance in the ground layer.

Some studies have shown that there can be a delay in the biodiversity responses after restoration in forested areas (Bouget et al., 2014, De Keersmaeker et al., 2011). Therefore, long-term studies are needed in order to detect biodiversity trajectories (Rudolphi and Strengbom, 2016) and take long-term knowledge as a base for management decisions (Hylander et al., 2012). Consequently, this study will also take into account the time after the treatments were applied. Data was collected in one inventory prior to (2010) and two post restoration (2012 and 2019) allowing me to analyse differences in short- versus long-term responses (one and eight years respectively). Furthermore, the before-after-control-impact study design allowed me to control for environmental stochasticity and between years variation (Hägglund et al., 2020). The experimental design, based on responses under natural conditions, can potentially help the comprehension of long-term ecological dynamics (Wardle et al., 2012).

The aim of this study is to test the effectiveness and adequacy of the two restoration methodologies (prescribed burning and gap cutting) to improve vegetation biodiversity at field and ground level in managed boreal forests. To achieve the goal, I focused on two biodiversity measures, richness and Shannon diversity, as well as in community composition changes, vegetation response patterns and species indicators analyses (ISA).

My hypotheses were the following:

- Prescribed burning will affect both in field and ground layer similarly. In the short-term, with a decrease in diversity and an important change in community composition because of fire impact. However, in the long-term a rebound effect will overtake the initial pre-restoration diversity values due to the appearance of opportunistic and pioneer species and therefore a different community composition from before fire.
- Gap cutting will affect differently depending on the layer. In the short-term: field layer diversity will increase due to an augment of light availability; however canopy openings will also bring drier conditions to the ground and therefore impact negatively bryophytes diversity in the ground layer. In addition, both field and ground layer will suffer minor changes in community composition due to the lower intensity impact created by canopy gaps. In the long-term the initial light availability effect will fade and dominant species in the field layer would take over the few opportunistic species that might appear. In the ground layer, bryophytes will remain affected by the canopy openings.
- Reference stands would serve as control and I will not find any variation through the different inventories.

2. Material and Methods

2.1. Study Area

This study was conducted in northern Sweden in a region (63˚24’ to 64˚30’ N and 17˚22’ to 20˚12’ E, Figure 1) classified as middle boreal zone (sensu Ahti et al. (1968). In the area predominates conifer forests with Scots pine (*Pinus sylvestris)* and Norway spruce (*Picea abies)* as the most abundant tree species while deciduous broadleaves trees (mainly birch *Betula spp.)* appear sparse in the area (Esseen et al., 1997). The field layer in these forests is dominated by ericaceous dwarf-shrubs (Esseen et al., 1997). The normal precipitation (calculated from the period 1961-1990) registered in the area is 514 mm and mean annual temperatures range between 0 and 4 degrees (Open data extracted from SMHI, 2020) .

The study design consists of 18 forest stands, distributed over six geographic areas. Stand characteristics were collected and standardized prior to restoration (see Table 1). Subsequently, stands were assigned to different treatments to obtain comparable variation across all groups (Hjältén et al., 2017).

The stands are part of voluntary set-asides from the forest company Holmen Skog AB. This company follows FSC certification criteria, which requires that 5% of the productive forest is set aside for biodiversity conservation purposes (Anonymus, 2014). The stands have never been clear felled, only historically subjected to selective felling (Hjältén, J. personal communication).

Table 1. Stand characteristics before restoration (2010), mean and standard deviation per treatment. Data were provided by the land owner (Holmen Skog AB) or collected by the baseline surveyors.

Treatment		Area (ha)	Productivity ($m^3ha^{-1}year^{-1}$)	Tree age (years)	Standing volume (m^3ha^{-1})	Tree species distribution (%) Pine	Spruce	Broadleaves	CWD volume (m^3ha^{-1})
Untreated	Mean	10.02	4.02	113.5	206.07	50	35	15	4.18
	SE	2.99	0.14	13.49	11.77	5.16	5.63	2.24	0.63
Gap cutting	Mean	6.82	3.97	121.83	231.68	51.67	36.67	11.67	4.88
	SE	1.80	0.16	9.27	13.52	6.01	6.15	1.67	1.13
Restoration burning	Mean	6.10	4.23	120.33	186.72	58.33	31.67	20	4.45
	SE	0.53	0.12	12.10	42.71	5.43	4.01	2.58	1.49

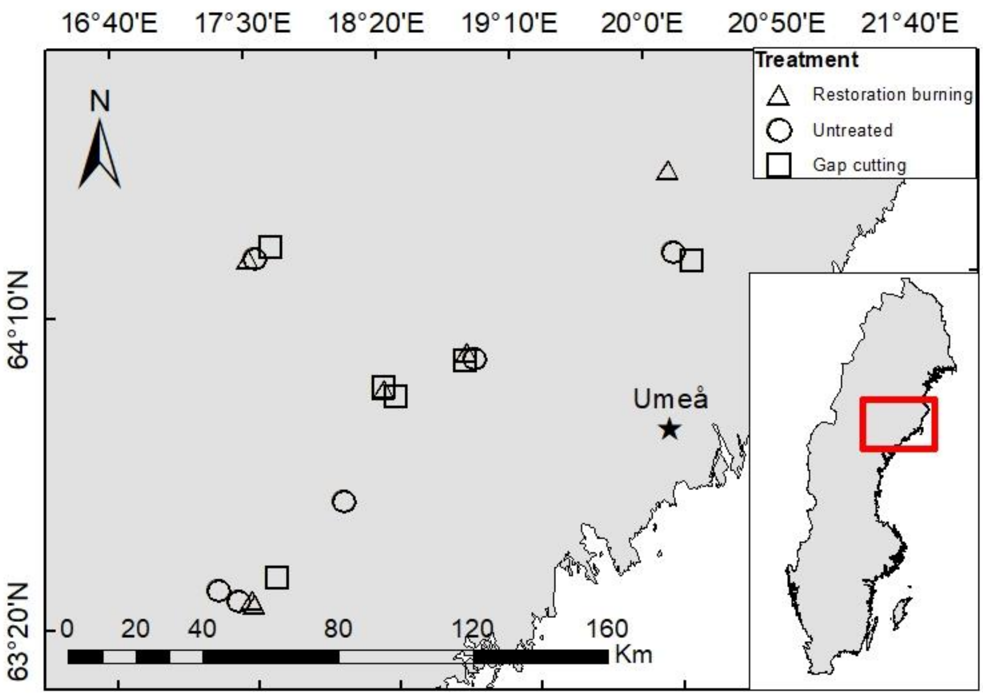

Figure 1. Map of Sweden with the location of the stands. The star represents the location of Umeå city. Base map (1:10m vector) from Natural Earth (Anonymus, 2020) modification made with Arc GIS (Anonymus, 2017).

2.2. Restoration methodologies

Two treatments: (1) prescribed burning and (2) gap cutting; were applied during spring/summer of 2011 on six stands each and six stands were left untreated. The prescribed burned stands are hereafter referred to as *burned* stands; gap cutting stands are referred to as *gap cut* stands and untreated stands as *control* stands. These management operations were chosen to mimic natural disturbances historically present in boreal forests (Angelstam, 1998).

In prescribed burning, fire was conducted between June 10 and August 3, 2011. There was a pre-fire extraction of timber (between 5-30%) to facilitate the drying of forest floors and compensate restoration costs (Olof Norgren, head of forestry treatment at Holmen Skog AB in a personal communication to Hjältén et al. (2017)). Approximately 2-5 m^3/ha of cut trees were left on site to promote establishment of dead-wood dependent species (Hjältén et al., 2017).

In gap cut stands six gaps, measuring 20 meters in diameter, were created per hectare, amounting to approximately 19% of stand area. Each gap had one deciduous tree in the centre when possible or Scots pine when not. The rest of trees were cut down and retained as dead wood in 50% of the gaps while in the other 50% trees were extracted for timber to cover costs (Hjältén et al., 2017).

Finally, untreated stands were left without performing any restoration and considered as reference.

2.3. Data collection

This study has a before-after-control-impact design. First inventory took place in August-October of 2010 before the intervention and considered as a baseline, henceforth referred to as *before*. Second inventory took place in August-October of 2012; one year after the methodology was applied, henceforth referred to as *after*. Third inventory took place in July 2019, 8 years after restoration, henceforth referred to as *follow up*. First and second inventories were performed by partly overlapping surveyors working in the Wildlife, Fish and Environmental Studies Department at Sveriges Lantbruksuniversitet (SLU) while third inventory was performed by the author with Jörgen Sjögren's assistance (associate professor at SLU). In addition, total precipitation and mean temperature data (from SMHI open database) was gathered from one year previous to every inventory, take into account significant variations that might have impacted the area.

In each stand two parallel transects were placed of approximately 400 meters in total. Sometimes, when stand area was shorter than 200 m, an extra third or fourth transect was used to retain enough plots. Transects were spaced 50 meters from each other and at least 25 meters away from the stand edge (Figure 2). In total 25 permanent plots of $0.25m^2$ (50 cm by 50 cm) were marked every 15 meters. In gap cut stands, only 17% of the plots were placed inside gaps in order to achieve representability for the whole stand. To allow repeatability and facilitate posterior inventories start and end coordinates positions for each transect were written down during baseline inventory (2010).

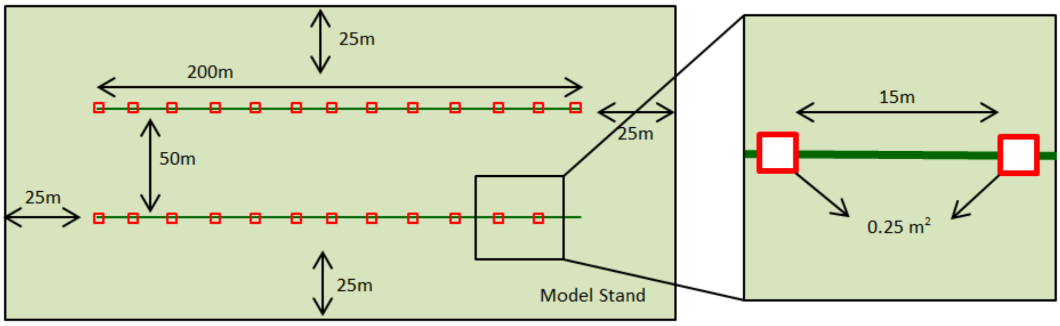

Figure 2. Model stand showing the placement of transects and plots.

In the field a GPS device (GPSMAP® 60CSx – Garmin) was used to locate start and end points of transects and, together with maps and a compass, individual plots were located. A wooden frame was placed to facilitate data collection (Figure 3). Due to that some permanent stick markers were missing, a few plots had to be relocated following the original design instead.

Figure 3. Example of a plot with permanent plastic sticks (visible in blue in lower right and in red in higher right corner) in at least two corners and wooden frame to facilitate the delimitation of the area to be surveyed.

In all inventories same methodology was followed. At each plot, field and ground layer were inventoried collecting presence/absence data. All occurring vascular plants build the field layer and were identified to species level at each inventory, resulting in a total of 34 species. In the case of bryophytes, which constitute the ground layer, *before* (2010) and *after* (2012) surveyors identified all species present. In *follow up* inventory (2019) only common Swedish species were recorded. However, to avoid misidentifications genera with very similar species were kept to genus level and, as a result, I collected data on eight common species/genera. Subsequently data from *before* (2010) and *after* (2012) inventories was adapted, grouping and counting species according to the level of detail used in 2019's inventory, in order to allow comparisons between all inventories.

Raw data contains information on presence/absence data from 450 plots resurveyed at each inventory. Data from plots in the same stand was pooled together to obtain relative frequencies of each species per stand.

2.4. Alpha diversity measures

This study focuses on two alpha diversity measures. First of all, richness (S); which importance relies on the simple and logic interpretation of this measure (Whittaker, 1972).

In addition to this rather simple approximation of diversity and to incorporate information about abundance, the study will also focus on "true diversity" or effective number of species (Jost et al., 2010), henceforth called Shannon Diversity. This "true diversity" measure is derived from diversity indexes, such as Shannon or Gini-Simpsons indexes. These indexes are measures of entropy that can cause some misunderstanding when it comes to data interpretation (Jost, 2006) and therefore their use was discarded. Shannon Diversity was calculated using the following function:

$$\text{Shannon Diversity} = e^{(\sum_{i=1}^{S} p_i \ln p_i)}$$

Where S= species richness; p = frequency of S_i

2.5. Statistical analyses

Analyses on diversity measures, ISA and response pattern were performed using R software (R Core Team, 2019), whereas Primer+ (Clarke and Gorley, 2006) was used for community composition changes. Ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2019) and dyplr (Wickham et al., 2018) packages were employed to build diversity measures graphs. Vegan package (Oksanen et al., 2019) was used for plotting NMDS graphs.

For nomenclature I made use of Svensk fältflora (Mossberg and Stenberg, 2018) for vascular plants and Mossor: en fältguide from Hallingbäck and Holmåsen (2016) for bryophytes.

Stand characteristics variables were analysed with linear models in order to check pre-existing differences between stands before restoration took place.

Diversity measures were calculated using "renyi" function included in Vegan package (Oksanen et al., 2019). Differences for both measures were tested with linear mixed-effects models from Lme4 package (Bates et al., 2015), specifying *treatment* and *time* as fixed factors and *stand ID* as a random factor nested within *treatment*. I used Maximum Likelihood (ML) as estimation method to incorporate the variability of the random factor but without testing its significance. Data distribution of response variables was assessed based on graphical techniques (Razali and Wah, 2011), thus Gaussian distribution was assumed. Subsequently, pairwise comparison was made using Emmeans package (Lenth, 2019). In Shannon Diversity lmer model for the field layer, it failed to converge and therefore I specified Nelder-Mead optimization method to find local convergences and make the model converge.

Community composition changes were analysed using PERMANOVA+ add-on package (Anderson et al., 2008) in PRIMER+ software (Clarke and Gorley, 2006). All species were included in analyses. Count data was fourth-root transformed and Bray-Curtis dissimilarity was used to create a distance matrix. In the Permanova design, *treatment* and *time* are considered as fixed factors and *stand ID* as random factor nested within *treatment*. In addition, the highest order interaction was removed from analyses, following recommendations from Anderson et al. (2008). Permutation limit was set to 999. Assumption of exchangeability of samples was tested using PERMDISP function in PRIMER+ software. The assumption was fulfilled for the field layer but violated for the ground layer. Data was plotted using Vegan package (Oksanen et al., 2019) with a 2-dimensional NMDS, based on Bray-Curtis dissimilarity for non-transformed data with subsets created for each *treatment* and *time*.

Based on species responses analyses from Hylander et al. (2012) I analysed patterns in species responses among treatments. I calculated the percentage change from count data between inventories at each stand. When the change was ±20% or higher, positive (+) or negative (-) responses were noted, if it was lower the response was registered as neutral (=). To avoid major contribution of abundant species the number of responses were standardized as ratio per species. Meaning that each species' responses summed up to 1, independently if they were present in one or six stands. Responses were divided according the changes observed in each stand and the number of stands where the species were present (e.g. 1/5 positive response, 2/5 negative response and 2/5 neutral response, in the case the species was present in 5 stands). Finally, the above mentioned ratios were grouped per treatment and then tested with Cochran-Mantel-Haenszel test to find out if there were differences between treatments and if these differences were consistent in the *after* and *follow up* inventories.

Indicator Species Analyses (Dufrene and Legendre, 1997) was performed, with "multipatt" function included in Indicspecies package (De Caceres and Legendre, 2009), to identify indicator species for the different treatments. This method gives maximum value to a species when all individuals of that species are exclusive of a single treatment and also when that species occurs in all sites belonging to a singular treatment. To analyse our data I apply phi coefficient of association, which is a correlation index that allow us to determine ecological preferences of the species. This method will test and identify to which group or combinations of groups better matches the observed species distribution (De Cáceres et al., 2010). Permutation limit was set to 2999.

3. Results

In total, I found 34 species of vascular plant and eight species/genera of bryophytes. The most abundant vascular plant species were *Vaccinium myrtillus* and *Vaccinium vitis-idaea* and among the bryophytes *Hylocomium splendens* and *Pleurozium schreberi* (see table 8 in the Appendix for species' abundance list).

Regarding the environmental variables gathered from one year prior to each inventory (2010, 2012 and 2019); the annual mean temperatures remained within the normal range values, 0-4 ºC. Nevertheless, the total amount of precipitation registered in 2009 (611 mm) and 2011 (603 mm) was higher than normal (513 mm, average for the period 1961-1990) while 2018 was a dryer year (439 mm). All the values have been extracted from SMHI open database (2020).

Stand characteristics (Table 1) did not differ between treatments before restoration measures were applied: Area (p: 0.375), Productivity (p: 0.372), Tree Age (p: 0.868), Standing volume (p: 0.256), Pine, Spruce and Broadleaves distribution (p: 0.544, 0.799 and 0.289 respectively) and CWD volume (p: 0.902).

3.1. Diversity measures

I found no differences prior to restoration and main differences post restoration appeared related to *burned* stands in both field and ground layer (see table 3).

Fire treatment created a complex landscape with various degrees of burning and some plots within stands were not burned. To take into consideration the heterogeneous fire impact I analysed the dataset by splitting burned and not burned plots within stands, but sample sizes were unbalanced (only three stands present unburned plots (four, eight and five respectively)) and no conclusions could be drawn. Another extra consideration was taken in the *gap cut* stands where some of the plots were located inside the gaps and some outside. I split the datasets and tried to analyse them separately but, as in the previous case, the design was too unbalanced to draw conclusions. Therefore in both field and ground layer all presented analyses focus on stand level diversity with all the variability included.

When analysing the field layer more in detail; I found significant differences in *after* inventory (2012) between *burned* and *control* stands. By contrast *before* and *follow up* did not show differences between all treatments. When analysing differences within treatment, only *burned* stands displayed significant differences between time points in richness as well as in Shannon diversity (see table 3 for further details); both values initially decreased in *after* inventories followed by a substantial increase in the *follow up* inventories (see figure 4A and 4B). This pattern was particularly noticeable in the comparison of the Shannon diversity that was significantly lower *after* (2012) than *before* (2010); while it was significantly higher in the *follow up* (2019) survey as compared to both *before* and *after*. *Gap cut* and *control* stands did not show any significant changes among time points.

In the ground layer, both time points post restoration (*after* and *follow up*) showed significant differences between *burned* and *control* stands as well as between *burned* and *gap cut* stands, but no differences were found between *control* and *gap cut* stands (see table 3 for further details). Looking specifically at each treatment; *burned* stands showed a significant decrease from pre to post restoration but no variation in between *after* and *follow up* inventories. Interestingly, in the *gap cut* stands I found a significant decrease in *follow up* inventory for both diversity measures (see figures 4C and 4D). *Control* stands did not statistically differ between time points.

*Table 2. Linear mixed models in richness and Shannon diversity for both layers. The α-probability was set to 0.05 and N=18. Statistically significant results are shown in bold. LMER: x ~ Treatment*Time+ (1|Treatment: ID), Gaussian. *likelihood ratio value for random nested factor.*

	Field layer						Ground layer					
	Richness			Shannon diversity			Richness			Shannon diversity		
	Df	F	P	Df	F	P	Df	F	P	Df	F	P
Treatment	2	0.50	0.613	2	0.89	0.427	2	6.97	**0.005**	2	9.755	**0.001**
Timeline	2	2.63	0.085	2	6.18	**0.004**	2	20.09	**<0.001**	2	25.69	**<0.001**
Treatment*Timeline	4	4.45	**0.005**	4	5.74	**0.001**	4	6.85	**<0.001**	4	6.16	**<0.001**

Table 3. Pairwise comparisons of species richness and Shannon diversity between treatments and time points for field and ground layer. The α-probability was set to 0.05 and N=6 for the pairwise post hoc tests. Statistically significant results are shown in bold

		Pairwise comparison	Field layer				Ground layer			
			Richness		Shannon Diversity		Richness		Shannon Diversity	
			Estimate	P	Estimate	P	Estimate	P	Estimate	P
Timeline	Before	Burned-Control	-0.167	0.917	-0.595	0.465	0.167	0.811	-0.536	0.388
		Burned-Gap cut	0.5	0.757	0.124	0.878	0.5	0.474	-0.176	0.776
		Control-Gap cut	0.667	0.411	0.719	0.379	0.333	0.633	0.36	0.561
	After	Burned-Control	-3.333	**0.046**	-1.743	**0.039**	-2.833	**<0.001**	-2,.735	**<0.001**
		Burned-Gap cut	-2	0.221	-0.879	0.283	-2.333	**0.001**	-2.381	**<0.001**
		Control-Gap cut	1.333	0.411	0.863	0.292	0.5	0.474	0.354	0.567
	Follow up	Burned-Control	-0.167	0.917	0.042	0.957	-2.667	**<0.001**	-2.598	**<0.001**
		Burned-Gap cut	1.167	0.471	0.936	0.254	-1.667	**0.02**	-1.77	**0.006**
		Control-Gap cut	1.333	0.411	0.893	0.276	1	0.155	0.828	0.185
Treatment	Burned	Before-After	-2.5	**0.001**	-0.834	**0.018**	-2.833	**<0.001**	-2.157	**<0.001**
		Before-Follow up	-0.5	0.509	-0.959	**0.007**	3.5	**<0.001**	2.848	**<0.001**
		After-Follow up	-3	**<0.001**	-1.794	**<0.001**	0.667	0.23	0.691	0.117
	Control	Before-After	0.667	0.379	0.312	0.362	0.167	0.762	0.042	0.922
		Before-Follow up	-0.5	0.509	-0.321	0.349	0.667	0.231	0.786	0.062
		After-Follow up	0.167	0.825	-0.008	0.979	0.833	0.136	0.828	0.076
	Gap cut	Before-After	0	1	0.168	0.621	0	1	0.047	0.912
		Before-Follow up	0.167	0.825	-0.147	0.666	1.333	**0.019**	1.254	**0.004**
		After-Follow up	0.167	0.825	0.021	0.95	1.333	**0.019**	1.302	**0.005**

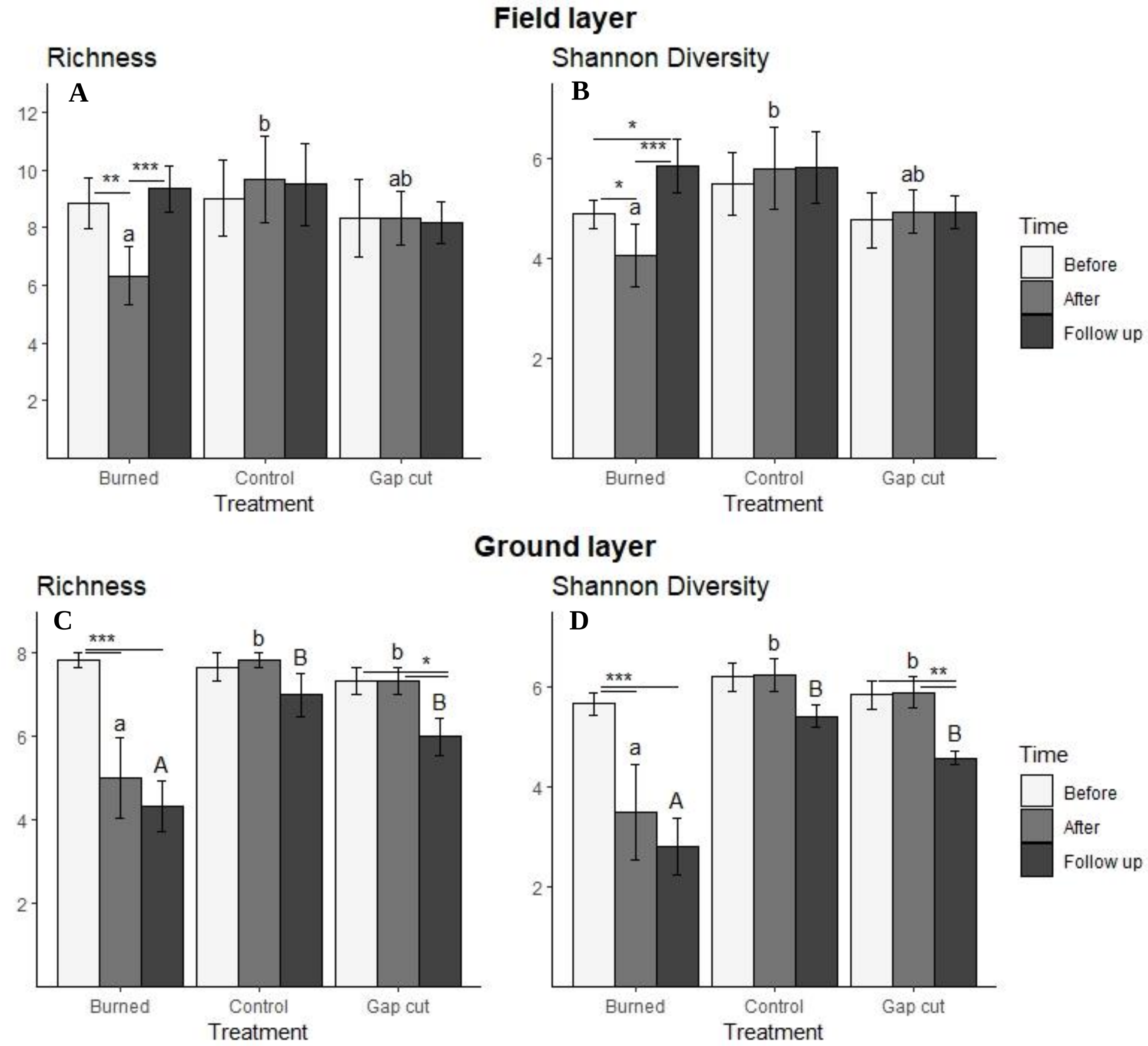

Figure 4. Mean richness (panel A and C) and Shannon diversity (panel B and D) in the field and ground layer respectively. Horizontal lines and stars above bars show significant differences within treatment (<0.05; **<0.01; ***<0.001) and letters indicate significant differences within time points, small letters for after (2012) and capital letters for follow up (2019). Error bars show standard errors*

3.2. Community composition

Community composition changes were assessed by Permanova analyses. The main test revealed a significant interaction effect (*treatment* * *time*) for both field and ground layer (Table 4). In the subsequent post hoc analyses I found no differences prior to restoration and main dissimilarities after restoration appear related to *burned* stands (Table 5). These results were not sensitive to singletons or doubletons as analysis where these were removed showed the same outcome as when included.

In line with the results previously obtained, both inventories post restoration (*after* and *follow up*) displayed significant differences, both in field and ground layer, between *burned* and each of the other two treatments. By contrast, no change was detected between *control* and *gap cut* stands. When looking at each treatment individually; *burned* stands showed compositional changes in both field and ground layer while *control* and *gap cut* stands differed solely in ground layer between *after* and *follow up* communities (see table 5 for exact p-values). All results, significant and non-significant are supported by the graphical visualization on NMDS plots (Figure 5 and 6, for field and ground layer respectively).

*Table 4. Permanova main test statistics for both field and ground layer. Field layer analysis is based on count data of 34 vascular plant species. Ground layer analysis is based on counts of 8 species/genera. The α-probability was set to 0.05 and N=18. Statistically significant results are shown in **bold**.*

	Field layer			Ground layer		
	Df	Pseudo-F	P	Df	Pseudo-F	P
Treatment	2	1.201	0.27	2	10.856	**<0.001**
Timeline	2	8.296	**<0.001**	2	15	**<0.001**
ID (Treatment)	15	11.88	**<0.001**	15	3.324	**<0.001**
Treatment * Timeline	4	6.917	**<0.001**	4	7.629	**<0.001**
Residuals	30			30		

*Table 5. Permanova pairwise comparisons statistics between each level of treatment and time for both layers. Field and ground layer comparisons are shown in the following NMDS figures. To facilitate the interpretation each layer has a figure associated (Fig. 4 and 5 respectively) and each level for both factors a specific letter. The α-probability was set to 0.05 and N=6 for the pairwise post hoc tests. Statistically significant results are shown in **bold**. NaN appear due to low replication and low variation between some of the specific pairwise comparisons therefore t-statistic cannot be calculated.*

		Pairwise comparison	Field layer (Fig.4)		Ground layer (Fig.5)	
			T	P	T	P
Timeline	Before (A)	Burned-Control	0.826	0.729	1.086	0.373
		Burned-Gap cut	NaN	1	1.373	0.159
		Control-Gap cut	0.714	0.858	1.006	0.398
	After (B)	Burned-Control	2.495	**0.003**	2.919	**0.006**
		Burned-Gap cut	2.263	**0.005**	3.014	**0.004**
		Control-Gap cut	0.484	0.929	1.064	0.358
	Follow up (C)	Burned-Control	1.979	**0.007**	2.871	**0.005**
		Burned-Gap cut	1.82	**0.011**	3.99	**0.004**
		Control-Gap cut	0.711	0.758	1.361	0.168
Treatment	Burned (D)	Before-After	3.353	**0.005**	3.112	**0.016**
		Before-Follow up	3.238	**0.007**	5.114	**0.003**
		After-Follow up	3.441	**0.007**	1.319	0.225
	Control (E)	Before-After	2.548	0.087	NaN	0.921
		Before-Follow up	1.571	0.172	NaN	0.996
		After-Follow up	1.716	0.134	4.572	**0.012**
	Gap cut (F)	Before-After	2.198	0.083	2.114	0.102
		Before-Follow up	1.7	0.137	NaN	0.998
		After-Follow up	1.58	0.125	10.825	**0.002**

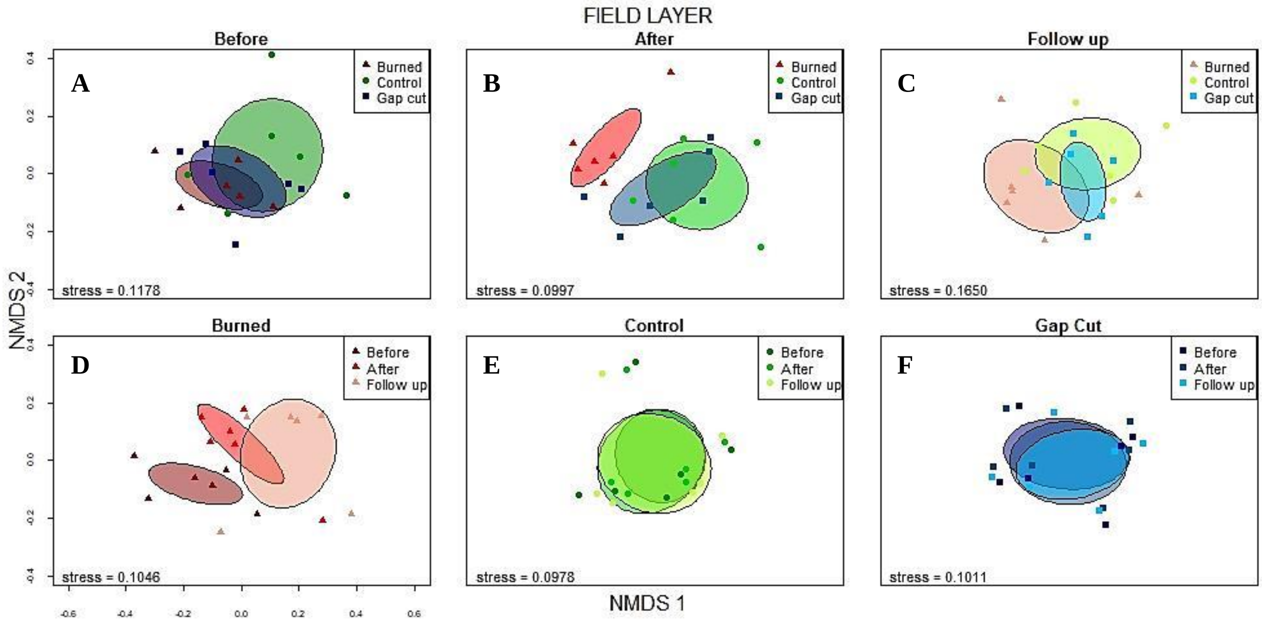

Figure 6. Two-dimensional NMDS visualization of community composition in field layer. Upper panels show the communities from the three treatments at each inventory. Lower panels show the communties amongst time within the same treatment. Letters indicate the correspondent pairwise analyses with significance levels specified in table 3. Symbols and colours represent treatment. Color intensities are assigned to different inventories. Ellipses represent standard deviations.

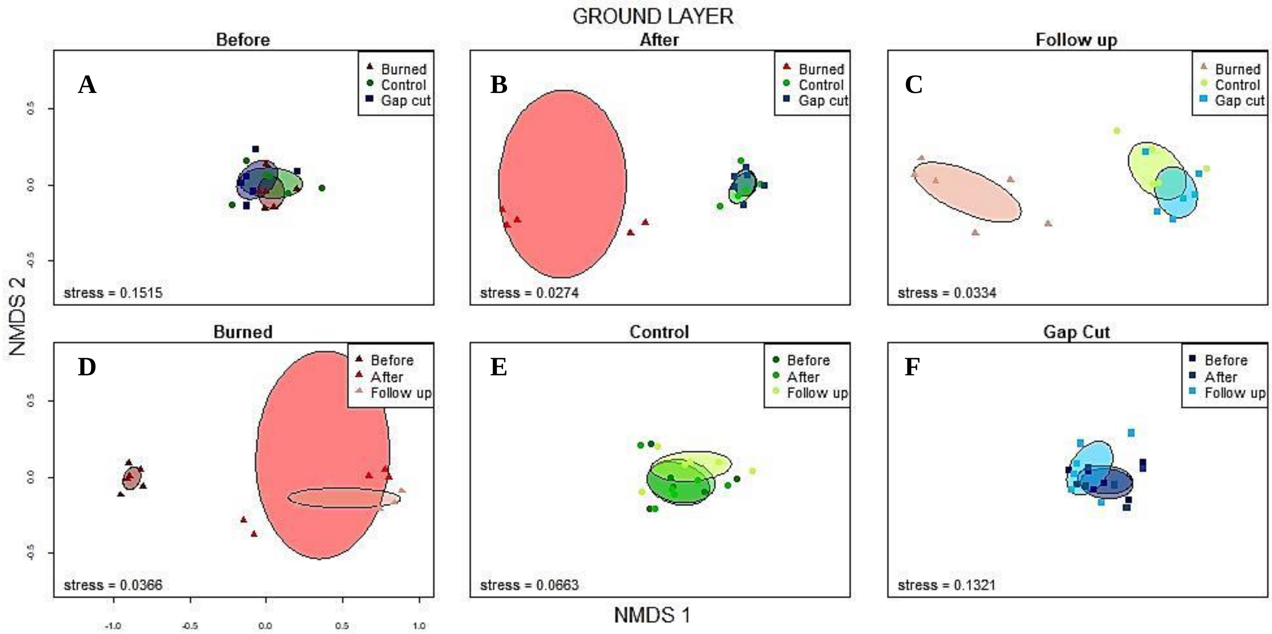

Figure 5. Two-dimensional NMDS visualization of community composition in ground layer. Upper panels show the communities from the three treatments at each inventory. Lower panels show the communties amongst time within the same treatment. Letters indicate the correspondent pairwise analyses with significance levels specified in table 3. Symbols and colours represent treatment. Color intensities are assigned to different inventories. Ellipses represent standard deviations.

3.3. Response patterns

Among treatments species displayed diverse responses over time (as defined and classified in the methods section). The different responses' percentages were analysed with Cochran-Mantel-Haenszel test resulting in no different responses between treatments neither in field layer (p: 0.257) nor ground layer (p: 0.944). Nevertheless, I could observe some general trends in both layers (see figure 7). Between *before* and *after* inventories (BA) both layers showed more neutral responses in *control* and *gap cut* stands while negative responses accumulated in *burned* stands. Between *after* and *follow up* inventories (AF) neutral and negative responses had similar frequencies among treatments, whereas more positive responses appear in *burned* stands.

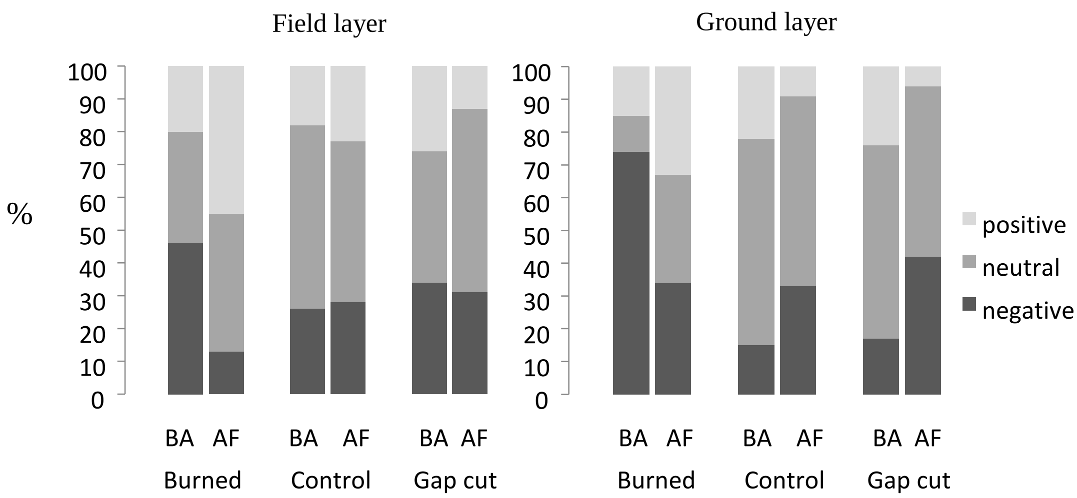

Figure 7. Percentages of positive, neutral and negative responses observed for field and ground layer between before and after (BA) inventories and between after and follow up (AF) inventories.

3.4. Indicator Species Analyses

The test detected one vascular plant (*Epibolium angustifolium*) and one moss genera (*Polytrichium spp.)* significantly associated with *burned* stands in both inventories post restoration. The test did no detect species exclusively associated to control or gap cut treatments. Nevertheless several species were significantly associated to the combination of *control* and *gap cut* stands (one vascular plant and six bryophytes for *after* inventory; and four bryophytes in *follow up* inventory, see table 6).

*Table 6. Indicator Species Analyses statistics after restoration took place. The association value is given for each species and the significance, after 999 permutations, is given by stars (*p<0.05, **p<0.01, ***p<0.001).*

	Burned				Control + Gap cut			
Species	After		Follow up		After		Follow up	
Epibolium angustifolium	0.792	***	0.846	***				
Linnaea borealis					0.562	*		
Polytrichium sp.	0.596	*	0.913	***				
Pleurozium schreberi					0.967	***	0.921	***
Hylocomium splendens					0.882	***	0.884	***
Dicranum sp					0.851	***	0.809	***
Ptilidium sp					0.784	**		
Ptilium crista-castrensis					0.781	***	0.723	**
Barbilophozia sp.					0.586	*		

4. Discussion

This study can potentially increase the comprehension of restoration outcomes under more natural conditions. Here I included the analyses of two distinct methodologies mimicking boreal forests natural disturbances. Their effects are tested over two of the main organism groups in boreal understory vegetation considering both short- and long-term responses.

4.1. Control stands

As predicted, I did not observe any significant changes in diversity measures or community change analyses in *control* stands. Except, in ground layer where I did observe a distinct community composition in *follow up* inventory, analogous to the pattern I observed in *gap cut* stands. This result could be explained by the fact that 2018 was an extremely dry year according to SMHI precipitation data.

4.2. Burned stands

I found strong and partial support, in field and ground layer respectively, for my hypothesis in *burned* stands. As predicted, the results showed an initial decrease in both layers, for richness as well as for Shannon diversity, showing that both organism groups were heavily impacted by fire. In the long-term, diversity values peaked in the field layer which suggested a rebound effect. The results suggested that fire-related species sprouted after the fire such as the ones detected by the ISA. Nevertheless, ground layer diversity values remained significantly lower after the treatment, showing no signs of diversity recovery after eight years from the fire disturbance. In line with the above mention results, community composition changes followed the same pattern. Field layer communities were significantly different at each time point while in the ground layer *before* community (2010) was different from both post restoration inventories: *after* (2012) and *follow up* (2019) communities. In the ground layer I observed a higher dispersion of the data in *after* inventory (2012). This variability of the data could be explained due to the heterogeneous fire impact. However considering that I focussed my research at stand level I decided that I could perform the analyses and draw reliable conclusions. Vegetation response pattern seemed to follow different trajectories in *burned* stands compared to *control* and *gap cut* stands.

According to my results, fire generated a distinctive effect in understory vegetation. The effects depend on the time since restoration and also on the target study group. While I found a positive impact in the long term for vascular plants, bryophytes showed a consistent detrimental impact. My results show that diversity values were not higher in burned than in reference stands. However, after eight years from the disturbance the community composition shifted in a significant different direction. This suggests that, at landscape level, burned patches within a forest matrix allow the cohabitation of fire-related, pioneer and opportunistic species that otherwise will not be present in managed forests.

My results support are in line with the study presented by Hekkala et al. (2014a) where burned stands did not show a significant increase in species richness but did display a clear shift in community composition. In other studies, burning treatment has been proved to increase vascular plant richness (Rees and Juday, 2002, Marozas et al., 2007, Laarmann et al., 2013) while bryophytes suffered a highly negative impact (Rees and Juday, 2002, Marozas et al., 2007). The dominant feather mosses in my study area, *Pleurozium schreberi* and *Hylocomium splendens,* have been prove to negatively affect the germination and regeneration of understory vegetation (Soudzilovskaia et al., 2011). Without disturbances, specially fire, the thick moss layer may lead the ecosystem functioning into a retrogression (Mallik, 2003). These results suggest that the lack of fire disturbance will negatively affect the ecosystem functioning and productivity.

Other studies in saproxylic beetles have observed positive responses to burning treatments in the short-term for richness (Hägglund et al., 2020, Hjältén et al., 2017). Nevertheless, burning treatment in boreal forests generates divergent responses depending the organism group and time since disturbance. Some groups might not recover after an intense fire event and therefore prescribed burning should be carefully implemented and other alternative considered (Hjältén et al., 2017).

4.3. Gap cut stands

I found no support for my prediction in *gap cut* stands. In contradiction to my hypothesis I did not observe significant changes in diversity measures for the field layer neither in short- nor long-term, suggesting that this methodology might have a limited effect in boreal forest vegetation. Interestingly and against my prediction in the ground layer both richness and Shannon diversity values decrease significantly in the *follow up* inventory. One possible explanation can be the fact that 2018 was an extremely dry year, recorded by SMHI (2020), and might have affected the ground layer. Community composition analyses followed a similar pattern as the one obtained in diversity analyses. I observed no differences in field layer whereas only *follow up* communities differed in ground layer. Vegetation responses in the field layer remained mainly neutral along inventories. By contrast in the ground layer I observed a noticeable increase of negative responses from short- to long-term inventories, consistent with the results obtained in diversity and community analyses. ISA did not find any species exclusively associated to *gap cut* stands. This could be explained by the fact that boreal vegetation is well buffered against light disturbances (Hekkala et al., 2014a).

Surprisingly, *gap cut* and *control* stands showed concordant results across my analyses. Therefore, my study found no support to argue that gap cutting generated a differential impact that was not already observed in reference stands. Even though my analyses did not detect effects of gap cutting on understory vegetation, there could still be some time-lagged responses, especially for bryophytes in the ground layer (Hylander et al., 2012) and long term studies are still needed.

My results are in line with previous studies where gap cutting did not generate any impact or shift in field or ground layer (Hekkala et al., 2014a, Laarmann et al., 2013). These results suggest that gap cutting is not an effective restoration methodology in boreal forest vegetation. Studies in other organism groups from the same study area, like saproxylic beetles, did not show any positive impact in richness or abundance either (Hjältén et al., 2017, Hägglund et al., 2020). Gap cutting could be replaced by another methodology studied by Hekkala et al. (2014a), called "storm simulation". It combines the creation of canopy gaps with tree uprooting and has showed promising results as an effective restoration method.

4.4. Limitations and further studies

When analysing the data I found some variability that was not accounted for. First of all, the heterogeneous impact created by the fire in *burned* stands. Some of the plots positioned before the fire were not completely burned and therefore the data collected had higher variability than the other treatments. The scope of my study was at stand level and therefore this variability was appropriate to achieve wildfire representability at larger scales. However if I would like to detect fire effects at plot level I would argue to place some extra plots in the first inventory, as baseline. Consequently if some of the plots were not affected by the fire those could be removed from posterior inventories and still have a satisfactory sample size for posterior analyses. Secondly, in *gap cut* stands I could not detect significant differences with my study design focused at stand scale. If the goal of the study would have been to detect canopy openings effects at plot level I would suggest distributing equivalently the amount of plots inside and outside the gaps.

My study focused on diversity measures and community composition changes, neither of these analyses take into account species identity as a variable. To get more insight I decided to analyse also vegetation response pattern and look for species ecological preferences through the ISA. All of my analyses (except ISA) aimed at understanding and identifying main trajectories at stand scale after restoration. If I would have had more time I would have included species individual coverage changes as well as changes in vegetation functional types to have more information about how ecosystem functioning might be affected by restoration. I think it would have been particularly interesting analyse if dominant species outcompete pioneers in the long term after a disturbance and also how berry producers are particularly affected by restoration.

Another particular limitation was the identification of bryophytes down to species level. This group is particularly complex and in many cases expert skills and microscopic details are required to properly identify them. To deal with this situation I would contact an expert to assess my identification and spend time in the laboratory.

5. Conclusion

My study highlights the importance of including different organisms groups and long-term studies in the evaluation of restoration success. Field layer showed opposite responses in short- versus long-term analyses whereas ground layer show a consistent negative response after eight years since restoration. Focusing only in one organism group can lead to misinterpretations of the real impact of restoration in the ecosystem. In addition, the lack of long-term differential responses found in bryophytes as well as in Hylander et al. (2012), suggests that the ground layer might need more time to recover after disturbances and further long-term studies are needed in order to properly evaluate the restoration outcome.

Eight years after restoration, neither of the methods resulted in a higher diversity at stand level when compared to reference stands. However burning treatment shifted the communities in a significantly different direction and the community after eight years does not resemble to the pre-restoration community. These results suggest that implementing recurrent prescribed fires, blending within the managed forest matrix, can help recreate a heterogeneous landscape. This habitat variability will allow for a higher total diversity, including different organisms groups, at landscape level (Kuuluvainen and Aakala, 2011). Accordingly, Hekkala et al. (2014b) claimed that in order to achieve a successful restoration, different treatments need to be regularly applied in the ecosystem.

Other studies conducted in the same study area have focused on other organism groups. Looking at their results it is needed to bring up to attention that in *burned* stands many species are also disfavoured, not only the dominant ones, and therefore other restoration methods need to be considered (Hjältén et al., 2017). This consideration is especially important when populations of red-listed species are present in the area or when the goal is to recover old-growth associated species (Hjältén et al., 2017).

Although the lack of effects due to gap cutting in my study, Hägglund et al. (2020) showed that gap cut stands could sustain both disturbance favoured and late successional state beetle species. Therefore gap cutting might offer a promising outcome when it comes to restoration, allowing the coexistence of different successional-stages species. Other alternative methods like storm simulation has been shown to generate greater positive impacts on the boreal forests (Hekkala et al., 2014a) and therefore should be consider as a more effective alternative.

6. Appendix

Table 7 *Descriptive stand characteristics data before restoration. Data were provided by the land owner except for data on CWD and tree species distribution that were collected by the baseline surveyors..*

Treatment	Stand ID	Area (ha)	Productivity ($m^3ha^{-1}year^{-1}$)	Tree age (years)	Standing volume (m^3ha^{-1})	Tree species distribution (%)			CWD volume (m^3ha^{-1})
						Pine	Spruce	Broadleaves	
Control	3191	11.4	4.4	88	190.7	60	30	10	4.2
	3298	4.5	3.8	110	241.1	30	60	10	4.2
	4725	21.6	4.1	172	226.4	40	40	20	6.4
	6083	3.9	3.7	130	223.6	60	30	10	5.1
	6232	15	4.4	86	189.9	60	20	20	3.4
	8668	3.7	3.7	95	164.7	50	30	20	1.8
Gap cut	505	3.5	4.1	141	198.7	60	30	10	-
	4848	14.8	4.4	96	231.3	40	50	10	4.3
	5655	8.4	3.7	135	257.5	50	30	20	5.7
	6323	3.6	4.4	121	254.7	60	30	10	2.8
	7315	3.8	3.5	93	263.2	30	60	10	4.2
	8570	6.8	3.7	145	184.7	70	20	10	7.4
Burned	1935	6.8	4.4	96	151.7	50	40	10	4.4
	2746	4.7	4.4	113	283.1	70	20	10	2
	3126	7.2	4.4	82	149.5	50	30	20	1.9
	4402	5.8	4.4	153	-	50	40	10	10.4
	6210	7.6	4.1	123	128	50	40	10	1
	7552	4.5	3.7	155	221.3	80	20	0	7

***Table 8**. Species list from field and ground layer with relative abundance at each inventory in each treatment. Sorted my abudance, frst vascular plants and then bryophytes.*

	Burned			Control			Gap cut		
Species	2010	2012	2019	2010	2012	2019	2010	2012	2019
Vaccinium myrtillus	0.96	0.90	0.89	0.93	0.95	0.94	0.96	0.96	0.95
Vaccinium vitis-idaea	0.92	0.87	0.91	0.89	0.94	0.91	0.89	0.91	0.93
Deschampsia flexuosa	0.24	0.26	0.50	0.53	0.62	0.58	0.33	0.40	0.40
Linnaea borealis	0.26	0.03	0.11	0.23	0.21	0.26	0.26	0.21	0.28
Luzula pilosa	0.01	0.02	0.03	0.05	0.06	0.05	0.02	0.03	0.01
Juniperus comunis	0.01	0.00	0.00	0.00	0.01	0.02	0.01	0.00	0.01
Melampyrum sylvaticum	0.01	0.00	0.05	0.02	0.07	0.14	0.03	0.03	0.07
Lycopodium annotinum	0.03	0.00	0.00	0.01	0.01	0.02	0.03	0.02	0.01
Maianthemum bifolium	0.02	0.01	0.03	0.00	0.01	0.01	0.03	0.01	0.01
Empetrum nigrum	0.15	0.01	0.01	0.12	0.13	0.12	0.11	0.13	0.11
Calluna vulgaris	0.01	0.00	0.00	0.08	0.08	0.08	0.01	0.01	0.01
Andromeda polifolia	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00
Rubus chamaemorus	0.03	0.03	0.04	0.03	0.05	0.05	0.03	0.03	0.02
Vaccinium uglinosum	0.01	0.01	0.05	0.00	0.00	0.01	0.01	0.01	0.01
Gymnocarpium dryopteris	0.01	0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.00
Trientalis europaea	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.03	0.01
Melampyrum pratense	0.02	0.00	0.17	0.05	0.10	0.02	0.01	0.06	0.04
Epibolium angustifolium	0.00	0.16	0.30	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum pratense	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum sylvaticum	0.01	0.02	0.02	0.01	0.01	0.02	0.01	0.03	0.03
Orthilia secunda	0.01	0.00	0.00	0.03	0.03	0.03	0.01	0.00	0.00
Deschampsia cespitosa	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Rubus idaeus	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Solidago virgaurea	0.00	0.00	0.00	0.03	0.01	0.01	0.00	0.00	0.00
Calamagrostis purpurea	0.00	0.00	0.00	0.01	0.01	0.01	0.00	0.00	0.00
Godyera repen	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Vaccinium oxycoccos	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Diphasiastrum complanatum	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Listera cordata	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Ranunculus lapponicus	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Melampyrum sp.	0.00	0.00	0.00	0.09	0.00	0.00	0.01	0.00	0.00
Carex sp	0.01	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Rhododendron tomentosum	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Equisetum palustre	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
Barbilophozia sp.	0.07	0.03	0.00	0.27	0.30	0.07	0.27	0.30	0.03
Dicranum sp.	0.66	0.09	0.09	0.67	0.72	0.54	0.74	0.79	0.66
Hylocomium splendens	0.84	0.13	0.12	0.73	0.77	0.73	0.73	0.73	0.70

Pleurozium schreberi	0.87	0.10	0.22	0.86	0.86	0.82	0.86	0.91	0.85
Polytrichum sp.	0.18	0.54	0.87	0.25	0.27	0.27	0.16	0.25	0.15
Ptilidium sp.	0.17	0.01	0.00	0.15	0.12	0.02	0.21	0.16	0.03
Ptilium crista-castrensis	0.55	0.09	0.03	0.48	0.49	0.44	0.49	0.49	0.38
Sphagnum sp.	0.08	0.09	0.08	0.14	0.16	0.17	0.05	0.05	0.03

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