Influence of prescribed burning on reindeer winter pastures at landscape scale in northern Sweden: A modelling approach

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Abstract While the re-introduction of fire can contribute to biodiversity conservation in Fennoscandian forests, the effects on reindeer herding remain uncertain. To assess the short- and long-term effects of prescribed burning on lichen supply in a productive forest landscape, we developed a model simulating lichen biomass available for reindeer grazing, covering 300 years and 1500 pine stands, under different soil preparation scenarios, including different prescribed burning regimes and mechanical scarification. Our simulations revealed that burning 25-50% of yearly clear-cuts has the potential to stop, or even reverse, reindeer lichen decline at landscape scale after 70 years, greatly surpassing the short-term losses caused by burning. No burning, or burning 5% of yearly clear-cuts, as required by the FSC certification, compounded the negative effects of fire suppression and scarification on lichen. Compared to the scenario with no soil preparation, all our simulations resulted in a continuous decrease of lichen supply in Lichen-type stands, indicating that any form of disturbance in these habitats can strongly limit future gains.

Keywords *Cladonia* · fire · Forest Stewardship Council · forestry · *Rangifer* · reindeer herding

INTRODUCTION

Fire is a key socio-ecological process in many ecosystems worldwide. The complex relationship between fire disturbance and ecosystem composition depends on fire regimes, i.e. a regular pattern of fires over a period of time, in which humans have played a significant role in the boreal forest (Granström and Niklasson 2008) and elsewhere (Trauernicht et al. 2015). In the Fennoscandian boreal region, wildfire was historically the most important natural disturbance in Scots pine forests (Esseen et al. 1997). It is estimated that, prior to the modern era, stand-replacing fires occurred at a mean interval of 80 years in Northern Sweden (Zackrisson 1977, Niklasson and Granström 2000). The development of commercial forestry in the late 19th century was associated with active fire suppression and considerably reduced the occurrence and extent of forest fires during the last 150 years (Wallenius 2011). This is now a major challenge for the conservation of fire-dependent species and restoration of fire-prone habitats (Halme et al. 2013). Another possible consequence of fire suppression, combined with forest management during the 20th century, is the notable decrease in lichen-rich winter pasture for the domesticated reindeer (*Rangifer tarandus tarandus* L.) of the Indigenous Sami people. Epigeous reindeer lichens (*Cladonia* spp.) represent vital winter grazing resources for reindeer herds and natural pastures are thus a key element in preserving traditional herding practices and cultural diversity in the region. Sandström et al. (2016) estimated that 71% of lichen-rich forests have been lost over the past 60 years as a consequence of large-scale logging, intensive reforestation efforts including mechanical soil scarification, and fire suppression.

Although fire destroys reindeer lichen for several decades, thus having an obvious short-term detrimental effect on reindeer winter pastures, the prolonged absence of fire induces changes in below- and aboveground properties that result in feather mosses and Ericaceous dwarf shrubs outcompeting ground lichens in the mid- to long-term (Ahti and Oksanen 1990, Nilsson and Wardle 2005). However, in dry oligotrophic conditions, reindeer lichen can become dominant after a century, even excluding

vascular plants from the system for decades (Crittenden 2000). These pathways also depend greatly on reindeer herbivory and forest stand management, which structure the competition between plants and lichens (Olofsson et al. 2010). In particular, soil preparation for forest regeneration after harvest is a key stage that shapes the understorey community.

Until the 1970s, prescribed burning was extensively used after clear-cutting in some areas before being completely replaced by mechanical soil scarification (Östlund et al. 1997). Since the 1990s controlled burnings have mainly taken the form of conservation fires used to restore fire-shaped habitats to benefit locally threatened species (Naturvårdsverket 2005). In this respect, the main driver of fire regimes in the boreal forest is the Forest Stewardship Council (FSC) certification, which requires large forest companies to burn at least 5% of the clear-cut area in dry and mesic forests over a 5-year period (Forest Stewardship Council 2019). Ramberg et al. (2018) estimated that, at the beginning of the 21st century, fire affected only 0.006% of the Swedish forest per year, including 65% of prescribed burns; this is far below historical levels of 0.8 to 2.8% in the region (Niklasson and Granström 2000).

Future fire regimes will be influenced by changing climate (MSB 2017) but will mainly depend on objectives set by humans, in a trade-off with biophysical conditions, as always in the complex history of human-fire relationships (Granström and Niklasson 2008, Hörnberg et al. 2018). We believe that the objectives of prescribed burning could serve forest production as it was during the 20th century, biodiversity conservation as has been encouraged by the FSC since the 2000s, but also the restoration of lichen-rich pastures for reindeer herded by Indigenous Sami people, possibly providing converging benefits.

Because data on the long-term effects of past and present fire regimes on lichen pastures is scarce and because a wide range of ecological factors and shifting patterns are involved, modelling is a relevant approach. Recently, several studies have developed models to estimate lichen biomass or its decline in northern Fennoscandia, but none has included the effects of fire suppression/re-introduction (Sandström et al. 2016, Horstkotte and Moen 2019, Uboni et al. 2019, Miina et al. 2020).We, therefore, developed a model based on current forest management standards and practices plus published literature in forest ecology, to simulate the effects of prescribed burning on lichen supply for reindeer in a landscape used by commercial forestry and reindeer herding. More specifically, the objectives were: (i) to explore the long-term dynamics of lichen biomass available for reindeer grazing in a landscape following different soil preparation scenarios, including mechanical scarification and different prescribed burning regimes; (ii) to quantify and compare the short-term negative effects with potential long-term positive effects of prescribed burning on lichen biomass between different scenarios; and (iii) to examine the consequences of various scenarios on the structure (ground vegetation and time since last fire) of lichen stands grazed by reindeer. We conclude with suggestions concerning the place of prescribed burning in current Swedish forestry and the integration of Sami reindeer herding into future fire management.

MATERIALS AND METHODS

Modelling lichen biomass dynamics at the landscape level

We constructed a model to simulate reindeer lichen biomass dynamics in relation to the management of Scots pine (*Pinus sylvestris* L.) forest stands in a forest landscape grazed in winter by reindeer. Modelling spatially independent stands was chosen to represent the lichen dynamics driven by forest management at stand scale, thus constituting a non-spatially explicit landscape. Therefore, for each year, the reindeer lichen biomass modelled for each stand was used to calculate the lichen biomass available for grazing within the landscape (B). At stand level, the lichen biomass depended on four processes: yearly growth, removal through grazing, burning and soil scarification. All varied according to stand-dependent factors (stand characteristics and management), and landscape-dependent factors (prescribed burning regime and reindeer grazing). The values of the stand-dependent factors were based on data from the Swedish National Forest Inventory (SNFI) and forestry standards for Scots pine forests applicable in Norrbotten (Anon. 1985), the northernmost county in Sweden. In addition, a one-day workshop was organized with one forest ecologist, two forest managers and three Sami reindeer herders operating in Norrbotten. After being introduced to the objectives of the modelling, we organized focused discussions about variables and parameters for which there was a lack of information in the scientific or grey literature, in order to confirm, parametrize or refine values and make them more relevant to the context of reindeer herding and commercial forestry in the area. Hereafter, we refer to the information from this workshop as "workshop pers. comm.". Different prescribed burning regimes varying in their extent

of prescribed burning, i.e. the area burnt as a percentage of the yearly clear-cut area, and in the condition for burning, i.e. whether or not the stands that are most lichen-rich are preserved from burning, were considered as sources of variation between different scenarios.

Herein, an area of 280 km² of forestland was considered a functional landscape area from a reindeer herding perspective in northern Sweden (workshop pers. comm.). Based on herders' experience in their respective communities, it was estimated that in Norrbotten county, under today's conditions, this area could feed zero to three reindeer winter herds depending on the grazing conditions and herd size. According to the SNFI for Norrbotten, 38% of the landscape is covered by productive pine forests and 62% by spruce forests, mires, and impediments (https://www.slu.se/nfi). Therefore, the modelled landscape was defined as 105 km² of productive pine forests divided into 1500 stands of 7 ha (in accordance with median prescribed fire size, Ramberg et al. 2018).

Lichen dynamics at stand level

Every stand was assigned fixed parameters and variables which determined its lichen biomass dynamics (Table S1). The variables were: stand age given by the time since the last cut (*TSLC* in years), time since the last fire (*TSLF* in years), *post*-grazing lichen biomass (b^{po} in kg), lichen biomass growth rate (*r*), and lichen cover (*C* in %), which represented the percentage of the surface of a stand colonized by reindeer lichen. The fixed parameters were: altitude, soil fertility, site productivity index (SI) as defined by the Swedish forestry classification system (Anon. 1985) and the maximum lichen cover (C_{max}), i.e. the potential for lichen colonization in the stand. At year *t* the post-grazing lichen biomass in a stand, b_t^{po}, was given by:

$$b_t^{po} = b_t^{pr} - b_t^{gr}$$

Where b^{pr} and b^{gr} (both in kg) are, respectively, the *pre*-grazing lichen biomass and the lichen biomass *grazed* during winter.

Lichen biomass before grazing

The lichen biomass before grazing was modelled using the Beverton-Holt model, a discrete-time analogue of a logistic growth model (Kumpula et al. 2000):

$$b_{t+1}^{pr} = b_t^{po} \times \frac{exp(r)}{1 + b_t^{po} \times \frac{exp(r)-1}{b_{max}}} \qquad (1)$$

where *r* and b_{max} are, respectively, the lichen growth rate and the potential maximum lichen biomass. A feature of the model is that *r* and b_{max} both vary in time.

The value of *r* was calculated with the best simplified model explaining variation in annual lichen growth, following Jonsson-Čabrajić et al. (2010):

$$r = 51{,}5 - 0{,}63 * BA - 1{,}67 * T_{June} \qquad (2)$$

where *BA* is the stand basal area (m² ha⁻¹) and T_{June} is the mean June temperature. The *BA* varied over the *TSLC* as a result of tree growth and forest management, including the number, the timings and the intensity of thinnings, and the stand age at final harvest. The forest management was defined at stand level for each combination of SI and altitude. The potential maximal lichen biomass b_{max} (in kg) was calculated following the biomass equation (Akujärvi et al. 2014):

$$b_{max} = 1.3536 * C * h_{max} * A \qquad (3)$$

where 1.3536 is a coefficient set for *Cladonia stellaris*, the dominant reindeer lichen species, h_{max} is the maximum height of a fully-grown lichen mat (100 mm), *A* is the stand size (7 ha), and *C* is the percentage of the stand covered by lichen. Changes in *C* over time simulate vascular plant competition within the post-fire chronosequence at stand level. To simulate the effects of plant competition on reindeer lichen, depending on soil fertility and altitude, three vegetation categories (Lichen-, Mixed- and *Vaccinium*-types) were defined. Based on a literature review (Table S1), changes in *C* were simulated by the linear decrease in *C* from C_{max} to 0 over the *TSLF* and following different slopes for each vegetation category (Figure S1).

Lichen removal through grazing

Recent studies show the complexity of modelling lichen consumption by functional reindeer herds, including different sex and age classes (Tahvonen et al. 2014). On a landscape scale, the grazing conditions depend greatly on complex interactions between snowfall, temperature changes, forest structure and vegetation types (Roturier & Roué 2009); the various strategies developed by herders to cope with them in space and time made it virtually impossible to estimate yearly lichen biomass removal by reindeer in a satisfactory way with the reindeer herders during the workshop. Therefore we considered heavily grazed conditions where reindeer consumed all the lichen available for grazing in the landscape down to the minimum

lichen height (h_{min}). The consequent b_{min} (in kg) was calculated as:

$$b_{min} = 1.3536 * C * h_{min} * A \qquad (3')$$

For each stand, b_t^{gr}, the biomass grazed in year t was thus calculated as:

$$b_t^{gr} = b_t^{pr} - b_{min} \quad \text{if} \quad b_t^{pr} > b_{min}$$

$$b_t^{gr} = 0 \qquad \text{otherwise.}$$

This led to:

$$b_t^{po} = b_{min} \quad \text{if} \quad b_t^{pr} > b_{min}$$

$$b_t^{po} = b_t^{pr} \qquad \text{otherwise.}$$

As a consequence, the lichen biomass available for reindeer (or lichen supply) at the landscape level is given by:

$$B = \sum b^{gr}.$$

Influence of forest management on lichen biomass at stand level

Forest management was defined at stand level for each combination of SI and altitude, resulting in 60 different BA dynamics within the landscape. The BA dynamics were modelled using BA values before and after thinnings, before clear-cutting, according to the stand age at the time of the thinnings and at clear-cutting (Table S2). The values of these parameters were defined using an online free-access simulator for decision support to assist small forest owners in forest management (Skogsforsk 2008, https://www.skogforsk.se/produkter-och-evenemang/verktyg/ingvar/). The simulator followed the growth curves and silvicultural recommendations applied in commercial forestry in Sweden. To be more consistent with commercial forestry practices in northern Sweden, we advanced the clear-cutting ages by 10% (workshop pers. comm.). The effects of seedling density and precommercial thinning on BA were ignored. Depending on SI and altitude, we modelled one to two thinnings of stands, before the final clear-cutting at 96-131 years. In our model, all clear-cuts were followed by soil preparation either in the form of mechanical soil scarification or prescribed burning in the same year as clear-cutting. To apply the most current practices in forestry with respect to reindeer herding, soil preparations were only permitted in stands with a lichen cover $C < 35\%$ for mechanical scarification (C_{scar}), and $C < 15$ or $< 30\%$ for prescribed burning ($C_{burning}$) (workshop pers. comm.). When soil scarification was applied, we assumed a sudden decrease in pre-grazing lichen biomass b^{pr} and a sustained decrease in lichen cover C, both by 30%, to simulate respectively short- and long-term negative effects of soil preparation on ground lichen (Roturier et al. 2011, workshop pers. comm.).

In the year of clear-cutting, the stand entered the pool of stands that could be burnt only if its lichen cover C was below $C_{burning}$. Because burning could not take place on a fraction of a stand, the number of stands to be burnt within this pool was calculated as the random rounding of the product of the number of clear-cut stands and the proportion of burned land specified for each scenario. When this number was larger than the pool of stands available for burning, the entire pool was burnt, giving a lower proportion of burning than defined in the scenario. Otherwise stands to be burnt were randomly selected from the pool.

When prescribed burning was applied, the lichen cover C was reset to its maximum C_{max} and lichen biomass b^{pr} was totally removed for a period of 50 years, which is the estimated time before reindeer return and graze after a fire (workshop pers. comm.), and also corresponds approximately to the return of wild caribou ca. 60 years after large forest fires in Canada (Collins et al. 2011). After 50 years, the biomass value was set to the minimum (b_{min}) calculated using Equation 3'.
Figure 1 illustrates the effects of time and management on the main variables described above at stand level.

Simulation at the landscape scale

Landscape initialization

The 1500 stands were distributed according to their lichen cover class, age class (*TSLC*) and site productivity index (SI) given by the SNFI for Norrbotten (Figure S2). Since SNFI data only provide value classes for lichen cover and *TSLC*, values of initial lichen cover C_0 and $TSLC_0$ were randomly assigned based on the class of the stand, assuming a uniform distribution. For each stand, BA_0 at $TSLC_0$ was deduced from the simulated BA dynamics. Altitude and soil fertility distributions were randomly applied to express the range of variability observed in the area, allowing us to determine the distribution of the stands within the three vegetation categories. Temperatures were calculated as a monthly average of June temperature data at 6 a.m. and 6 p.m. from 1964 to 2011 at four weather stations located in northern Sweden (Table S1).

The initial distribution of *TSLF* in the landscape was based on literature and field data (Table S1), and each stand was then allocated a $TSLF_0$. Since no lichen biomass data were available
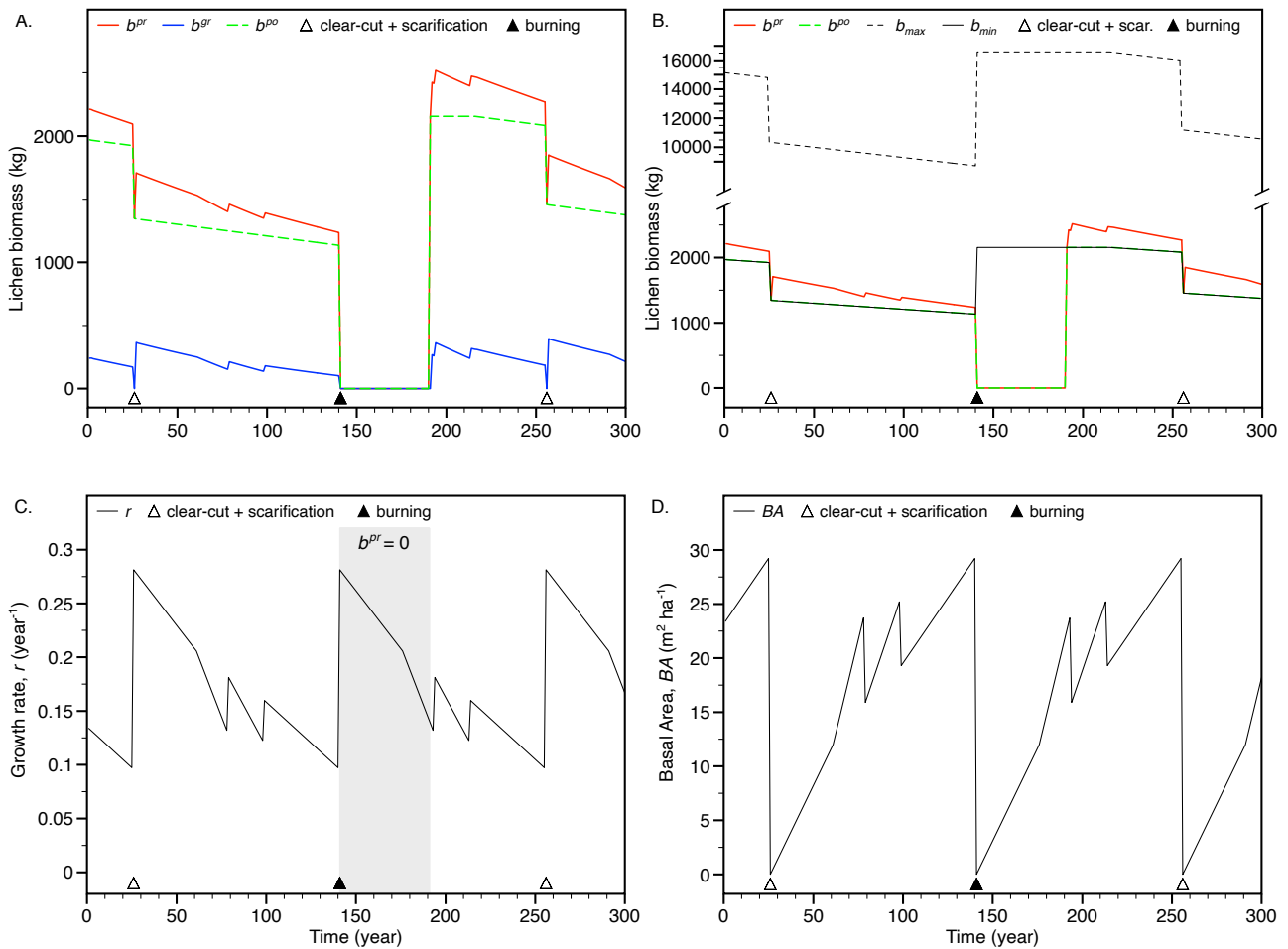
Fig. 1 Simulated effects of time and forest management (including clear-cutting followed by mechanical scarification, thinnings and prescribed burning) in a stand on: (A) pre-grazing (b^{pr}), grazed (b^{gr}) and post-grazing (b^{po}) lichen biomasses; (B) b_{max} and b_{min}; (C) the growth rate (r); and (D) basal area (BA) at stand level. The scenario applied in this simulation was *Burn50*. The stand characteristics were: Site productivity index (SI) = T18; Soil fertility: poor; Altitude: 0 m a.s.l.; Vegetation category: Lichen-type; $TSLC_0 = 89$ year; $TSLF_0 = 175$ year.

from the SNFI, the initial lichen biomass for each stand (b_0^{po}) was calculated using Equation 3 with $C = C_0$ and $h = h_{min}$.

The initial value of C_{max} for each stand was calculated from C_0 and $TLSF_0$ by working backwards from relationships shown in Figure S1.

Soil preparation scenarios and prescribed burning regimes

Six scenarios were tested by changing the prescribed burning extent from 0 to 50% of total yearly clear-cut area and by changing the condition for burning lichen-rich stands ($C_{burning} < 15$ or $< 30\%$). One scenario assumed no prescribed burning and only mechanical soil scarification after clear-cutting (*Burn0*). The *FSC* scenario applied prescribed burning in 5% of the yearly clear-cut area, i.e. the objective set in the FSC standard (Forest Stewardship Council 2019). The *Burn25* and

Burn50 scenarios applied prescribed burning in 25% and 50% of the yearly-clear-cut area, respectively. Variations of these scenarios (*Burn25+* and *Burn50+*) assuming a higher $C_{burning}$ were also tested, i.e. where prescribed burning was permitted in stands with higher lichen cover. In addition, we included a *Control* scenario with no burning and no scarification (Table 1). We performed one 300-year simulation for each scenario using the R software (version 3.2.0, R Core Team 2015).

RESULTS

As expected, the mean number of clear-cuttings per year was the same for the seven scenarios following the initial age structure of the landscape (Table 2). The mean number of mechanical scarifications per year decreased proportionally with increasing extent of prescribed burning among the scenarios.

Table 1 Description of the various scenarios.

Scenario name	Description	Prescribed burning extent (in % of yearly clear-cut area)	Condition (in % lichen cover) for	
			burning ($C_{burning}$)	soil scarification (C_{scar})
Control	No prescribed burning + no mechanical soil scarification	0	0	0
Burn0	No prescribed burning	0	0	<35
FSC	Restricted extent of prescribed burning, meeting the FSC standard	5	<15	<35
Burn25	Medium extent of prescribed burning	25	<15	<35
Burn25+	Medium extent of prescribed burning, including on the most lichen-rich stand	25	<30	<35
Burn50	Great extent of prescribed burning	50	<15	<35
Burn50+	Great extent of prescribed burning, including on the most lichen-rich stand	50	<30	<35

Table 2 Simulated forest management and fire regime components for each scenario.

Parameter	Prescribed burning scenarios						
	Control	*Burn0*	*FSC*	*Burn25*	*Burn25+*	*Burn50*	*Burn50+*
Number of clear-cuts per year							
Mean ($n = 300$)	13.4	13.4	13.4	13.4	13.4	13.4	13.4
SD	5.7	5.7	5.7	5.7	5.7	5.7	5.7
Range	[2-33]	[2-33]	[2-33]	[2-33]	[2-33]	[2-33]	[2-33]
Number of stands with mech. scarificat. per year							
Mean ($n = 300$)	0	12.7	11.9	8.8	8.8	5.1	5.0
SD	0	5.4	5.1	3.9	3.9	2.5	2.5
Range	-	[2-31]	[2-29]	[1-22]	[1-22]	[0-15]	[0-15]
Number of prescribed burnings per year							
Mean ($n = 300$)	0	0	0.7	3.4	3.4	6.6	6,7
SD	0	0	0.5	1.5	1.5	2.9	2,9
Range	-	-	[0-2]	[0-8]	[0-9]	[1-17]	[1-16]
Burnt area (% of clear-cutting) per year							
Mean ($n = 300$)	0	0	5.2	25.2	25.2	49.1	50.0
SD	0	0	5.2	4.2	4.5	4.8	4.2
Burnt area (% of landscape) per year							
Mean ($n = 300$)	0	0	0.04	0.23	0.22	0.44	0.45
SD	0	0	0.03	0.10	0.10	0.19	0.19
Mean TSLF (year) ($n = 1500$)							
t = 0	150.7	150.7	150.7	150.7	150.7	150.7	150.7
SD	41.7	41.7	41.7	41.7	41.7	41.7	41.7
t = 300	450.7	450.7	409.8	273.2	277.6	154.9	163.1
SD	41.7	41.7	115.3	169.5	170.7	132.7	141.1

Prescribed burning was effectively applied following the objectives set for different scenarios, giving on average 0.7, 3.4 and 6.6 prescribed burns per year in *FSC*, *Burn25/25+*, and *Burn50/50+* scenarios, respectively. For all the scenarios except *Burn50/50+*, the mean TSLF greatly increased over the simulation period (Table 2). In all scenarios, the mean yearly burnt area remained low. On average, it represented 0.04% of the 1500 stands over the simulation period in the *FSC* scenario, and 0.23% and 0.44% in the *Burn25* and *Burn50* scenarios, respectively.

The effects of the various scenarios on the lichen biomass available for grazing (*B*) over the

300 years are presented in Figure 2. The *Control* scenario showed a continuous decline in the lichen supply, exclusively driven by the decreasing effect of the lichen cover dynamics (*C*) on lichen biomass (*b*), i.e. with no management directly removing the lichen biomass. In all scenarios, *B* decreased at a faster pace than in the *Control* during the first 50 years of the simulations, as a result of direct lichen removal through mechanical scarification alone (*Burn0*), or in combination with burning for the other scenarios. After 50 years, i.e. the delay for the return of lichen biomass in the stands that were burnt at the beginning of the simulations, *B* stopped decreasing and stabilized at ca. $300 \cdot 10^3$ kg in
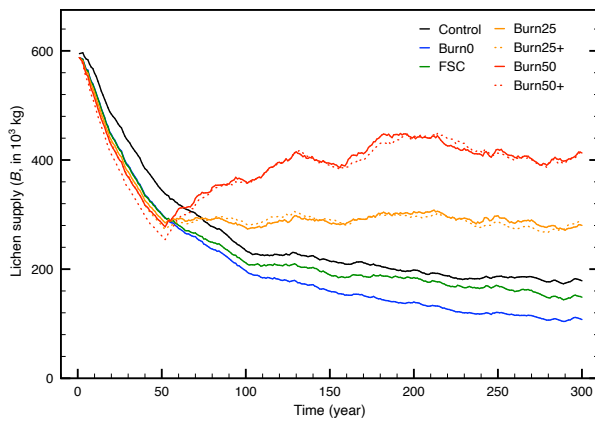
Fig. 2 Lichen biomass available for grazing (B, in 10^3 kg) per year in 1500 pine stands for the different scenarios over 300 years.

scenarios, and far surpassed the short-term losses. Higher $C_{burning}$ in scenarios *Burn25+* and *Burn50+* did not result in any clear effect on the cumulated lichen supply compared to *Burn25* and *Burn50*, respectively (Figure 3).

The different scenarios also had a strong influence on the lichen biomass grazed by reindeer (b^{gr}) in the landscape (Figure 4). In the scenarios *Control*, *Burn0* and *FSC*, the forest management with no or a restricted extent of burning led to a situation at $t = 300$ where reindeer grazing was virtually absent from two third of the stands. This proportion decreased with increasing extent of burning in *Burn25/25+* and *Burn50/50+*, still accounting for 43 to 56% of the 1500 stands. However a shorter TSLF in these scenarios suggests that the absence of grazing was due to stands being recently burnt. In the scenarios *Control* and *Burn0*, the grazed biomass at $t = 300$ originated exclusively from Lichen-type stands due to the decrease in lichen cover (C) being faster in the absence of burning in Mixed- and *Vaccinium*-types than in Lichen-type stands. In contrast, in the scenarios *Burn25/25+*, *Burn50/50+*, and *FSC* to a lesser extent, burning allowed the maintenance of a larger number of Mixed and *Vaccinium* stands supporting high b^{gr}, as shown by the lower mean TSLF in these scenarios for these stands. Finally Lichen-type stands with a $b^{gr} > 750$ kg were not scarified or burnt in any scenarios. However the lower mean TSLF in *Burn25/25+* and *Burn50/50+* shows that burning also created Mixed and *Vaccinium* stands with high b^{gr} in the long run.

Burn25/25+, while it increased up to $400 \cdot 10^3$ kg in *Burn50/50+*. The *FSC* scenario showed a positive effect of burning on B, especially compared to *Burn0*, but remained below the *Control* scenario in the long run. Allowing stands exhibiting higher lichen cover to be burnt ($C_{burning} < 30\%$) did not result in positive long-term effects on the lichen supply in *Burn25+* and *Burn50+* compared to *Burn25* and *Burn50*, respectively, and there was a somewhat greater decrease for *Burn50+* during the first 50 years.

For the different scenarios, the cumulated lichen supply compared to the *Control* scenario exhibited a constant net loss over time in Lichen-type stands, representing the largest loss of lichen in the landscape (Figure 3). In Mixed- and *Vaccinium*-types of vegetation, the losses were limited to the first 70 years. The subsequent gains in lichen supply were proportional to the area burnt in different
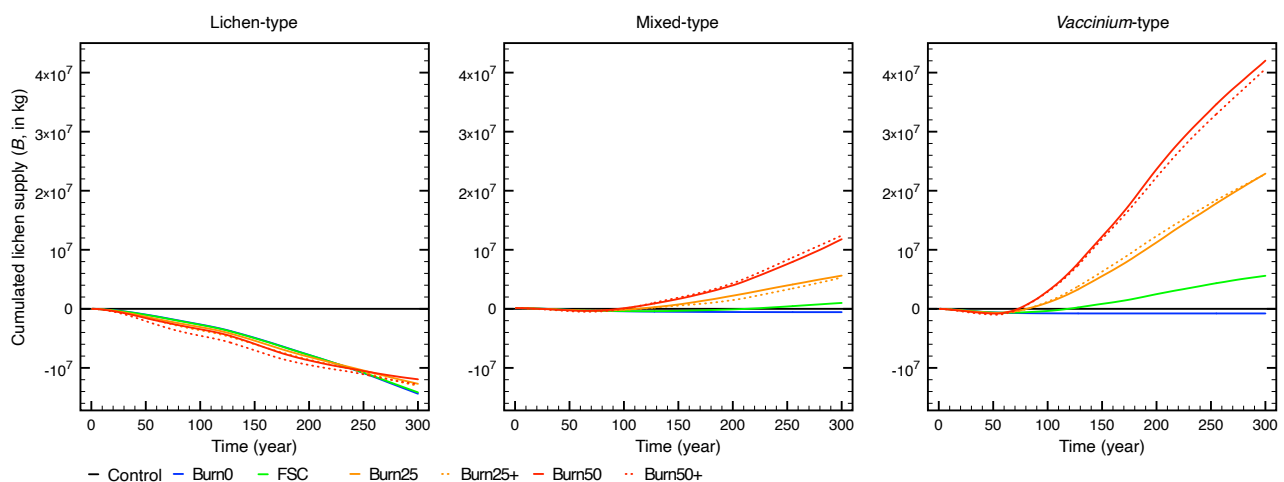

Fig. 3 Cumulated lichen biomass available for grazing (in kg) over time in Lichen- (n = 580), Mixed- ($n = 276$) and *Vaccinium*-type ($n = 644$) stands for different scenarios compared to the *Control* scenario.
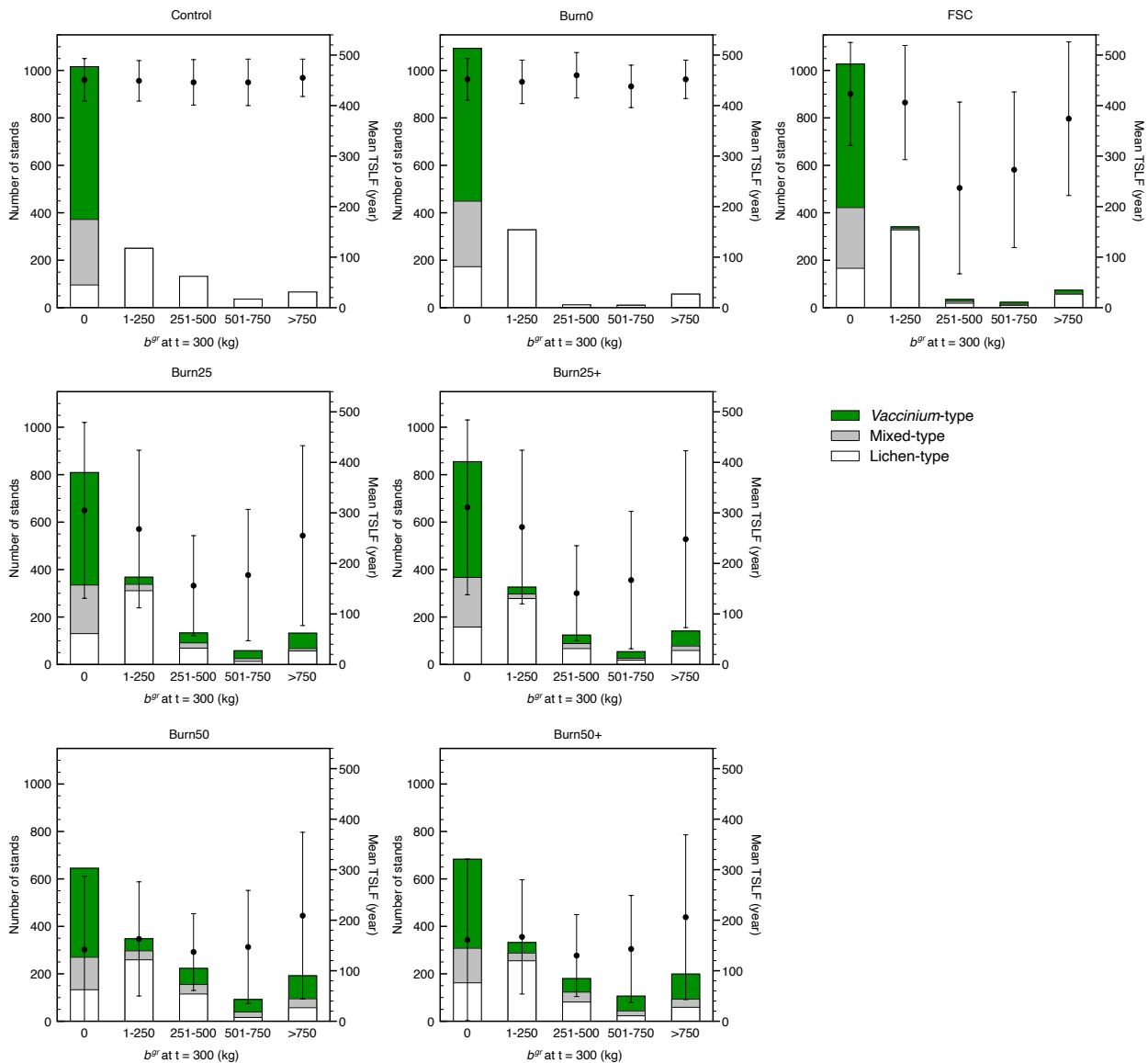
Fig. 4 Distribution of the Lichen-, Mixed- and *Vaccinium*-type stands (*n* = 1500) according to the lichen biomass grazed during winter (b^{gr}) and corresponding mean TSLF ($\pm$ SD) at t = 300 years for the different scenarios.

DISCUSSION

Effects of prescribed burning on lichen supply for reindeer

Our study simulated various soil preparation scenarios, allowing us to compare the effects of different prescribed burning regimes (area burnt and conditions for burning), in combination with soil scarification, on reindeer lichen supply in northern Sweden. Our model showed that scenarios with no (*Burn0*) or a restricted extent of prescribed burning (*FSC*) compounded the negative effects of fire suppression and systematic use of scarification, which both affected the lichen supply in the landscape through time. These results are consistent with observations collected within other time

frames and using other methodologies, showing that current forest management, including mechanical soil scarification, strongly affects ground lichen pastures and does not provide favourable conditions for lichen-rich habitats (Berg et al. 2008, Roturier et al. 2011, Sandström et al. 2016). Conversely, the scenarios with a greater extent of burning (*Burn25/25+* and *Burn50/50+*) stopped the decrease in lichen supply at the landscape scale and maximized the lichen biomass available for reindeer (Figure 2). This reflected the reduced removal of lichen biomass through soil scarification, and above all the increased number of stands supporting reindeer lichen, especially Mixed- and *Vaccinium*-type, as a direct result of prescribed burning in the model (Figure 4). This suggests that negative short-term effects of prescribed burning on lichen supply at the landscape scale are weak compared to the

systematic use of mechanical soil scarification, and largely compensated for in the long run. However, compared to the *Control* scenario, all our simulations resulted in a continuous decrease of lichen supply in Lichen-type stands, indicating that any form of disturbance in these habitats can strongly reduce future gains.

In this respect our study confirmed the position of reindeer herders, that the most lichen-rich stands should be protected from prescribed burning resulting in high losses at stand level in the short-term (Cogos et al. 2021). Our results showed that changing the condition for burning lichen-rich stands ($C_{burning}$ < 15 to < 30%) has no effect on lichen supply in the long run. Our simulations also highlight the fact that beside the extent of lichen cover in a stand at the time of burning, the vegetation type and future dynamics are extremely important with respect to increasing lichen supply at the landscape scale (Figure 3). The FSC standard prioritizes burning dry and mesic soils based on the historical role of fire in the natural functioning of these habitats. Historic references can indeed be of help, whilst acknowledging that decades of fire suppression have already modified past successional pathways (see Swetnam et al. 1999). However, the potential effects of burning should also be examined with respect to soil properties and vegetation responses to fire severity, which can vary greatly, between, and within, natural and controlled fires (Schimmel and Granström 1996, Angelstam 1998, Sulyma and Coxson 2001), and as a result of subsequent stand management, especially in the early regeneration stages.

Interests and limits of the modelling approach

Several studies have used statistical models to identify the main determinants of lichen presence or abundance in North America as well as in Fennoscandia, some of them underlining the impact of fire regime (Angelstam 1998, Kumpula et al. 2014, Silva et al. 2019). However mechanistic models of long-term lichen biomass dynamics under fire regimes are scarce. Rupp et al. (2006) showed that, in Alaska, an increase in fire frequency may lead to a severe decrease in lichen availability, but they assumed that the oldest forest stands are the most lichen-rich while we simulated a severe decrease in lichen cover with stand age, as suggested by previous studies (Sandström et al. 2016, Horstkotte and Moen 2019, Miina et al. 2020). One limit of the approach developed in this study is that it considered some processes, e.g. herbivory or changes in lichen cover, as purely deterministic and unchanging in the long-term. Including more uncertainty in the model would involve

characterizing and quantifying the variability of these processes for which collecting empirical data is a true challenge. In addition, in the long run, the assessment of climate change impacts remains uncertain considering the numerous feedbacks it will generate in relation to management policies (fire and forest management), reindeer herding and vegetation growth (Moen 2008, Venäläinen et al. 2020). Although consistent with the literature, the absolute values of predicted biomasses should be considered with care in this context. However, the fundamental aim of this work was to assess the relative performance of the different soil preparation scenarios and there is no reason to expect that some of them would be more subject to uncertainty than others.

The expert-based evaluation of parameters and factor values guaranteed that the main mechanisms simulated matched empirical observations in the field. The most difficult mechanism to model was herbivory, which reindeer herder experts could not quantify. In this respect the workshop revealed the importance of forage availability on feeding behaviour ("the more lichen there is, the less the reindeer graze" (workshop pers. Comm.)), which have been explored for other ungulates (e.g. by Månsson et al. 2007). Although very relevant, our model could not include variations in herbivory, thus forcing us to assume that all available ground lichen was grazed without considering any limit in herd size or social regulation of common pasture use, both of which occur in the real world. In a sense, the biomass of grazed lichen modelled in this study can be seen as a measure of the maximum annual productivity of the forest from a reindeer herding perspective. In our simulations, the mean annual grazed biomass ranged between 19 and 37 kg ha^{-1} among the scenarios. This corresponds to lichen production during the early stages after fire or in heavily grazed areas (Kumpula et al. 2000), indicating that the landscape has the potential to exhibit higher standing biomass and production of lichen under lower grazing pressure.

The sharp decrease in the biomass available for grazing during the first 50 years (Figure 2) played an important role in the cumulated lichen supply modelled through time. This decrease has been potentially overemphasized by the extreme grazing pressure applied in the model and by the severely decreasing lichen cover dynamics over the *TSLF*. In addition, the initial conditions for lichen biomass relied on the best available large-scale data for the region, but only provided lichen cover classes, and there is an obvious lack of long-term survey data pertaining to ground lichen biomass. However this decrease is consistent with other studies (Sandström et al. 2016, Horstkotte and Moen 2019) and does not

challenge the relative long-term dynamics between different scenarios.

Implications for forest and fire management

Fire is one of the main drivers of vegetation dynamics in the boreal pine forests, and thereby influences the distribution and abundance of ground lichen at different scales, from stand to landscape level (Foster 1983, Silva et al. 2019). Our results reinforce the hypothesis that more proactive fire re-introduction is necessary to compensate for the effects of fire suppression and mechanical scarification on lichen decline during the 20th century (Berg et al. 2008). However, during the last 30 years, there has been renewed interest in burning, especially to deliver biodiversity conservation goals. This study demonstrates the urgent need to integrate reindeer herding by Indigenous Sami people into fire management policy to maintain future potential reindeer grazing.

Our results show that fire management following FSC certification standards has no positive effect on lichen supply at the landscape scale. The application of the FSC standard to commercial forestry actually encourages burning smaller areas with standing trees, instead of larger clear-cut areas (Forest Stewardship Council 2019). This is extremely important for the conservation of threatened fire-dependent species and for the restoration of natural processes and structures (Halme et al. 2013), but produces marginal positive effects on reindeer lichen supply. A more balanced use of different soil preparation methods before forest regeneration is needed (Hallsby et al. 2015), including prescribed burning in a wider diversity of vegetation types instead of mechanical scarification, which causes enormous losses of lichen (Fries et al. 1997), to maintain a forest landscape adapted to reindeer herding in northern Sweden. Our model shows that burning 25-50% of yearly clear-cuts is feasible within the management framework (from 24 to 47 ha annually out of 105 km^2 in our model), still far below historic reference levels during the golden age of prescribed burning (Cogos et al. 2020).

The results of this model also address the more general issue of fire restoration in fire-prone pine forests through prescribed burning. Burning 50% of the yearly clear-cuttings (*Burn50*), i.e. a tenfold increase compared to today's FSC certification, allowed the mean TSLF in the landscape to be maintained, rather than increasing over the simulation; however, it did not drop to the lower historical levels (Zackrisson 1977, Niklasson and Granström 2000). Considering that we only modelled productive Scots pine forests, which

according to the SNFI represent 38% of the total forest landscape in Norrbotten, we estimated that our scenarios resulted in 0.02%, 0.09% and 0.17% of the total landscape area burnt annually for *FSC*, *Burn25* and *Burn50*, respectively. These proportions are all lower than the annual burnt area during the first half of the 20th century, when prescribed burning was used on a large scale in northern Sweden, reaching 0.6% of the national forest being burnt annually in some areas (Cogos et al. 2020), indicating that there is a wide margin for greater progress.

Our results show that burning represents a possible common ground between various interests including timber production, reindeer herding and biodiversity conservation in boreal Sweden. However, many challenges remain to be addressed such as technical obstacles, lack of coordination between forest owners (Ramberg et al. 2018), burning skills vanishing in large forestry companies and the effects of burning on reindeer behaviour and movements (Cogos et al. 2021). A democratic and collaborative fire management system, from planning to implementation, should be based on a deeper understanding of human–fire relationships as has been tested in other contexts (Rodríguez et al. 2018, Eloy et al. 2019).

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