Restoration strategies in boreal forests: Differing field and ground layer response to ecological restoration by burning and gap cutting

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A B S T R A C T

The boreal biome is one of the largest in the world and its forests have been widely exploited for centuries. Consequently, large areas have suffered ecological simplification and loss of biodiversity. Under the current circumstances passive conservation measures are no longer enough and active restoration techniques need to be developed and assessed to preserve and recover the loss of biodiversity. We evaluated short- and long-term effects of two restoration methods aimed at mimicking natural disturbances on species richness, Shannon Diversity and community composition of vascular plants in the field layer and bryophytes in the ground layer. The experiment consisted of 18 forest stands in northern Sweden; each assigned to a different treatment: prescribed burning, gap cutting and untreated stands left as controls. A before-after control-impact (BACI) study design was applied and data was collected on three occasions: once prior to restoration (2010) and twice post restoration; one year (2012) and eight years after (2019). We analysed the differences in species richness and Shannon Diversity with linear mixed effect models and community composition changes with multivariate methods. Fire treatment caused an initial decline in diversity for both field and ground layer, but in the long-term, field layer surpassed the species richness and Shannon Diversity values found prior to restoration. Ground layer bryophytes species richness and Shannon Diversity remained lower than pre-treatment. Prescribed burning should, therefore, be used with caution in core areas for bryophyte diversity. Community composition in burned stands differed significantly between each time point as well as when compared to other treatments, for both layers. By contrast, we found no significant differences in diversity measures or community composition after gap cutting. The absence of effects from gap cutting suggests that minor changes in canopy cover does not affect the vegetation structure of forest stands. The organism group-specific responses, and temporal variability to restoration, highlight the importance of including more than one organism group, different restoration methodologies, and long-term studies in order to properly assess restoration outcomes at landscape level.

1. Introduction

Historically, boreal forests were shaped by naturally occurring disturbances such as fire, wind and pest outbreaks (Kuuluvainen and Aakala 2011) creating a highly heterogeneous landscape (Bergeron et al. 1999). During the last century, these agents of disturbance have largely been replaced by forestry as the main factor affecting forest structure and composition (Esseen, et al 1997, Bouchard & Pothier, 2011). Moreover, forestry practices changed over the last decades, especially in the boreal zone (sensu Ahti et al. (1968)) where today's forestry has been directed towards thinning, clearcutting and even aged mono-culture plantations (Esseen et al., 1997, Östlund et al., 1997, Wallenius,

2011). At the same time as forestry was intensified, fire protection programmes, as for example in some parts of the boreal Fennoscandia, efficiently reduced the occurrence of naturally induced fires. The annual fire area in Sweden is, today, only a fraction of historical values. Less than 0.02% of the forest area burns each year in Sweden compared with approximately 1% per year before 1900 CE (Granström, 2001, Zackrisson, 1997).

The previously highly diverse and heterogeneous boreal ecosystem (Esseen et al., 1997, Östlund et al., 1997) has suffered ecological simplification and a biodiversity decrease due to intensive forest management and the suppression of natural disturbances. Many species that are adapted to fire (Granström and Schimmel, 1993), dead wood

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dependant or associated with old growth continuity forest are now threatened with extinction (Kuuluvainen, 2009, Virkkala, 2016, Paillet et al., 2010) due to the current forest exploitation system, with the fire suppression program and shorter rotation times. Natural disturbances, such as wildfires and canopy openings by wind fell trees, not only shaped the tree layer, but also the understory vegetation. Understory vegetation, mainly composed of ericaceous dwarf shrubs and feather mosses and lichens, plays a key role for ecosystem functioning (Nilsson and Wardle, 2005, Wardle et al., 2012) influencing conifer regeneration (Mallik, 2003), nutrient recycling and microbial activity (Wardle and Zackrisson, 2005). Thus, changes in natural disturbance regimes likely impacted ecosystem functions (Mallik, 2003, Wardle et al., 2012). Studies have shown that ecosystem functions are largely influenced by the fluctuation in abundance of common species (Winfree et al. 2015), and that rare species do not contribute to ecosystem stability (Schwartz et al. 2000).

To cope with biodiversity loss and degraded ecosystems, traditional conservation measures have been the establishment of national parks or nature reserves. However, these passive conservation measures are not enough (Kuuluvainen, 2009), partly due to the limited area available for protection. Internationally, a commitment to restore at least 15% of degraded forest ecosystems was established at the Aichi Convention on Biological Diversity 2010 (CBD, 2010) and echoed in the EU Biodiversity Strategy for 2020 (EU, 2011). Thus, active ecological restoration methods need to be applied to restore degraded forest habitats (Kuuluvainen, 2009, Angelstam et al., 2011, Halme et al., 2013, Johansson et al., 2013). In addition, some types of ecological restoration have been included in the FSC certification requirements in some countries, e.g., Sweden. Ecological restoration is commonly conducted in protected areas were natural disturbance processes have been lost. It is, therefore, of outmost importance to develop cost-efficient and easily implemented methods for ecological restoration.

Restoration theory is generally based on the assumption that it is favourable to mimic natural processes in degraded landscapes (Lindenmayer et al. 2006, Kuuluvainen 2009) like wildfires and gap dynamics. High intensity boreal wildfires can drive vascular plant communities towards earlier successional states (Hekkala et al., 2014a), while low intensity fires and prescribed burning allow the expansion of pioneer and opportunistic species (Schimmel and Granström, 1996, Wang and Kemball, 2005, Faivre et al.,2016). Bryophyte species composition has been shown to respond in a similar way. In a study from eastern Canada, Paquette et al. (2016) showed that perennial species decreased whereas colonist species increased as a result of fire. Small-scale forest gap dynamics, like canopy openings, are particularly important in mature boreal forest (Esseen et al., 1997) allowing more light to reach the ground which can boost the diversity and abundance of certain vegetation species (Thomas et al., 1999, Prévost and Raymond, 2012) and allow multiple successional stages (Hekkala et al. (2014b). The restoration methods assessed in this study aim to mimic both large- and small-scale natural disturbances, specifically fires (prescribed burning) and gap dynamics (gap cutting), to recreate a more structurally diverse forest and allowing the coexistence of more plant species.

Several studies have shown differential effects of gap cutting and prescribed burning depending on the studied species group (Versluijs et al., 2017, Hjältén et al., 2017, Hekkala et al., 2014a, Baker et al., 2004). Inclusion of several organism groups when assessing restoration effects can improve our comprehension the ecosystem responses. Here we present a study that includes two of the main organism groups present in the boreal understory vegetation (Nilsson and Wardle, 2005): (1) vascular plants dominated by ericaceous dwarf shrubs in the field layer and (2) bryophytes, with feather mosses dominating in the ground layer.

Previous studies have shown short-term effects after restoration in forested areas, but that there can also be a delay in biodiversity responses (Bouget et al., 2014, De Keersmaeker et al., 2011). In this study, we address both short- and long-term responses using vascular plants and bryophytes. These organism groups have previously been used in

order to detect long-term biodiversity trajectories (Rudolphi and Strengbom, 2016). The before-after-control-impact study design allowed us to control for environmental stochasticity (Eberhardt, 1976; Hägglund et al., 2020).

The aim of the study was to assess the effect of two restoration methods: prescribed burning and gap cutting, recreating large- and small-scale dynamics; on vegetation biodiversity at stand level.

We tested the following hypotheses:

(1) Prescribed burning will, in the short-term, decrease field layer richness and Shannon Diversity due to fire impact. In the long-term, an increase of species richness and Shannon Diversity values is predicted due to colonisation of opportunistic pioneer species. Community composition is predicted to exhibit a notable shift at each time point.

(2) Prescribed burning is predicted to influence the ground layer in the same way as the field layer, in both short- and long-term.

(3) Gap cutting is predicted to increase field layer species richness and Shannon Diversity in the short-term due to augmented light availability; in the long-term the light increase effect will fade and dominant species will take over, outcompeting the few opportunistic species that might have appeared. Community composition will have minor changes due to the lower intensity impact created.

(4) Gap cutting openings will bring drier conditions to the ground layer and is predicted to have short-term negative impacts on bryophytes species richness and Shannon Diversity. In the long-term, ground layer bryophytes are expected to remain negatively affected by the canopy openings compared to before state. Community composition will show minor changes due to the lower intensity impact created.

2. Material and methods

2.1. Study area

The study was conducted in northern Sweden in a region (6324′ to 6430′ N and 1722′ to 2012′ E, Fig. 1) classified as the middle boreal zone (sensu Ahti et al. (1968)). In this region conifer forests predominate, with Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.) Karst.) as the most abundant tree species. Deciduous broadleaved trees (mainly birch, *Betula* spp.*)* are 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 average precipitation (calculated from the period 1961–1990) registered in the area (from 9 weather stations located around the study area, see table 1 in Appendix) is 514 mm and mean annual temperatures range between 0 and 4 ̊C (Open data extracted from SMHI, 2020).

The study design consisted of 18 forest stands, distributed over six geographic areas. Stand characteristics were determined 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, and thus were already allocated for conservation purposes. 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).

2.2. Restoration methods

The restoration experiment was developed in close collaboration with the forest company Holmen Skog based on the principles that treatment should: 1) be based on the best knowledge of biodiversity
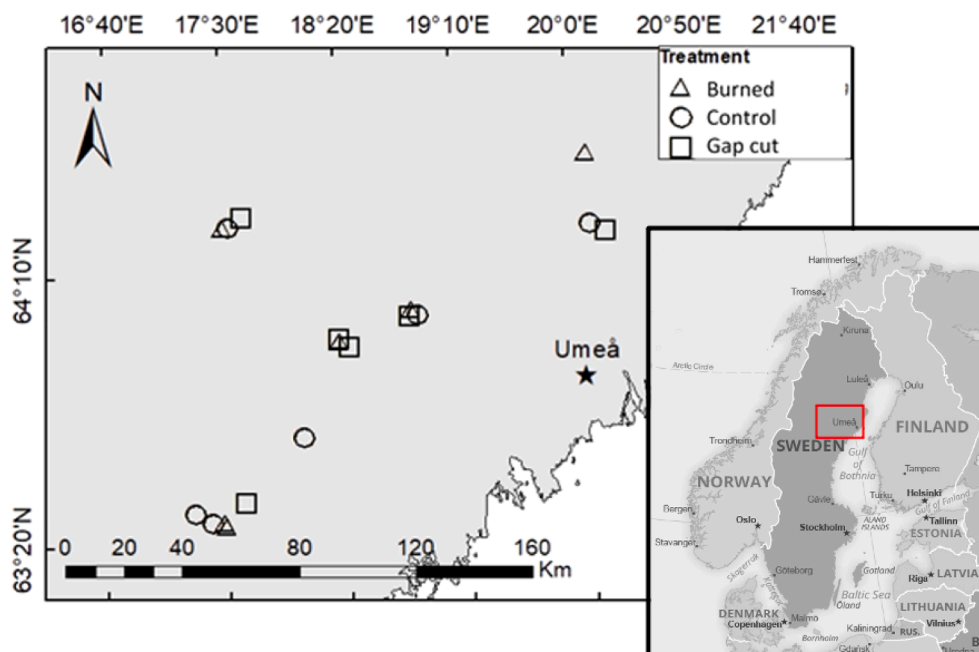
Fig. 1. Map of Sweden with the location of the stands.

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. Differences between treatments were tested with One-way ANOVA, no significant differences were found. Treatment.

Area	Productivity	Tree age	Standing volume	Tre species distribution (%)			CWD volume
(ha)	$(m^3ha^{-1}\ year^{-1})$	(years)	(m^3ha^{-1})	Pine	Spruce	Broadleaves	(m^3ha^{-1})
Control 10 ±2.9	4. ±0.1	113.5 ±13.4	206.1 ±11.7	50 ±5	35 ±5	15 ±2	4.1 ±0.6
Gap cut 6.8 ±1.8	3.9 ±0.1	121.8 ±9.2	231.6 ±13.5	51 ±6	36 ±6	11 ±1	4.8 ±1.1
Burned 6.1 ±0.5	4.2 ±0.1	120.3 ±12.1	186.7 ±42.7	58 ±5	31 ±4	20 ±2	4.4 ±1.4

conservation; 2) allow for a quantitative evaluation of different treatments; 3) be easily conducted with today's techniques/machinery; and 4) be cost neutral. These principles were designed to enable a rapid application of the restoration measures if found effective.

When conducting experimental studies under natural conditions, it is important to use an experimental design that can control for environmental stochasticity and between-year variation. We therefore applied a before-after-control-impact approach (Eberhardt, 1976), including baseline inventories of vascular plants and bryophytes one year prior to restoration and follow-up inventories conducted after restoration. Two treatments: (1) prescribed burning and (2) gap cutting; were applied during spring/summer of 2011 on six stands per treatment and six stands were left as control. The prescribed burned stands are, hereafter, referred to as *burned* stands and gap cutting stands are referred to as *gap cut* stands. These particular management operations were chosen to mimic natural disturbances historically present in boreal forests (Angelstam, 1998).

The prescribed burning was conducted between June 10 and August 3, 2011, depending on local weather conditions at the different forest stands. In the early spring of 2011, there was a pre-fire extraction of timber (between 5 and 30%) to facilitate the drying of forest floors and to compensate for restoration costs (Olof Norgren, head of forestry treatment at Holmen Skog AB in a personal communication to Hjältén et al., 2017). Approximately 2–5 m³/ha of cut trees were left on site to promote establishment of dead-wood dependent species (Hjältén et al., 2017). The intensity of the fire was mostly moderate, killing most of the spruce and birch trees whereas most of pine trees survived. However, the fire intensity was higher in two stands killing about 50% of the pines. The fires can be classified as medium to light with no crown fires but no quantitative measures on intensity or severity were taken.

In gap cut stands, six gaps each measuring 20 m in diameter, were created per hectare (during the winter/spring of 2011 before snowmelt) amounting to approximately 19% of stand area. Each gap had one large deciduous tree retained in the centre when possible or Scots pine when not. The rest of the trees in the gap 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 restoration costs (Hjältén et al., 2017) and to reduce the risk of creating more fresh coarse woody debris (CWD) than is prescribed by Swedish forestry legislation (5 m³ ha⁻¹).

2.3. Data collection

The first inventory took place in August-October of 2010 before the intervention, and is considered the baseline, henceforth referred to as *before*. The second inventory took place in August-October of 2012; one year after the restoration was applied, henceforth referred to as *after*. The third inventory took place in July 2019, eight years after restoration, henceforth referred to as *follow up*. Total precipitation and mean temperature data (from nine weather stations available at SMHI open database; locations reproduced in Appendix, Table 1) were gathered from one year prior to every inventory, to help explain potential between-year variations that might have impacted the study area.

Each stand had two parallel transects of approximately 400 m in total. In smaller stands, extra transects were established to compensate for shorter transect lengths. Transects were spaced 50 m apart and at least 25 m from the stand edge. In total, 25 permanent plots of 0.25 m² every 15 m were established and marked with plastic or metal sticks in the corners. In gap cut stands, 17% of the plots were placed inside gaps

in order to achieve representability for the whole stand and focus on the responses and changes observed at stand level, not only inside the gaps. To allow repeatability and facilitate posterior inventories, start and end positions for each transect were marked with large poles in the field, and coordinate positions were recorded during baseline inventory (2010).

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. Some permanent stick markers were missing, thus ten plots had to be relocated following the original design using a measuring tape from the transects' starting points to be included in the analyses.

At each plot, field and ground layer were inventoried by collecting presence/absence data. All vascular plants in the field layer were identified to species level at each inventory. In the case of bryophytes, which constitutes the ground layer, *before* (2010) and *after* (2012) surveyors identified all species present. In the *follow up* inventory (2019), common Swedish species were recorded, mostly feather mosses. These common species are the most abundant ones and have a larger impact in ecosystem functionality according to Winfree et al. (2015). To avoid misidentifications, genera with very similar species were kept to genus level and, as a result, we collected data on eight common taxes (four species and four clusters of species with two or three species each). Subsequently, data from *before* (2010) and *after* (2012) inventories were adapted by grouping and counting species according to the level of detail used in 2019s inventory in order to allow comparisons between all inventories.

The raw data contains information on the presence/absence of species data in 450 plots resurveyed at each inventory. For analysis, data from plots in the same stand were pooled together to obtain relative frequencies of each species per stand.

2.4. Diversity measures

This study focuses on two alpha diversity measures. Species richness (S) and effective number of species (Jost et al., 2010), henceforth called Shannon Diversity, to incorporate information about abundance. The effective number of species (referred as Shannon Diversity) is a measure derived from Shannon Index, which is a measure of entropy that can cause some misunderstanding when it comes to data interpretation (Jost, 2006). Therefore, Shannon Index was discarded in the present study and instead, Shannon Diversity was calculated using the following function:

$$ShannonDiversity = e^{(-\sum_{i=1}^{S} p_i \ln p_i)}$$

where S = species richness; p = frequency of S_i.

2.5. Statistical analyses

Analyses on diversity measures and Indicator Species Analyses 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. The Vegan package (Oksanen et al., 2019) was used for plotting NMDS graphs. For nomenclature, we used Svensk fältflora (Mossberg and Stenberg, 2018) for vascular plants and Mossor: en fältguide from Hallingbäck and Holmåsen (2016) for bryophytes. Each stand characteristic variable was analysed with general 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*. We 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). The Shannon Diversity lmer model for the field layer failed to converge and therefore we used the Nelder-Mead optimization method to find local convergences and make the model converge.

The 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 we analysed the dataset by splitting burned and not burned plots within stands, but sample sizes were unbalanced 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. We 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.

Community composition changes were analysed using PERMANOVA + add-on package (Anderson et al., 2008) in PRIMER + software (Clarke and Gorley, 2006). PERMANOVA has been shown to be robust in cases with a balanced study design also with relatively small sample sizes as in our study (Anderson and Walsh 2013). All species were included in the 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 the 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*.

Indicator Species Analyses (Dufrene and Legendre, 1997) was performed, with the "multipatt" function included in the 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 exclusively found in a single treatment and also when that species occurs in all sites belonging to a singular treatment. To analyse our data, we applied the phi coefficient of association, which is a correlation index that allowed us to determine ecological preferences of the species. This method will test the observed species distribution and identify to which group, or combinations of groups, better matches (De Cáceres et al., 2010). Permutation limit was set to 2999.

3. Results

In total, we found 34 species of vascular plants and eight taxes of bryophytes. The most abundant vascular plant species were *Vaccinium myrtillus* and *Vaccinium vitis-idaea* (ericaceous shrubs) and among the bryophytes *Hylocomium splendens* and *Pleurozium schreberi* (feather mosses) (see table 2 in the Appendix for species' abundance list). No rare or red-listed species were found in any of the inventories.

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 of 0–4 ̊C. Nevertheless, the total amount of precipitation registered in 2009 (611 mm) and 2011 (603 mm) was higher than average (514 mm, average for the period 1961–1990) while 2018 was a dryer year (439 mm). Stand characteristics (see Table 1) did not differ between treatments before restoration measures were applied.

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	F	P	F	P	F	P
Treatment	2	0.50	0.613	0.89	0.427	6.97	**0.005**	9.76	**0.001**
Time	2	2.63	0.085	6.18	**0.004**	20.09	**<0.001**	25.69	**<0.001**
Treatment*Time	4	4.45	**0.005**	5.74	**0.001**	6.85	**<0.001**	6.16	**<0.001**

3.1. Species richness and Shannon Diversity

We found significant effects of both treatment and time, and the interaction between these two factors, on both layers and both species richness and Shannon Diversity (see Table 2 for more details).

Further analyses of the interaction term for field layer data revealed significant differences between *burned* and *control* stands, both for species richness and Shannon Diversity, for the time *after* but not for *before* and *follow up*. When analysing differences within treatment, only *burned* stands displayed significant differences between time points in species 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 Fig. 2A and 2B). 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 between *after* and *follow up* inventories. Interestingly, in *gap cut* stands we found a significant decrease in *follow up* inventory for both diversity measures (see Fig. 2C and 2D). *Control* stands did not statistically differ between time points.

3.2. Community composition

The main test revealed a significant interaction effect (*treatment * time*) for both field and ground layer (Table 4). These results were not sensitive to singletons or doubletons as analysis where these were removed showed the same outcome as when included.

In the subsequent post hoc analyses we found no differences prior to restoration, and main dissimilarities after restoration appear related to *burned* stands (Table 5).

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 (Figs. 3 and 4, for field and ground layer respectively).

3.3. Indicator species analyses

The test detected one vascular plant (*Epilobium 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).
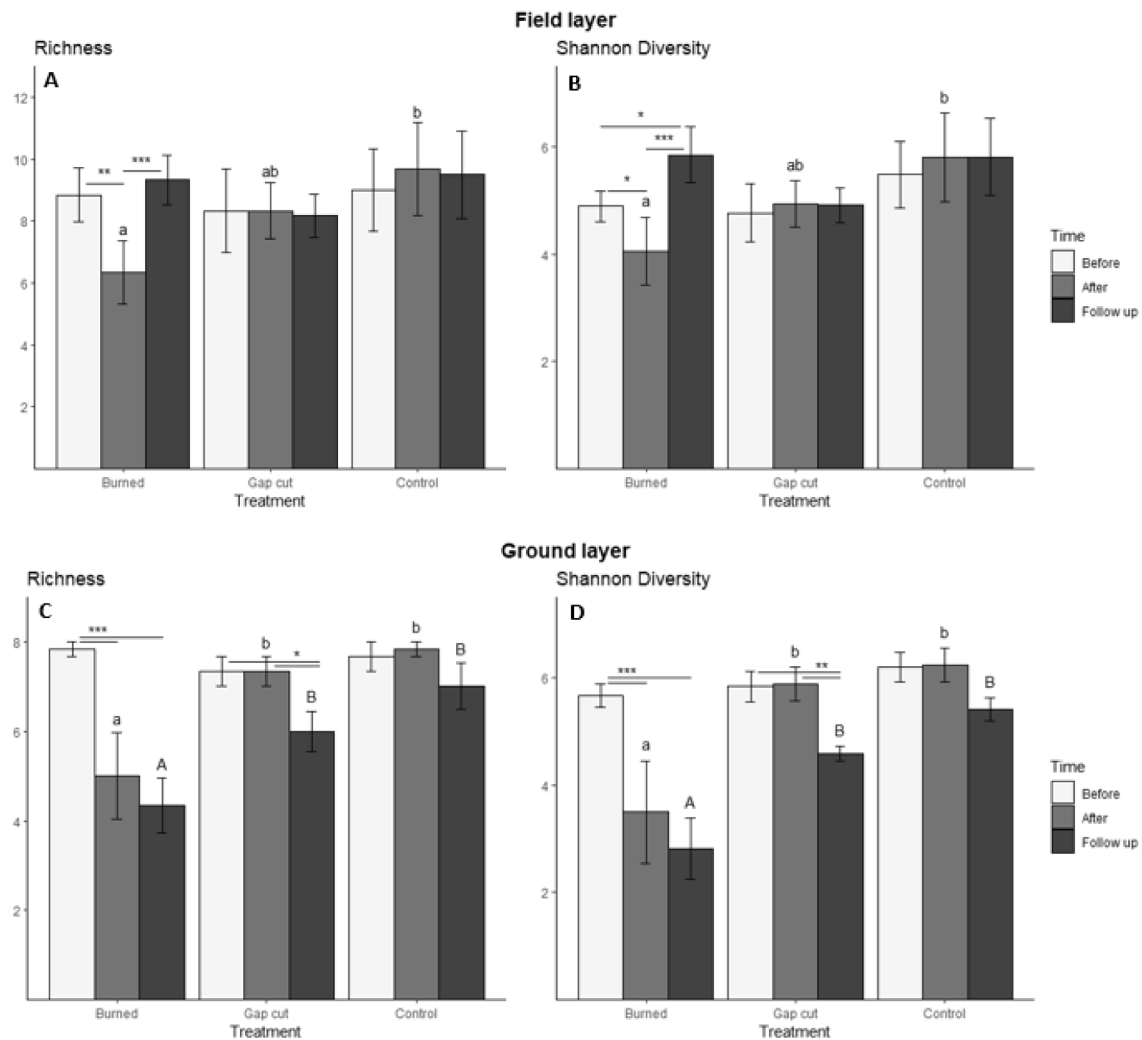
Table 3

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
Time	Before	Burned-Control	−0.17	0.917	−0.60	0.465	0.17	0.811	−0.54	0.388
		Burned-Gap cut	0.50	0.757	0.12	0.878	0.50	0.474	−0.18	0.776
		Control-Gap cut	0.67	0.411	0.72	0.379	0.33	0.633	0.36	0.561
	After	Burned-Control	−3.33	**0.046**	−1.74	**0.039**	−2.83	**<0.001**	−2.74	**<0.001**
		Burned-Gap cut	−2.00	0.221	−0.88	0.283	−2.33	**0.001**	−2.38	**<0.001**
		Control-Gap cut	1.33	0.411	0.86	0.292	0.50	0.474	0.35	0.567
	Follow up	Burned-Control	−0.17	0.917	0.04	0.957	−2.67	**<0.001**	−2.60	**<0.001**
		Burned-Gap cut	1.17	0.471	0.94	0.254	−1.67	**0.020**	−1.77	**0.006**
		Control-Gap cut	1.33	0.411	0.89	0.276	1.00	0.155	0.83	0.185
Treatment	Burned	Before-After	−2.50	**0.001**	−0.83	**0.018**	−2.83	**<0.001**	−2.16	**<0.001**
		Before-Follow up	−0.50	0.509	−0.96	**0.007**	3.50	**<0.001**	2.85	**<0.001**
		After-Follow up	−3.00	**<0.001**	−1.79	**<0.001**	0.67	0.230	0.69	0.117
	Control	Before-After	0.67	0.379	0.31	0.362	0.17	0.762	0.04	0.922
		Before-Follow up	−0.50	0.509	−0.32	0.349	0.67	0.231	0.79	0.062
		After-Follow up	0.17	0.825	−0.01	0.979	0.83	0.136	0.83	0.076
	Gap cut	Before-After	0.00	1	0.17	0.621	0.00	1	0.05	0.912
		Before-Follow up	0.17	0.825	−0.15	0.666	1.33	**0.019**	1.25	**0.004**
		After-Follow up	0.17	0.825	0.02	0.950	1.33	**0.019**	1.30	**0.005**

Fig. 2. 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 among treatments, small letters for after (2012) and capital letters for follow up (2019). Error bars show standard error.

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	1.20	0.270	2	10.86	**<0.001**
Time	2	8.29	**<0.001**	2	15	**<0.001**
ID (Treatment)	15	11.88	**<0.001**	15	3.32	**<0.001**
Treatment * Time	4	6.92	**<0.001**	4	7.63	**<0.001**
Residuals	30			30		

4. Discussion

As predicted, we did not observe any significant changes in diversity measures or community change analyses in *control* stands, except in ground layer where we did observe a change in community composition in *follow up* inventory, analogous to the pattern we observed in *gap cut* stands. This result could be explained partly by the fact that 2018 was an extremely dry year according to SMHI precipitation data. Bryophytes do not have a proper water circulation system and therefore, they are more susceptible to negative effects in periods of drought (Proctor, 1982).

4.1. Effects of fire restoration

In the field layer we found strong support for our hypothesis. As predicted, we observed an initial decrease in both species richness and Shannon diversity. The significant change in before and after community composition further supports this, showing a strong effect of fire restoration. For example, *Linnaea borealis* and *Empetrum nigrum* decreased and *Epilobium angustifolium* increased in abundance following fire (See Table 1 in Appendix). However, at the follow up, eight years after restoration, species richness and Shannon Diversity values surpassed pre-restoration levels. But the fact that field layer communities were significantly different at each inventory also suggest that fire also resulted in changes in community composition allowing disturbance favoured species to colonize and become more dominant. *Melampyrum pratense*, *Linnaea borealis* and *Deschampsia flexuosa* are examples of species that show higher relative plot occurrences eight years after fire as compared to prior to fire (see Table 1 in Appendix). At the same time, it should be noted that the changes in relative plot occurrence of dominant dwarf shrubs were small because of fire probably due to their ability to re-sprout from below-ground rhizomes. Their stable dominance also suggest that ecosystem functionality was not heavily impacted in the long-term.

In the ground layer, we found partial support for our hypothesis. As predicted, we found an initial decrease in both species richness and

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 (Figs. 3 and 4 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		Ground layer	
			T	P	T	P
Time	Before (A)	Burned-Control	0.85	0.729	1.09	0.373
		Burned-Gap cut	NaN	1	1.37	0.159
		Control-Gap cut	0.71	0.858	1.01	0.398
	After (B)	Burned-Control	2.50	**0.003**	2.92	**0.006**
		Burned-Gap cut	2.26	**0.005**	3.01	**0.004**
		Control-Gap cut	0.48	0.929	1.06	0.358
	Follow up (C)	Burned-Control	1.98	**0.007**	2.87	**0.005**
		Burned-Gap cut	1.82	**0.011**	3.99	**0.004**
		Control-Gap cut	0.71	0.758	1.36	0.168
Treatment	Burned (D)	Before-After	3.35	**0.005**	3.11	**0.016**
		Before-Follow up	3.24	**0.007**	5.11	**0.003**
		After-Follow up	3.44	**0.007**	1.32	0.225
	Control (E)	Before-After	2.55	0.087	NaN	0.921
		Before-Follow up	1.57	0.172	NaN	0.996
		After-Follow up	1.72	0.134	4.57	**0.012**
	Gap cut (F)	Before-After	2.20	0.083	2.11	0.102
		Before-Follow up	1.70	0.137	NaN	0.998
		After-Follow up	1.58	0.125	10.83	**0.002**

Shannon Diversity. The significant change in before and after community composition further supports this, showing strong effect of prescribed burning. By contrast, we did not detect any increase in species richness, Shannon Diversity or community composition eight years after treatment. A likely reason for this is that the ground layer consists of slow growing bryophytes, an organism group that will take time to recover and recolonize after severe disturbances. No increase could be detected for relative plot occurrence in the follow up for species like *Dicranum* spp., *Hylocomium splendens* and *Ptilium crista-castrensis*.

However, *Polytrichum* spp. did increase in relative plot occurrence following fire suggesting that this taxonomic group might actually benefit from fire disturbance. Other studies like Marozas et al. (2018), also found *Polytrichium* spp. replacing late successional moss species after fire episodes.

Interestingly, studies of saproxylic beetles in the same experiment showed increased species richness shortly after fire (Hägglund et al., 2020, Hjältén et al., 2017). This is most likely an effect of these highly mobile organism being attracted from the surrounding landscape to the conditions (e.g., large amounts of dead and dying trees) created by the fire. The recolonization of vascular plants and bryophytes on the other hand will take much longer, emphasizing the importance dispersal ability for species response to disturbance.

Our results are consistent with other studies where burning treatment has maintained or increased vascular plant richness (Rees and Juday, 2002, Marozas et al., 2018, Laarmann et al., 2013) while bryophytes showed a highly negative impact (Rees and Juday, 2002, Marozas et al., 2018). Soudzilovskaia et al., (2011) found that feather mosses like *Pleurozium schreberi* and *Hylocomium splendens,* (dominants in our study area) negatively affect the germination and regeneration of understory vegetation. Therefore without disturbances, specially fire, the thick moss layer may result in ecosystem retrogression (Mallik, 2003) negatively affecting ecosystem functioning and productivity. Malik's results support that changes in common species like feather moss abundances modify ecosystem functioning as in Winfree et al., (2015). Consistent with this, Nilsson and Wardle (2005), found that the lack of fire episodes also allow the expansion of cowberry (*Empetrum nigrum*) which negatively affects forest regeneration.

4.2. Effects of gap cutting

In the field layer, we found no support for our prediction. In contradiction to our hypothesis, we did not observe significant changes in diversity measures for the field layer either in the short- or long-term, suggesting that this restoration method might have limited effects on boreal forest understory vegetation.

In the ground layer, we found no support for our prediction either. However, interestingly and against our prediction, in the ground layer both richness and Shannon diversity values decrease significantly in the
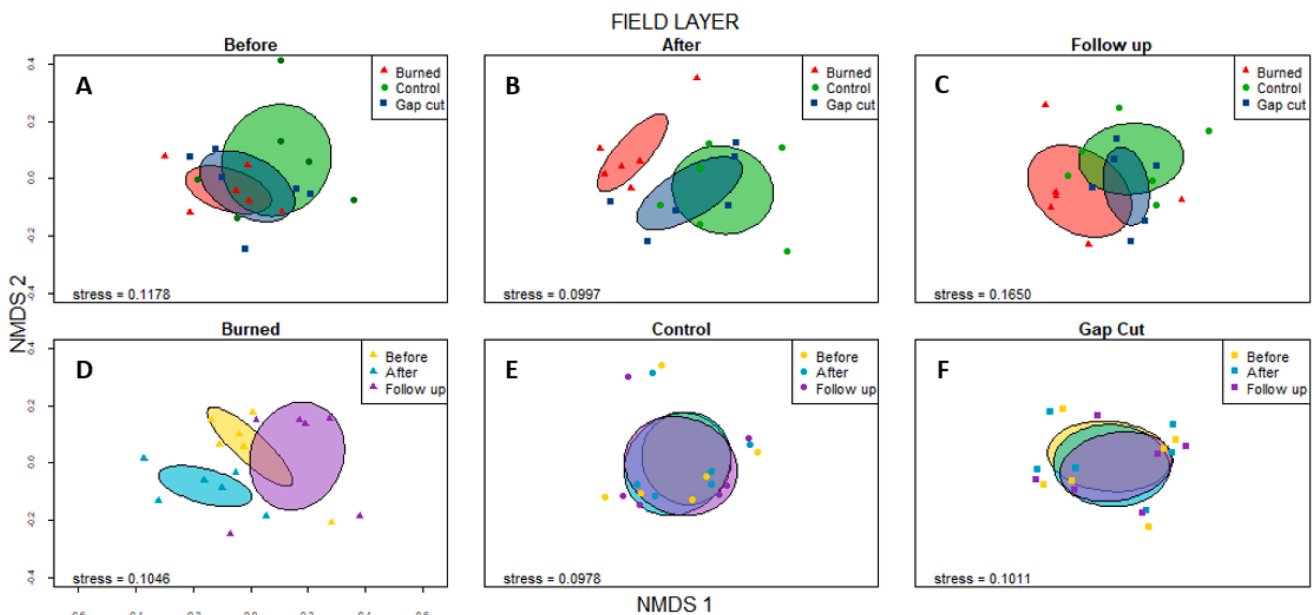

Fig. 3. Two-dimensional NMDS visualization of community composition in field layer. Upper panels show the communities from the three treatments at each inventory. Lower panels show the communities from the three inventories within the same treatment. Letters indicate the correspondent pairwise analyses with significance levels specified in Table 5. Ellipses represent standard deviations.
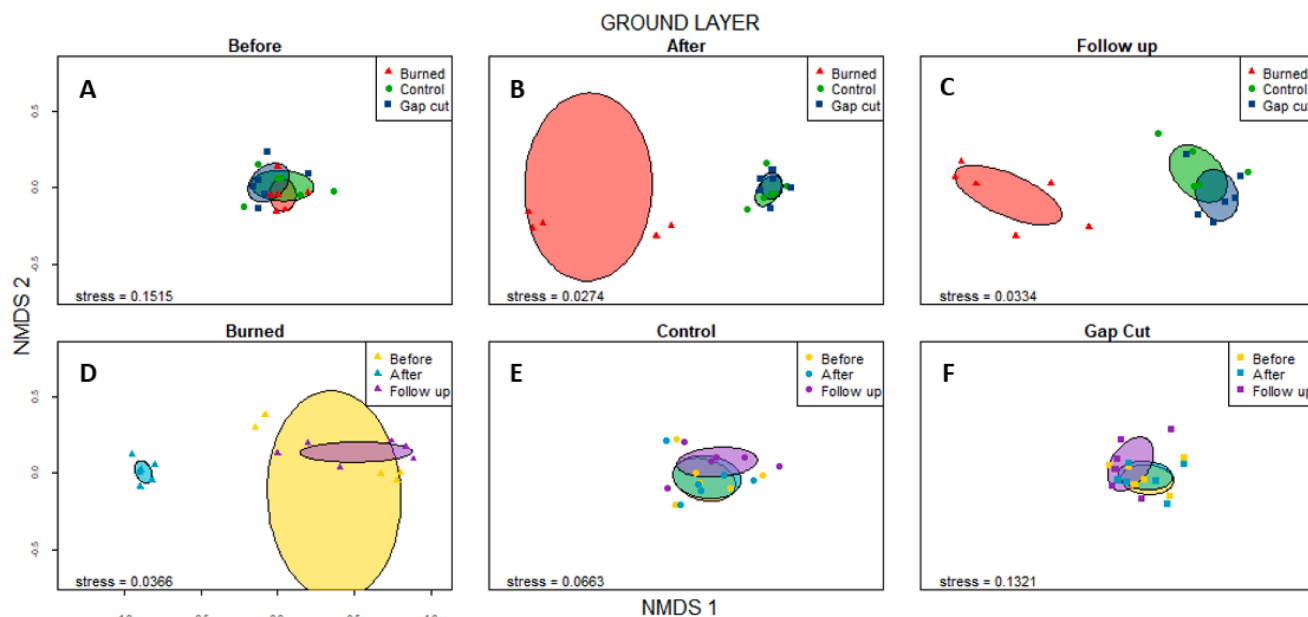
Fig. 4. Two-dimensional NMDS visualization of community composition in ground layer. Upper panels show the communities from the three treatments at each inventory. Lower panels show the communities from the three inventories within the same treatment. Letters indicate the correspondent pairwise analyses with significance levels specified in Table 5. Ellipses represent standard deviations.

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).

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

follow up inventory, which is the same pattern we observed in untreated stands (control).

Previous studies have shown little or no impact of gap cutting on ground vegetation diversity (Hekkala et al., 2014a, Laarmann et al., 2013), although Shure et al (2006) found an initial decline in species richness in the herbaceous layer in an experiment in southern Appalachian forests. This decline was mainly due to a shift towards early successional species, but when the community was followed for more than a decade, species richness increased again (Shure et al 2006). Our results are in line with these studies indicating that gap cutting generate only little impact or shift in field or ground layer diversity over a longer time span. Studies in other organism groups (saproxylic beetles and birds) in the same experiment as the present study, revealed no, or only weak effects, of gap cutting on species richness and community composition (Hjältén et al., 2017, Hägglund et al., 2020). However, in the case of beetles, the effect increased over time (Hägglund et al., 2020). Our community composition analyses showed a similar pattern as the one obtained in diversity analyses. Through our indicator species analysis, we did not detect 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).

Despite the lack of effects due to gap cutting observed in our study, there may be a promising outcome with particular groups, allowing for the coexistence of species from different successional stages (Hägglund et al. (2020) as fire disfavours species associated with old growth forest continuity.

4.3. Treatment comparison

According to our results, fire generated a distinctive effect in understory vegetation compared to *control* and *gap cut* stands. We found that species richness and Shannon Diversity values were not higher in *burned* than in *control* stands, however, eight years after the disturbance the community composition in *burned* stands shifted in a notably different direction compared to the other treatments. These results 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. This suggests that, at the landscape level, burned patches within a forest matrix increases structural variability, allowing the co-occurrence of fire-related, pioneer and opportunistic species that would otherwise not be present in monoculture-managed forests. Nevertheless, some groups might not be favoured at all after an intense fire event and therefore prescribed burning should be carefully implemented and other alternatives considered (Hjältén et al., 2017).

Surprisingly, *gap cut* and *control* stands showed concordant results

across our analyses, a result indicating that gap cutting had little or no effect on field or ground layer vegetation and might not be an effective restoration methodology when vascular plants and bryophytes are targeted. An alternative restoration approach to ensure vegetation effects was implemented 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 methodology by adding seedbeds of pioneer species, for example deciduous trees. Even though our 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 even longer term studies are still needed. In addition, an extra thought should be given about gap cutting effects in other ecosystem compartments. For instance, further research is needed to test if gap cutting modifies flowering and berry production, and consequently has an impact in pollinators' communities.

5. Conclusions and management implications

Our study highlights the strong impact of fire restoration on field and ground layer vegetation. Over time, field layer species richness increased (although not significantly compared to pre-treatment state) and fire provided opportunities for disturbance favoured species as we can observe differences in community composition, and at least to some degree, restarted succession. Thus, implementing recurrent prescribed fires within the managed forest matrix can help recreate a heterogeneous landscape, which are likely to increase species diversity at landscape level (Kuuluvainen and Aakala, 2011). In fact, prescribed burning of voluntary set-asides are conducted by Swedish forest companies as part of fulfilling FSC certification requirements (Anon. 2014) as well as by governmental authorities as management of protected areas were natural disturbance regimes have been lost. This study as well as earlier studies on other organism groups (Hägglund et al. 2020, Versluijs et al., 2017) provides support that prescribed burning benefits fire favoured and disturbance favoured species. This suggest that prescribed burning is a good management option for favouring this group of species. Gap cutting, by contrast, had little or no effect on field or ground layer vegetation in this study. Earlier studies report no or limited effect on bird communities and insect species, including red-listed species, associated with old growth forest with long forest continuity (Hägglund et al. 2020, Versluijs et al., 2017). However, gap cutting has been found to have a positive effect on abundance and species richness of some groups of wood living beetles (Hjältén et al. 2017, Hägglund et al. 2020), especially when combined with dead wood creation (Hägglund and Hjältén, 2018). Thus, in practical biodiversity management, gap cutting could be used to benefit certain groups of organisms, while avoiding negative effects on old growth associated species. This study also stresses the potential to use voluntary set-asides as a conservation tool in Fennoscandia. They cover a large percentage of the productive forest area, and this and other studies show that there is a cost-neutral way to utilize them in a more proactive way than is currently the case. However, our finding also stresses the importance of proper assessment of different methods for ecological restoration, e.g., including different organism groups and a long-term perspective when evaluating restoration effects. Field layer showed partly opposite short- versus long-term responses whereas ground layer shows a consistent negative response eight years after restoration. Thus, focusing only on one organism group can lead to misinterpretations of the real impact of restoration in the ecosystem.

CRediT authorship contribution statement

C. Espinosa del Alba: Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Writing - review & editing. **J. Hjältén:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition. **J. Sjögren:** Conceptualization, Methodology, Validation, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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