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Assessing the restoration and the dispersal of reindeer lichen after forest fire in northern Sweden: Results after eleven growing seasons

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ABSTRACT

In circumboreal regions, *Rangifer* populations depend heavily on ground reindeer lichens (*Cladonia* subgenus *Cladina*) during the winter, but this critical resource was depleted over the 20th century as a result of land encroachment and habitat loss. Fires, both wild and controlled, can also contribute to the decline of reindeer lichen. Depending on the context, accelerating the return of winter pasture through reindeer lichen transplantation after fire may be needed to conserve threatened caribou populations and semi-domestic reindeer herding. Following a field experiment established in 2008, two years after a forest fire, we evaluated the success of restoration through lichen transplantation, measuring biomass on restoration, control and reference sites. We also assessed the dispersal of lichen fragments from the restoration plots into the surrounding burnt area. Eleven growing seasons after lichen transplantation, the lichen biomass measured on restoration sites (62 g m^{-2}) was on average significantly higher than on control sites (0.8 g m^{-2}), but remained non-significantly lower than on reference sites (109 g m^{-2}). This confirms the success of the transplanting operation and the remaining progress towards a fully restored lichen mat. The distance distribution of lichen fragments showed that reindeer lichen had dispersed by at least 20 m from the restoration plots, and locally by much greater distances, of up to 60 m. The absence of a clear pattern of dispersal on all sites indicates the importance of microsite conditions and post-dispersal processes. Perspectives for future restoration operations are discussed, including the fire-lichen-*Rangifer* relationship, and implications for local and Indigenous populations who depend on them.

1. Introduction

In circumboreal regions, reindeer and caribou (*Rangifer tarandus* sspp.) populations rely on vast grazing areas, migrating between different seasonal pastures. In winter they depend on arboreal and ground lichens, a critical resource that became less abundant and accessible over the 20th century due to various forms of land encroachment and habitat loss (Cornelissen et al., 2001; Fraser et al., 2014; Esseen et al., 2022), to an extent that now threatens *Rangifer* populations and the associated local and Indigenous livelihoods (Vors and Boyce, 2009). In northern Sweden, it has been estimated that the area of lichen-rich forests has declined by 71 % over the last 60 years due to commercial forestry for industrial wood supply (Sandström et al., 2016). In addition to conservation measures to preserve these forest habitats from the most severe impacts of forest operations, such as mechanical soil preparation, measures to restore the lichen resource may be key to supporting the sustainable use of natural pastures for reindeer husbandry.

Options for restoring suitable habitat for ground lichens in the long run include conservation fire and prescribed burning prior to forest regeneration (Cogos et al., 2019). Although fire burns out the ground vegetation, including reindeer lichens (*Cladonia* spp.), for several decades, the prolonged absence of fire due to fire suppression in boreal forests over the 20th century induced changes in below- and

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aboveground properties that have resulted in feather mosses and ericaceous dwarf shrubs outcompeting ground lichens, particularly on mesic sites (Sulyma and Coxson, 2001; Nilsson and Wardle, 2005). Controlled burning can also promote the conservation of fire dependent species, most of which are considered to be under threat in the region (Halme et al., 2013), and can create favourable conditions for pine seedling recruitment (Nilsson and Zackrisson, 1992; Pasanen et al., 2015). However, depending on the severity of fire, mat-forming reindeer lichen become naturally dominant 50–100 years after burning (Morneau and Payette, 1989; Ahti and Oksanen, 1990), a timescale which is considered too long to be viable in terms of winter pasture use for reindeer herders. The transplantation of reindeer lichen after burning, through artificial dispersal of lichen fragments, thus offers a possible way of combining the long-term positive effects of fire and faster restoration of mat-forming lichen.

Experiments involving the transplantation of reindeer lichen on burnt ground have been conducted in boreal regions of northern Sweden (Roturier et al., 2017) and British Columbia, Canada (Rapai et al., 2023), and demonstrated that transplanted fragments survive and establish within a decade of a fire event. The next step forward in ecological restoration is to evaluate whether the system has recovered from disturbance, or is progressing along a trajectory of recovery, including cross-comparison with control and reference ecosystems (Wortley et al., 2013). A wide range of ecosystem attributes can be used to characterise ecosystems and monitor the degree of recovery, including structural diversity and ecosystem functions (Gann et al., 2019). Considering the recent development of studies on restoration of reindeer lichen after burning, it is important to investigate the level of growth of transplanted lichen and the rate of colonisation of the burnt environment in order to identify where to focus future restoration efforts (Mahlum et al., 2018). Such investigations could establish baselines for assessing whether or not the ecosystem can provide associated ecosystem services, i.e. winter pasture for reindeer. Studies of lichen mat colonisation can also provide a stronger basis for designing larger scale restoration strategies and operations based on natural expansion of transplanted lichen fragments.

In Fennoscandia, reindeer lichen represents a functional group of terrestrial lichen that includes *Cladonia stellaris* (Opiz), *C. rangiferina* (L.), *C. arbuscula* (Wallr.) and *C. uncialis* (L.), all of which are dispersed by multiple agents including wind, animals, and surface water runoff. They disperse as thallus fragments, i.e. large propagules which are less suited to long distance dispersal (Nelson et al., 2015). However, direct measures of dispersal distances for lichens remains scarce (Heinken, 1999), and studies of dispersal patterns primarily concern epiphytic lichens (e.g. Hilmo et al., 2012; Gjerde et al., 2015).

Following on from an earlier study (Roturier et al., 2017), we carried out a new series of field inventories at Klusåberget, northern Sweden, during the summer of 2020, 11 growing seasons after reindeer lichen transplantation, to assess reindeer lichen transplantation and further advance the development of reindeer pasture restoration after fire. More specifically, we aimed to: (i) assess reindeer lichen restoration using destructive lichen biomass sampling in lichen transplanted, control, and reference plots; and (ii) estimate reindeer lichen dispersal from the transplanted plots into the surrounding burnt area.

2. Material and methods

2.1. Study area and experimental design

The study area is located in Bodträskfors, Northern Sweden, on the hill Stora Klusåberget (66°8′N, 20°50′E, 273 m a.s.l.). In August 2006 a forest fire burnt an area of approximately 1900 ha. Before the fire, the forest was dominated by 75–150 year-old Scots pine (*Pinus sylvestris* L.). The field-layer vegetation was classified as lingonberry (*Vaccinium vitis-idaea* L.) type on sandy moraine soils. No data was available about the extent of reindeer lichen cover before the fire, although it can be inferred that the bottom layer was dominated by feather mosses with substantial patches of reindeer lichen. The fire was particularly severe at some locations due to extremely dry conditions, consuming all the soil organic material and leaving mineral soil exposed. Following the fire, burnt standing trees were clear-cut and the area has subsequently been planted with Scots and lodgepole (*Pinus contorta* Douglas) pine seedlings or been allowed to regenerate naturally, depending on the landowner. At the top of the hill the burnt forest was left untouched to become a set-aside area for biodiversity conservation.

The restoration experiment was established in early September 2008 at three locations within the burnt area, resulting in three sites with different environmental conditions with respect to light exposure, soil humidity, burning severity, and post-burning operations. A diversity of post-fire habitats was deliberately selected by the stakeholders involved at the time of establishment – specifically, reindeer herders and forest managers. Sites 1 and 2 were established in the clear-cut area on the southern slope of Stora Klusåberget, and site 3 was located closer to the top (Fig. 1a). Site 1 was located where the fire had been most severe, totally removing the understory vegetation and, in many places, the soil surface, exposing a rather dense rock field. In 2020, understory vegetation remained scarce and was composed of bryophytes, sparse ericaceous dwarf shrubs, and planted lodgepole pine seedlings. Site 2 was located further down the slope, adjacent to a moist-mesic area where the fire was less severe. A month prior to establishing the experiment, the forest owner gently scarified the top layer of soil on ca. 15 % of the surface of this site, using prototype equipment. By 2020, ericaceous dwarf shrubs had regenerated, bryophytes covered the ground surface, and birch (*Betula* sp.) and sown Scots pine seedlings reached breast height (i.e. 1.3 m above ground level). Site 3 was located near the top of the hill where burnt standing trees were retained (38 % of the estimated canopy closure in 2008). The fire was also less severe here, meaning that many Scot pines initially survived the burning and ericaceous dwarf shrubs regenerated rapidly. By 2020, the understory vegetation largely covered the ground surface and Scots pine seedlings had regenerated naturally. Fourteen years after the fire, almost all the remaining standing trees had fallen due to windstorms, leaving a great amount of deadwood (see Table A1 for a complete description of the different sites).

Between September 2008 and March 2009, a total of 540 kg DM (ca. 17 m^3) of fragmented reindeer lichen were transplanted across the three sites. In each, lichen was dispersed manually on eight adjacent 20 × 20 m plots, forming a 40 × 80 m area homogeneously covered with reindeer lichen (Fig. 1b). The composition of the lichen material (collected in Oulu, Finland) was estimated visually: *Cladonia stellaris* (75 %), *C. rangiferina* (12 %), *C. arbuscula* (7 %) and *Cetraria islandica* (L.) (6 %). In each site, two different doses were applied: 5.5 kg DM on one plot, corresponding to 14 g m^{-2} (or 0.45 L m^{-2}, dose 1 hereafter), and 28 kg DM on three plots, corresponding to 70 g m^{-2} (or 2.25 L m^{-2}, dose 2 hereafter), at two different time periods (late summer and late winter). This gave a total of 24 plots: 3 sites * 2 transplantation seasons * (1 plot with dose 1 + 3 plots with dose 2). Between 2010 and 2015, the establishment of lichen fragments was monitored on five permanent subplots (0.25 m^2), randomly placed within each plot (see Roturier et al., 2017 for a complete description of the results and the lichen transplantation operations). The study area has not been used by reindeer for winter grazing since the fire. Isolated reindeer have, though, been observed in the summer when they have been escaping harassment by insects.

2.2. Lichen biomass inventory and measurements

In June 2020, biomass inventories were carried out to assess reindeer lichen restoration 11 growing seasons after lichen transplantation. In each of the three sites, a total of 16 lichen samples were collected from 2 randomly selected spots on each plot, i.e. 4 samples collected from plots dispersed at dose 1 (14 g m^{-2}), and 12 samples from plots dispersed at dose 2 (70 g m^{-2}), giving 48 biomass samples from the restoration sites.

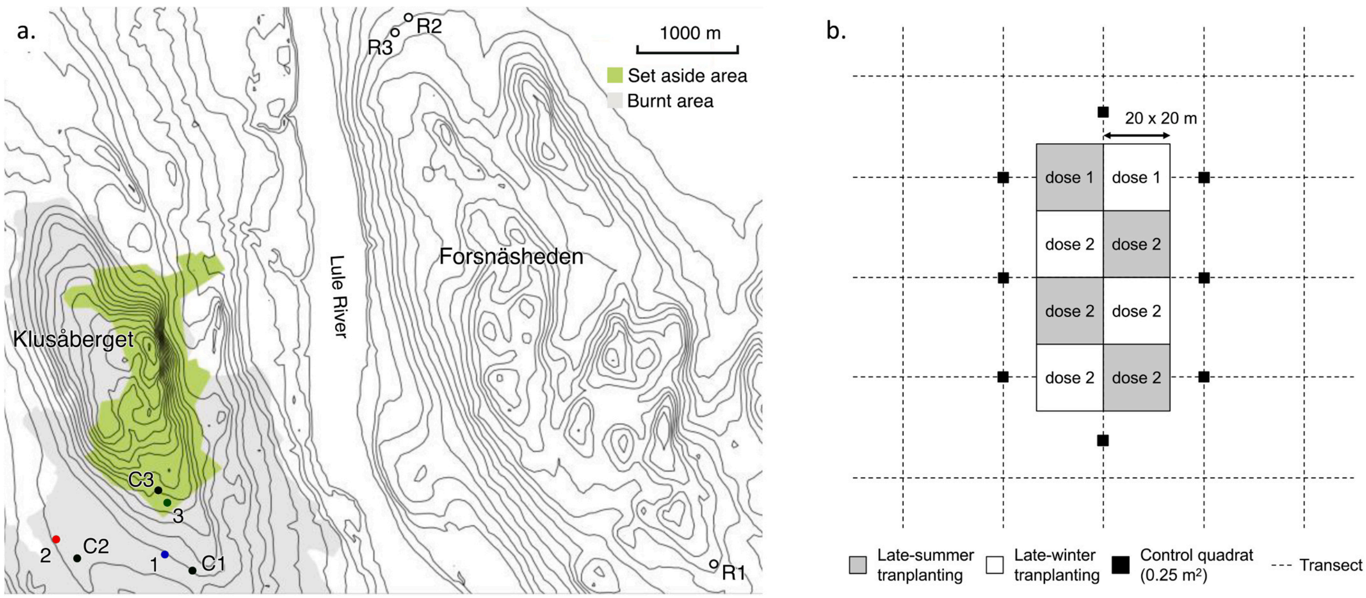

Fig. 1. (a) Location of the restoration (1,2,3) and control (C1, C2, C3) sites at Klusåberget, and reference (R1, R2, R3) site at Forsnäsheden. (b) Transplantation design and dispersal monitoring at each restoration site.

To evaluate the effects of restoration, lichen samples were also collected from degraded/control and undisturbed/reference sites (Fig. 1a). In 2020, three control sites were inventoried in the burnt area. Each control site was located 250 m from each restoration site, corresponding as closely as possible in terms of post-fire habitat, but at a distance where colonisation by transplanted lichen would be very limited. Since no data were collected in the study area prior to fire, three additional reference sites were inventoried in lichen-rich pine forests (lichen cover >25 % of the ground cover) grazed annually by reindeer herds, 5 km away from the study area at Forsnäsheden on the other side of the Lule River (see the appendix for a detailed description of the control and reference sites). These were used as a proxy for the pre-disturbed ecosystem. In both control and reference sites, 48 lichen samples were collected at randomly selected spots (16 in each site), giving a total of 144 biomass samples.

Lichen sampling was carried out using a cylinder (with an opening of 123 cm^2) lowered down to the soil. Prior to collecting each sample, average thallus height was measured to the nearest 0.1 cm in dry conditions. All samples were stored for 10 weeks in paper bags, sorted to remove the litter and the dead bases of the thalli from the lichen material, dried at 80 °C for 24 h, and weighed to obtain their dry weights. This measurement did not discriminate between species but *Cladonia stellaris* represented >95 % of the lichen collected.

2.3. Lichen fragment dispersal measurements

At the time of establishment in 2008, 10 permanent quadrats (0.25 m^2) were set up 10 m away from, and around, each restoration site. Lichen frequency was inventoried a total of four times following the establishment of the experiment, in September 2010, August 2013, September 2015, and June 2020, using the method described in Roturier et al. (2017). Frequency of viable fragments was estimated as the number of grid squares of 5 × 5 cm (out of 100) occupied by at least one fragment, in the quadrats. These repeated measurements gave a good estimate of the speed of lichen dispersal outside of the restoration sites.

However, to better assess the dispersal of lichen fragments from the restoration sites into the surrounding area, lichen frequency was measured using the same method at 5 m intervals along a grid of 5 × 5 transects, 150 m-long, with the restoration site at the centre (Fig. 1b). If a sampling point selected for inventory comprised more than 50 % impediment (e.g. rocks or machine path south of site 1), the sampling point was moved to the side until the presence of impediments was less than 50 %.

2.4. Statistical analysis

All statistical analyses were conducted using "R" software (R Core Team, 2022) and the additional packages lmer, lmerTest, emmeans and TcGSA. The analyses relied on the following mixed models, fitted on the whole dataset which included biomass measurements within the three site types (restoration, control, and reference):

$$Y_{ijk} = \mu + \alpha_i + U_{j(i)} + E_{ijk}$$

with $E_{ijk} \overset{i.i.d.}{\sim} N(0\sigma^2)$ independent of $U_{j(i)} \overset{i.i.d.}{\sim} N(0\sigma_U^2)$
(Model Biomass and Model Height)

where the site effect denoted by j ($1 \leq j \leq 3$) is nested in the site effect denoted by i ($1 \leq i \leq 3$), k is the replication index ($1 \leq k \leq 16$), and Y is equal to $\log(biom + 1)$ where *biom* is the biomass per square meter for the Model Biomass, and Y is equal to $\log(height + 1)$ where *height* is the height of the average thallus height for the Model Height. The logarithm transformation was done to enforce homoskedasticity in the residuals. Within this model, site and site type effects were tested with likelihood ratio tests, and the asymptotic distribution of the test statistics was computed by the pchisqmix function from the TcGSA package. When testing the effect on the site type effect the function corresponds to a χ^2_2 distribution while, when testing the site, the function corresponds to a mixture between a chi square distribution and a Dirac mass at 0: $\frac{1}{2}\chi^2_1 + \frac{1}{2}\delta_0$ (Self and Liang, 1987).

The comparisons of means were done by Student *t*-test with an asymptotic adjustment of the degrees of freedom, the *p*-values of which were corrected for multiple testing using a Bonferroni method. Note that using an asymptotic adjustment for the Student t-test amounts to using the standard normal distribution as the asymptotic distribution of the test statistic under the null hypothesis.

The dose effect was tested with a mixed model fitted on the subpart of data collected from restoration sites which was subject to two different dose levels:

$$Y_{ijk} = \mu + \alpha_i + U_j + E_{ijk}$$
$$\text{with } E_{ijk} \overset{i.i.d.}{\sim} N(0\sigma^2) \text{ independent of } U_j \overset{i.i.d.}{\sim} N(0\sigma_U^2)$$
$$\text{(Model Dose)}$$

where j denotes the site effect ($1 \leq j \leq 3$), i the dose effect ($1 \leq i \leq 2$), and k the replication index ($1 \leq k \leq 4$ if $i = 1$, i.e. dose 1, and $1 \leq k \leq 12$ if $i = 2$, i.e. dose 2). The dependent variable Y also corresponds to the logarithm transformation of the biomass, and the statistical tests on the dose and site effects were also likelihood ratio tests with the asymptotic distribution of the test statistics computed by the function pchisqmix as above. The effect of 'time of dispersal' was not tested in the models and was therefore included in the site effect.

3. Results

3.1. Lichen biomass

For the biomass inventory, the results of the tests within the mixed models (Table 1) showed that site type and site within the site type had a significant effect (p-value <0.0001 for site type and = 0.014 for site), indicating high variation in lichen biomass between the site types (Fig. 2). There was no significant difference between the restoration and the reference site types (p-value = 0.77). However, 11 growing seasons after transplantation, the lichen biomass measured in the unburnt reference sites remained higher on average (109 g m^{-2}, SE = 20) than on the restoration sites (62 g m^{-2}, SE = 9). Compared to the control sites (0.84 g m^{-2}, SE = 0.24) lichen biomass on the restoration sites was on average significantly higher (p-value <0.0001), confirming the clear positive effect of restoration actions on lichen biomass measured 11 growing seasons after transplantation. Biomass measurements on the control sites also revealed the emergence of lichen through natural dispersal: about one third of the samples collected in the control sites showed the presence of reindeer lichen.

Mean lichen height was significantly different between the site types, but not between the sites. On restoration sites, it was 23 mm (SE = 2) on average while on reference sites and control sites it averaged 28 mm (SE = 3) and 3.5 mm (SE = 0.9), respectively (results not shown).

On average, samples measured on dose 1 plots exhibited non-significantly (p-value = 0.46) lower biomass, of 43 g m^{-2} (SE = 14), than those from dose 2 plots, with 68 g m^{-2} (SE =11). The dose had no effect on the lichen height measured (results not shown).

3.2. Lichen fragment dispersal

The repeated inventories of lichen frequency in permanent quadrats established around the restoration sites, carried out between 2010 and 2020, showed that it took between 5 and 10 years for the lichen fragments to colonise at this distance (10 m) from their edges (Fig. 3).

In 2020, examination of lichen frequency by distance from the edge of the three restoration sites (Fig. 4) showed a rapid decrease with distance, from an average of 40 % and 25 % at the edge of sites 1 and 2, respectively, to 10 % at 20 m and beyond. In site 3, no such decrease was observed and lichen frequency was measured at 10 % on average, with no relationship to distance from the edge of the site up to 60 m. However, the results showed a wide range of lichen frequency, varying between 0 and 44 % between 20 and 60 m from the edge. We found no spatial pattern of dispersal relating to dominant wind direction during the days without snow (1773 days between September 2008 and June 2020, at Lakaträsk meteorological station, 185 m.a.s.l., 19 km from Kluså berget, www.smhi.se) or topography, on any of the three restoration sites (results not shown).

4. Discussion

4.1. Evaluation of lichen transplantation

A critical first step towards restoring winter pastures for reindeer following fire is to confirm that transplanted reindeer lichen can establish and start growing (Roturier et al., 2017; Rapai et al., 2023). Measuring biomass and fragment dispersal at Klusåberget, northern Sweden, and comparing these measurements with control and reference ecosystems, enables us to assess whether this ecosystem is progressing towards recovery.

In 2008–2009, after transplantation into burnt ground, the lichen biomass on the plots virtually equalled the transplanting doses, i.e. 14 g m^{-2} DM and 70 g m^{-2} DM for dose 1 and 2, respectively. Over the two following years a large proportion of the transplanted lichen biomass died off. No destructive sampling was carried out during the first years of the experiment, but Roturier et al. (2017) estimated that, on average, viable fragments occupied just 19 % and 57 % of dose 1 and 2 plots in 2010, before surging to 57 % and 85 % in 2015, respectively. In 2020, the biomass measured in dose 1 and 2 plots, 43 g m^{-2} DM and 68 g m^{-2} DM, respectively, showed continuing growth overtime, although for dose 2 this was only enough to compensate for the significant losses that had followed transplantation.

The biomass measured on the restoration sites in 2020 was found to be significantly higher than on the control sites, despite different conditions in terms of light and wind exposure, post-fire succession and management, and fire severity among the sites, indicating the clear positive effect of lichen transplantation after 11 growing seasons (Fig. 2). On the control sites reindeer lichen was inventoried 14 years after the fire, but lichen biomass and height remained extremely low. This finding aligns with all previous studies which have shown that

Table 1
Effects of the different factors on reindeer lichen biomass and height, and t-test results for the comparisons between site types (restoration, control, reference).

	Effect	p-value	Test statistics	Distribution of the test statistics under H_0
Lichen biomass *(Model Biomass)*	Site type	< 0.0001	21.4	χ^2_2
	Site	0.014	4.8	$\frac{1}{2}\chi^2_1 + \frac{1}{2}\delta_0$
Pairwise comparison (t-test)	Control – Reference	< 0.0001	−7.13	$N(0,1)$
	Control – Restoration	< 0.0001	−6.05	$N(0,1)$
	Reference – Restoration	0.83	1.08	$N(0,1)$
Lichen height *(Model Height)*	Site type	< 0.0001	24.21	χ^2_2
	Site	1.00	0.06	$\frac{1}{2}\chi^2_1 + \frac{1}{2}\delta_0$
Pairwise comparison (t-test)	Control – Reference	< 0.0001	−8.1	$N(0,1)$
	Control – Restoration	< 0.0001	−7.6	$N(0,1)$
	Reference – Restoration	1.0	0.5	$N(0,1)$
Lichen biomass *(Model Dose)*	Dose	0.46	0.53	χ^2_1
	Site	0.031	3.49	$\frac{1}{2}\chi^2_1 + \frac{1}{2}\delta_0$

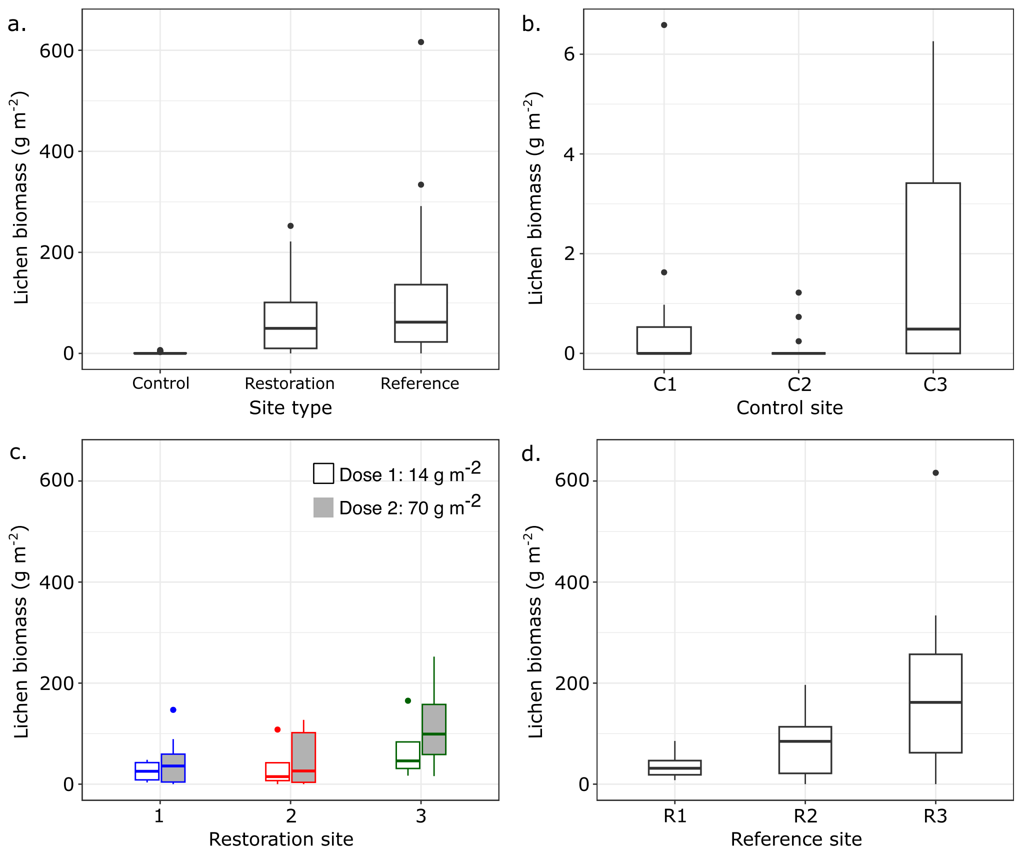

Fig. 2. Boxplots of lichen biomass (g m^{-2}) measured on degraded/control, restoration and reference site types (a); panels (b), (c), and (d) depict the different sites within the control, restoration, and reference site types, respectively (note the different scale for the control). In panel (c) the different treatment doses applied to restoration sites 1 (blue), 2 (red), and 3 (green) are depicted in white (dose 1: 14 g m^{-2}) and grey (dose 2: 70 g m^{-2}). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

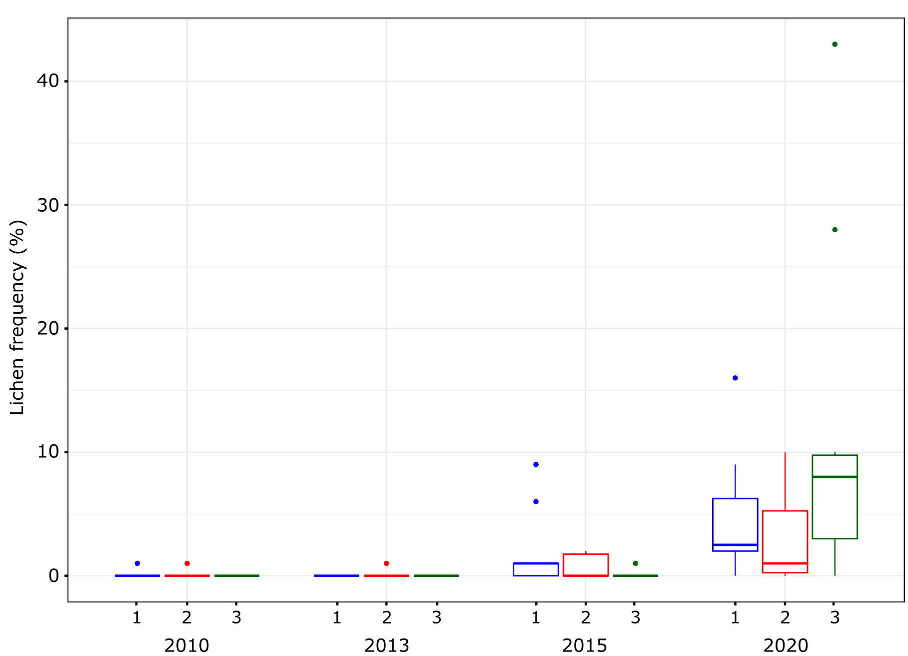

Fig. 3. Boxplots of fragment frequency (in %) measured in permanent quadrats ($n = 10$, each 0.25 m^2) at 10 m from restoration sites 1 (blue), 2 (red), and 3 (green), showing lichen fragment dispersal between 2010 and 2020. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

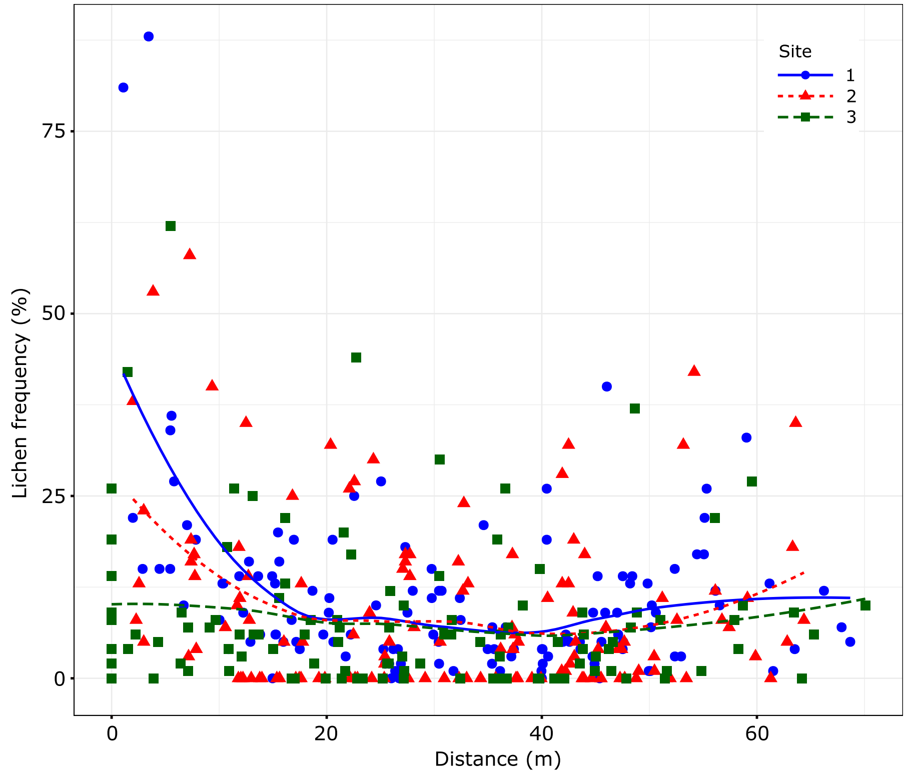

Fig. 4. Distance distribution of lichen fragments (fragment frequency, in %, with an average line and a 95 % confidence interval, according to distance from the edge) around the restoration sites 1 (blue), 2 (red), and 3 (green), 11 growing seasons after transplantation. The smoothing lines were obtained by local polynomial regression fitting. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

natural colonisation of reindeer lichen after fire takes several decades (Morneau and Payette, 1989; Coxson and Marsh, 2001; Jandt et al., 2008; Nelson et al., 2015; Russell and Johnson, 2019). The results showed that there were no significant differences between the restoration and reference sites in terms of both lichen biomass and height (Table 1). Apart from one reference site (R3) which averaged 180 g m^{-2} DM, a lichen type forest considered by reindeer herders to offer very good winter pasture, the mean lichen biomasses were similar between restoration and reference sites (Fig. 2). This result was surprising as the reference sites were in lichen-rich pine forests on dry soils, thus offering better conditions for lichen to compete with vascular plants than the restoration sites prior to burning. The timing of sampling, in June, certainly influenced the results as grazed lichen-mats had not yet recovered from winter grazing and the difference may have been much higher after a full growing season. However, the level of lichen growth 11 years after transplantation was encouraging (Fig. 1a), and should be confirmed by subsequent inventory.

The significant differences in lichen biomass between the three restoration sites confirmed previous results on lichen establishment by Roturier et al. (2017), who discussed extensively the influence of environmental conditions for lichen growth in the different sites involved in this experiment. Being poikilohydric organisms, lichen growth is restricted to times when the thallus is wet (Palmqvist and Sundberg, 2000), and thus it depends on light exposure, atmospheric temperature, and humidity, which in turn depend on atmospheric conditions but are also strongly regulated by vegetation. In the study area, variations in the severity of burning, post-fire vegetation responses, and post-fire management have definitely influenced reindeer lichen growth. Particularly on site 3, standing trees and windfallen logs created shelter from wind and solar radiation, and protected lichen fragments from desiccation so that they were able to continue photosynthesising for longer than those in more open, dry habitats.

4.2. *Colonisation of post-fire environment by transplanted lichen*

To evaluate the progress of restoration, and improve transplantation designs and strategies for future restoration efforts, the dispersal of propagules from the restoration sites must also be considered (Ruiz-Jaen and Mitchell Aide, 2005). Although our field experiment was not initially designed to monitor lichen dispersal over a long period, the repeated inventories between 2010 and 2020 of lichen frequency at 10 m from the edge of the restoration sites showed that colonisation occurred at a relatively slow, yet exponential pace (Fig. 3). The extended survey carried out in 2020 and the distance distribution of lichen fragments showed that reindeer lichen had dispersed by at least 20 m from the plots on all sites (Fig. 4 and 5b). In an earlier experiment, Heinken (1999) measured that the dispersal by wind of terricolous lichens, including *Cladonia arbuscula* and *C. uncialis*, occurred within an average radius of 0.2 m from the source within 15 days. Considering this pace and the number of days without snow since the restoration experiment started we would expect dispersal to have reached ca. 23 m from the source, which aligns with our empirical measurements. Following these results, using the same total amount of reindeer lichen as in the present study but in a pattern that includes a buffer zone of 20 m around individual plots (20 × 20 m) within which lichen could disperse, an area of 8.6 ha could be restored within the same time period. In this respect, it is worth noting that the average area of prescribed burning in Sweden is around 7 ha (Ramberg et al., 2018), and could therefore be completely restored in this way.

We also measured a substantial number of fragments at greater distances (> 20 m) on all sites, which we attribute to wind and other agents. Unfortunately, our transects were too short to record the absence of lichen at a greater distance, and to draw conclusions about the effect of transplantation between 20 and 60 m. The growth of understory vegetation, which was lower on site 1 and higher on site 3, combined with wind exposure, which was higher on site 1 and lower on site 3, also

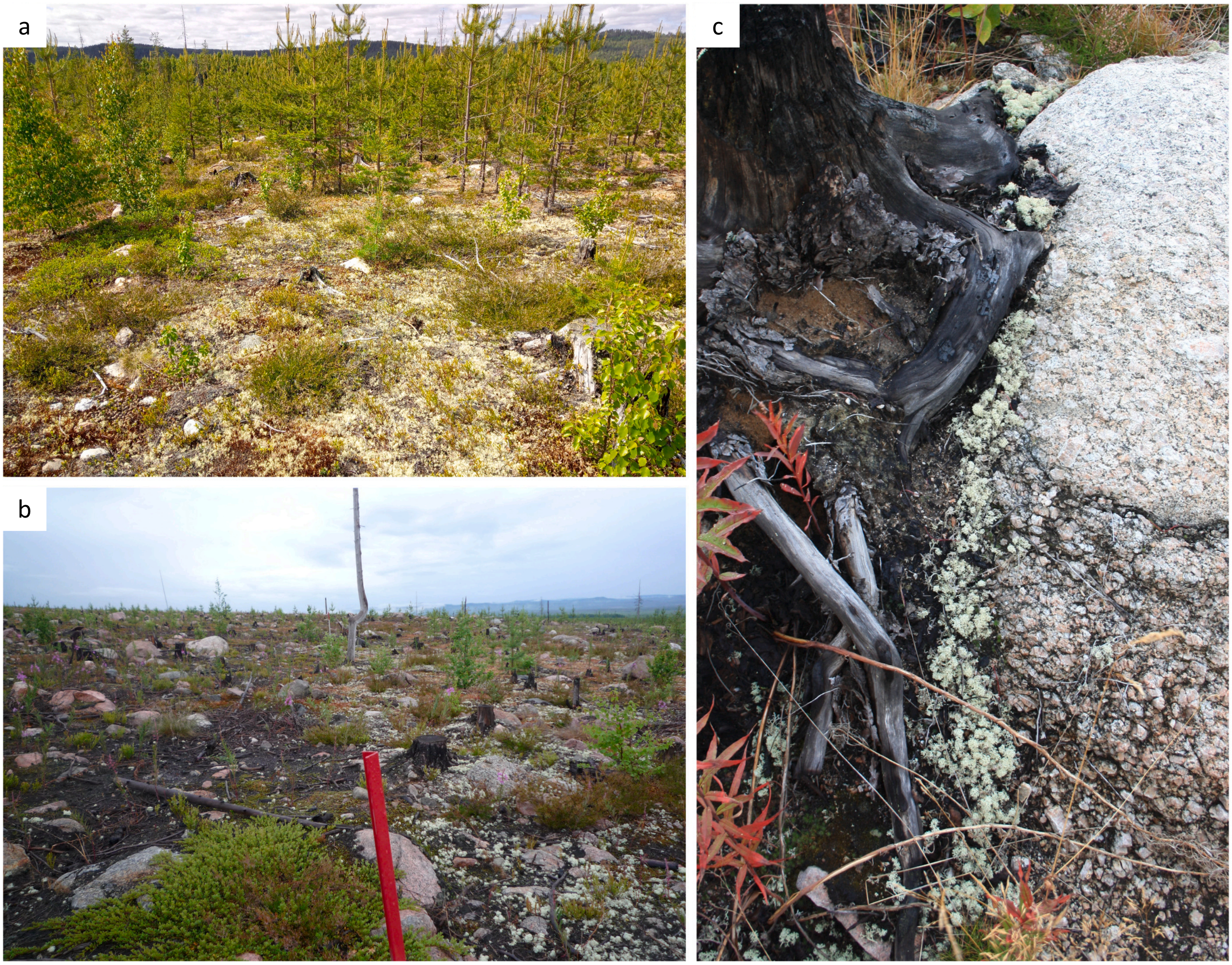

Fig. 5. (a) Transplanted reindeer lichen in a restoration plot in site 2, 11 growing seasons after transplantation (Photo: J. Jensen). (b) Dispersal of lichen fragments from a restoration plot, in site 1 (right of the pole) into the surrounding burnt area (left of the pole). (c) Influence of the microsites on fragment retention and post-dispersal establishment outside restoration site 1. (Photos: S. Roturier).

certainly influenced dispersal (Heinken, 1999; Roturier et al., 2007) and may explain the observed variations between sites. However, the absence of a clear relationship between the pattern of dispersal and dominant wind speed and direction on the restoration sites also revealed the importance of microsite conditions (Fig. 5c). Post-dispersal processes such as establishment in the ground strongly depend on the substrate, micro-climate (Nathan and Muller-Landau, 2000), and associated plant community and biological soil crusts that may promote fragments' survival and growth. Reindeer lichen colonisation may therefore be as much limited by their very branched growth form, which makes them prone to rapid desiccation, as by their ability to disperse over long distances. As underlined by Nelson et al. (2015), there is a clear trade-off between dispersal form and growth form in the successful establishment of lichens in post-fire environments.

4.3. Fire, lichen, and Rangifer: Perspectives for restoration

The absence of natural disturbances that structure forest habitats and dynamics is now widely recognised as one of the key issues for preserving biodiversity and the functioning of boreal forests (Kuuluvainen, 2009; Gauthier et al., 2015). It results from the dominant silvicultural approach based on clear-cut harvesting, mechanical soil preparation, and growing of even-aged stands (Kuuluvainen, 2009). If there is a need for more natural disturbance-based management of boreal forests (Shorohova et al., 2011; Kuuluvainen et al., 2021), including the use of fire which is the main natural disturbance in lichen dominated ecosystems (Zackrisson, 1977; Esseen et al., 1997), this will require sensitive negotiations with other interests and activities that also depend on boreal forests, including forest management, nature conservation, and Sami reindeer husbandry (Cogos et al., 2021). Reindeer herding is carried out by some of the last surviving pastoral societies in Europe, and it performs numerous ecological functions including shaping vegetation dynamics through grazing and trampling (Sundqvist et al., 2019), predation by large predators (Åhman et al., 2022), and carbon storage (Ylänne et al., 2021).

In boreal forests, fire is the most significant disturbance and it plays a major role in determining the distribution and composition of plant communities (Morneau and Payette, 1989; Schimmel and Granström, 1996; Coxson and Marsh, 2001). Changes in fire regimes, whether increases in frequency and severity or suppression, directly impact *Rangifer* populations (Klein, 1982) and the societies who depend on them and their pastures (Granström and Niklasson, 2008). Herds have evolved alongside major ecosystem disturbance by fire, which destroys their winter grazing lands and, in the long run, contributes to the availability

Table 2
Recommendations for transplanting lichen for *Rangifer* winter forage in a post-fire environment, based on Klusåberget experiment, northern Sweden.

Collection	Reindeer lichen should be collected outside of *Rangifer*'s winter range. Kauppi (1979) recommended that no more than 20 % of the lichen cover in an area should be harvested, with 5–6 year intervals between collections, to maintain good production. Good practice should draw on the experience of reindeer herders with regards to managing collection sites and lichen storage as it is a current practice to feeding starving animals with lichen during bad winters.
Fragmentation	Reindeer lichen should be roughly fragmented (from <1 cm-long fragments to ca. 5–7 cm in this experiment). Other vegetation debris, including dead parts of lichen thalli, and the bank of seeds and propagules, were considered to promote lichen establishment after dispersal (see Roturier et al., 2007). An alternative to fragmentation may be to transplant entire lichen mats (Rapai et al., 2023).
Time of dispersal	Dispersal should be undertaken at least two years after fire, ideally in late summer to promote lichen growth, or in late winter for easier transportation. In case of winter transplantation, care should be taken with storing the lichen to guarantee the viability of the material.
Dose	A minimum of 15 g m^{-2} (or 0.5 L m^{-2}) is suggested. Higher doses may result in significant losses during the first years following dispersal. However, depending on site conditions, higher doses can result in greater growth.
Transplanting pattern	Transplantation should be designed in patches with a buffer zone of ca. 20 m to benefit from natural dispersal of fragments from the transplanted plots.
Post-restoration management	Natural regeneration should be supported with indigenous pine species, and pre-commercial thinning applied to avoid high stem density detrimental to lichen growth.

of grazing habitats in the landscape, including lichen-rich habitats (Payette et al., 2000; Hörnberg et al., 2018). However, the current decline of pastures, driven by various successional pathways and causes (Fraser et al., 2014; Kumpula et al., 2014; Horstkotte and Moen, 2019), mean that negative short-term effects of fire, i.e. the decades-long destruction of the lichen mat, are extremely challenging to overcome (Greuel et al., 2021; Roturier et al., 2023). For this reason, controlled burning, mainly driven by Forest Stewardship Council certification, is considered by reindeer herders to constitute an increasing threat to reindeer winter pastures (Cogos et al., 2021). In Fennoscandia, while postfire treatments are generally not necessary or desirable, rehabilitation of degraded winter pastures following wildfire and conservation burning, or following prescribed burning associated with intensive silviculture for timber production (such as *Pinus contorta* plantation or nitrogen fertilisation), may be locally necessary. To achieve such rehabilitation, forest managers, reindeer herders, and other stakeholders need technical, ecological, and economic evidence to negotiate the effective management of forest ecosystems.

Based on Klusåberget experiment, we are able to make recommendations for further reindeer lichen restoration operations, in particular in post-fire environments (Table 2). After 11 growing seasons, we have confirmed that: (1) post-fire forestry management, from set-aside to stand regeneration, influences the growth of transplanted reindeer lichen through providing different habitats and resulting growing conditions; however, (2) transplanting has a clear positive effect on lichen biomass in all restoration plots, from intensive to moderately burnt, compared to control plots, progressing along a trajectory of recovery, compared to reference grazed lichen-rich forests; (3) a lower transplanting dose (14 g m^{-2}) can result in statistically similar levels of growth as a higher dose (70 g m^{-2}), which can suffer significant losses during the first year after transplantation; and (4) restoration plots can act as sources for further lichen dispersal at a pace of at least 20 m within a decade. These results complement previous studies (Roturier et al., 2017; Rapai et al., 2023), which have informed transplantation operations, from collection to lichen preparation and modes of dispersal (Table 2), and functional-based approaches to anticipating lichen colonisation of post-fire environments (Nelson et al., 2015).

The future of this specific restoration project, and the development of potential new ones, now depends on further development of methods and technologies to improve the cost-effectiveness of restoration work, and on applying management measures to provide the conditions for a fully functional lichen mat. To assess the success of restoration, it may be worth measuring additional attributes such as the diversity of lichen and bryophyte communities, succession dynamics within the lichen mat, and competition with bryophytes and ericaceous dwarf shrubs, all of which depend on the forest management approach adopted (Berg et al., 2008; Horstkotte and Moen, 2019). However, assessment of biomass over time remains a critical indicator for evaluating the potential for herbivory by *Rangifer* populations and, in the case of reindeer husbandry in Fennoscandia, the associated ecosystem services for Indigenous Sami communities. A fully functional lichen mat would thus include reindeer grazing and trampling, and lichen regeneration following grazing (Crittenden, 2000; Gaio-Oliveira et al., 2006). Finally, the social goals of a restoration project have taken on increasing importance in recent years (Gann et al., 2019). We believe that this experiment, described as a co-production of knowledge experience (Roturier et al., 2022), has also engaged Sami reindeer herders and forest managers, contributed to knowledge enrichment through participation by members of the reindeer herding community at different stages of the project, and has the potential to further benefits for reindeer herding communities through its contribution to designing new forest management strategies.

CRediT authorship contribution statement

Samuel Roturier: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Joel Jensen:** Methodology, Writing – review & editing. **Lars-Evert Nutti:** Conceptualization. **Pierre Barbillon:** Formal analysis, Writing – original draft, Writing – review & editing. **Sébastien Ollier:** Formal analysis, Methodology. **Dan Bergström:** Funding acquisition, Methodology, Writing – review & editing.

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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Data availability

Data will be made available on request.

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Appendix A. Appendix

Table A1
Environmental conditions at the different sites (restoration, control, and reference sites) in 2020 and at the time of lichen transplantation for canopy cover and top soil pH on the restoration site. (–) indicates no measurement undertaken; (n/a) indicates not applicable measurement.

	Klusåberget						Forsnäsheden		
	Restoration sites			Control sites			Reference sites		
Site	1	2	3	C1	C2	C3	R1	R2	R3
Alt. (m.a.s.l.)	135	128	175	135	125	175	170	90	90
Mean slope (%)	7	0	0	7	0	0	0	0	0
Soil type	Mesic-dry	Mesic	Mesic-dry	Mesic-dry	Mesic	Mesic-dry	Dry	Dry	Dry
Veg. type	Transplanted lichen following fire			Post-fire succession			Lichen-rich	Lichen-rich	Lichen
Fire severity	High	High-moderate	High-moderate	High	High-moderate	High-moderate	n/a	n/a	n/a
Post-fire operations	Clear-cut, lodgepole pine planted	Clear-cut, scarified, Scots pine sown	Set-aside, nat. reg.	Clear-cut, nat. reg.	Clear-cut, nat. reg.	Set-aside, nat. reg.	n/a	n/a	n/a
Deadwood (m^3 ha^{-1})	0	0	23	–	–	–	–	–	–
Canopy cover (%)									
2008	0	0	38	0	0	–	–	–	–
2020	4	15	14	–	–	–	26	34	15
Scots pine basal area (m^2 ha^{-1})	0	1	14.5	0	3	0	33	6	3
Seedlings (>1.3 m) ha^{-1}									
Pinus	490	1889	3008	70	3218	280	0	0	0*
Betula	210	2378	0	0	1679	70	0	0	0
Top soil pH									
2008	4.9	5.5	5.6	–	–	–	–	–	–
2020	4.2	4.2	4.4	4.3	4.3	4.1	–	–	–

* The site R3 was strongly affected by moose (*Alces alces* L.) browsing before pre-commercial thinning, resulting in a very high density of dead-top seedlings.

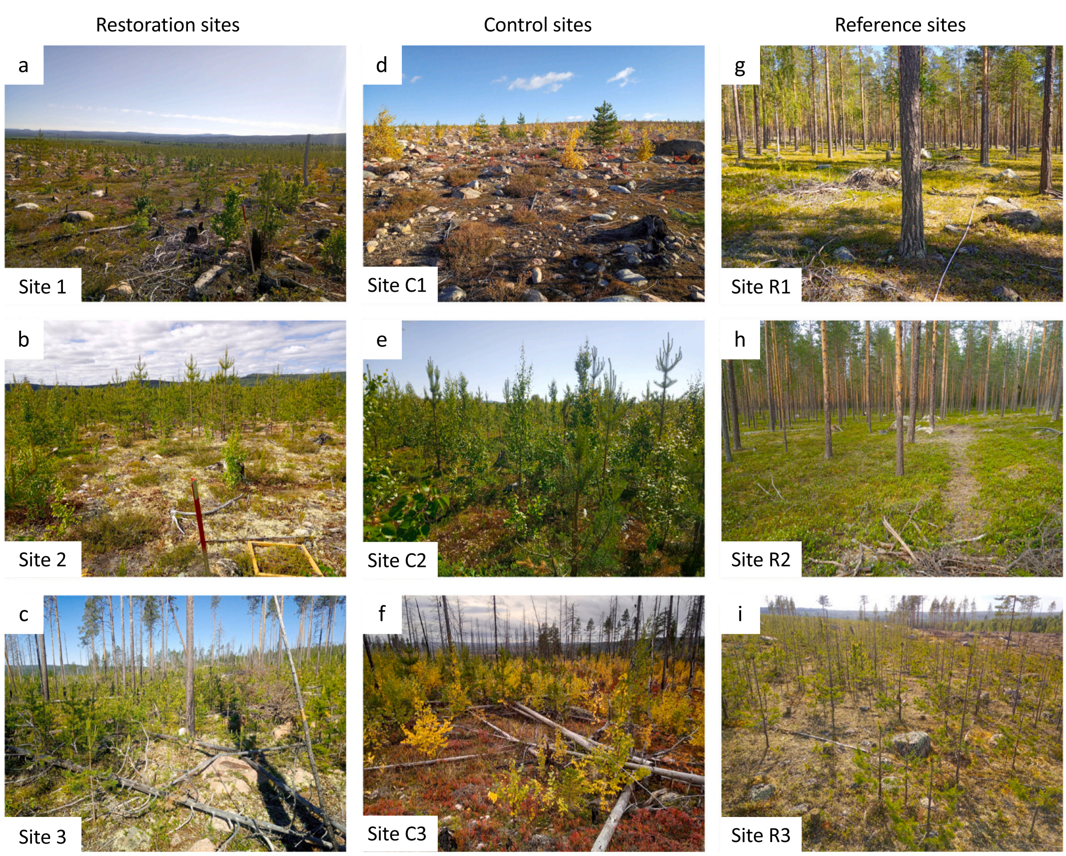

Fig. A1. Photos taken in June 2020 in the restoration (a, b, c), control (d, e, f) and reference (g, h, i) sites (3 in each). Note that the photos (d & f) were taken in September 2020, i.e. 2 months after the inventory.

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