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Wildfire and prescribed burning impact moose forage availability and browsing levels in the northern boreal forest

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ABSTRACT

Fire regimes and herbivore densities have in parts of the boreal been heavily impacted by human activities with consequences for vegetation, forage supply and ungulate use. In this study, we evaluate the effects of natural wildfires and prescribed burning on moose forage availability, use, and browsing in northern Sweden. We studied three wildfire locations, adjacent controls, and five prescribed burns 12 years after fire. To compare forage availability and browsing levels we combined related variables with Principal Component Analyses and used the first axis in a regression analysis. The wildfire locations had a different composition of forage compared with the controls with less forage in the field layer and more woody browse and deciduous saplings. Forage availability was best explained by the occurrence of fire and differed between wildfire and the unburned control areas. Browsing levels were higher in wildfire locations compared with unburned controls. Prescribed burns varied substantially and could resemble both unburnt control and wildfire in terms of forage availability and browsing. We conclude that prescribed burning as a restoration action potentially can improve forage availability, particularly of deciduous species, if they mimic the impact of wildfires in terms of larger area burned and high fire severity.

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Alces alces; browsing; fire disturbance; fire suppression; Fennoscandia; Sweden; ungulate

Introduction

In many ecosystems, fire interacts with other disturbances to shape the post-fire succession (den Herder et al. 2009; Foster et al. 2016; Smith et al. 2016). Co-occurring disturbances can interact to produce distinctly different outcomes from what would be expected based on individual effects. This means that changed disturbance regimes may result in changed successional pathways and forest structure (Didham et al. 2007; Tylianakis et al. 2008; Royo et al. 2010), e.g. if fire modifies the effect of herbivores on the vegetation with higher browsing pressure on severely burned patches (Lord and Kielland 2015) or if burned locations affect the behaviour of browsers by introduced obstacles (de Chantal and Granström 2007) and/or more open habitat (Mysterud and Østbye 1999). Burned locations can produce large amounts of forage, mostly in terms of deciduous trees (den Herder et al. 2009). Fire also increase productivity and subsequently impact forage quality (Nichols et al. 2021; Amiro et al. 2000). In Alaska, moose consumed relatively more of the available forage (49%) in sites that had burned with higher severity vs. low severity (24%) (Lord and Kielland 2015). However, both fire regimes and herbivore densities have in parts of the boreal zone been heavily impacted by human activities with consequences for vegetation, forage supply and ungulate habitat use (Mönkkönen et al. 2014; Felton et al. 2020; Rodriguez et al. 2021). On the other hand, intense browsing can alter the forest structure and in the long-term affect how prone the landscape is to fire events (Kramer et al. 2003). Historically, fire has been used to favour forage availability in many ecosystems (Andersson et al. 2020) and fire suppression has in many cases degraded the habitat for wildlife (Proffitt et al. 2019; van Wagtendok 2007).

Sweden has a highly developed and efficient forest management with more than 95% of the productive forest land managed for sustained yield (Gustafsson et al. 2010; Anonymous 2015). Consequently, natural disturbances such as fire, wind throw, and insect outbreaks have been altered in their severity, frequency, and area affected (Felton et al. 2020; Berglund and Kuuluvainen 2021). Effective fire suppression has reduced the total annual area burnt in Sweden to less than 1% compared to “natural” levels (Granström 2001) and the amount of mature deciduous trees has decreased (Felton et al. 2020) due to active management to promote conifers. As a result, many species (e.g. insects (Bell et al. 2015) and birds (Bütler et al. 2004)) have decreased in abundance and distribution. In the managed landscape, the economically important Scots pine (*Pinus sylvestris*, from here on pine) and Norway spruce (*Picea abies*, from here on spruce) dominate in Fennoscandian forests of all age classes >10 years. Modern forest management (including e.g. clear-

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cutting, planting, pre-commercial thinning etc.) also affects other natural processes such as browsing by ungulates, as their foodscape becomes heavily altered. As fire generally results in the regeneration of deciduous trees (den Herder et al. 2009) and ungulates have been shown to use burned locations in North America (Brown et al. 2018) it is highly probable that burned locations in Sweden also constitute a substantial forage supply.

Fire is heterogeneous in nature and can vary largely in how it affects the boreal landscape depending on weather conditions, available fuel, local abiotic factors, etc. It can cause high tree mortality, which creates dead wood as well as opens the canopy and allow regeneration of early successional species such as aspen (*Populus tremula*), downy birch (*Betula pubescens*) and silver birch (*B. pendula*) (Zackrisson 1977). Controlled fires of forest or clear-cuts are being performed by forest owners as part of their Forest Steward Certification (FSC 2015) or by County Administrative Boards for conservation purposes. These controlled fires, hereafter prescribed burns, are for safety reasons often small and burnt with low severity. A smaller and lower severity fire causes lower tree mortality, creates less dead wood and less opportunity for early successional species (Engelmark 1999). The predominant aim of prescribed burning in Fennoscandia is to create habitats for fire-associated species (e.g. beetles), of which many are rare (Toivanen and Kotiaho 2007). However, burning is expensive and labour-demanding and if additional benefits could be achieved the method might be implemented at larger scales.

Ungulates can have substantial impacts on their ecosystem not only by affecting vegetation dynamics by selective foraging but also through trampling and nutrient redistribution by urine and faecal deposits (Kielland and Bryant 1998; Persson et al. 2000). Five cervid species inhabit Sweden: reindeer (*Rangifer tarandus*), moose (*Alces alces*), roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). In the northernmost parts of the country, only the first three may be encountered (i.e. reindeer, moose and roe deer), with moose being the main browser of woody vegetation. The number of moose in Sweden has fluctuated greatly over the last hundred years with a peak in harvest numbers of almost 180 000 moose in 1982 (corresponding to 1.1 moose/km^2 productive forest) followed by an intentional reduction in population size by intense hunting (Hörnberg 2001). The large increase in the moose population up to ca 1980 was likely due to the implementation of modern forestry practising clear-cutting followed by pine plantation. This land use change increased the available forage, especially of the number of pine (Kardell 2016). Today the moose population in Fennoscandia is managed by hunting to fulfil local and national goals of browsing damage reduction and harvest quotas (Sandström et al. 2013; Dressel 2020) and predator densities are kept low (Hörnberg 2001).

Moose usually browse in the range of 0.5–2.5 m (Nichols et al. 2015) and have been shown to prefer deciduous trees such as rowan (*Sorbus aucuparia*), aspen and willow (*Salix spp*.) over coniferous trees such as pine and spruce (Bergström and Hjeljord 1987). However, pine within browsing range is highly abundant in the landscape due to the forest management practice (Bergqvist et al. 2018). Young pine trees are also available above high snow cover in winter. In all, the high availability of pine makes it an important food source for moose, especially in winter (Bergqvist et al. 2018). However, the composition of available forage is also of great importance with high variation being beneficial for moose (Felton et al. 2020). When available moose browse a wide range of vegetation (Spitzer 2019). Higher quality forage, usually defined based on chemical composition, has been connected to larger bite diameters by moose of pine (Danell et al. 1991). Browsing causes large economical losses every year and many management actions are taken to reduce this problem, e.g. hunting of ungulates, creating alternative forage, applying wildlife-adapted forest management etc. (Dressel 2020). Nonetheless, because hunting is highly valued there is also a large incentive to keep the population density of moose high.

In this study we evaluate the effects of forest fires on ungulate forage availability and browsing levels in northern Sweden, using moose as a model species. We hypothesise that the fire (>10 years old) will lead to increased forage availability, which can attract moose from the surrounding landscape and therefore result in higher browsing levels. Due to the expected increase in the total amount of forage after burning, we do not expect an increase in browsed proportion in wildfire locations compared with unburnt controls (Bergqvist et al. 2018). We also hypothesise that due to the smaller size and lower fire severity of the prescribed burns their effects will be less pronounced than those of wildfire.

Material and methods

Study area

The study area includes three wildfire locations, three paired controls and five prescribed burns, all located in the county of Norrbotten in northern Sweden (Figure 1), ranging between 65°35′N–67°51′N and 20°24′E–22°14′E. The study area is located within the northern boreal zone (Ahti et al. 1968) and the landscape is dominated by productive forest land (40%), followed by high mountains (33%), and mires (19%). The productive forest is most commonly of pine type (59%) followed by mixed conifer type (14%) and spruce type (10%) (Anonymous 2017). The vegetation found in the field layer across all sample locations was dominated by *Ericaceae* sp. (heather family, e.g. bilberry). The number of days with snow cover during the winter before the sampling 2017/2018 was 180–200 (mean value of 11 weather stations across Norrbotten (Anonymous 2020b)). The length of the growing season is 165–170 days in northern Sweden (Anonymous 2020a). Moose and roe deer were the only ungulates present, except for semi-domesticated reindeer. The number of moose reported shot during the winter of 2017/2018 was 2.1 per 1000 ha forested land in Norrbotten with the exception of the coastal areas where it ranged up to 4 per 1000 ha forested land (calculations based on game data from Anonymous (2021)). The number of roe deer reported shoot was 0.3 per 1000 ha in the

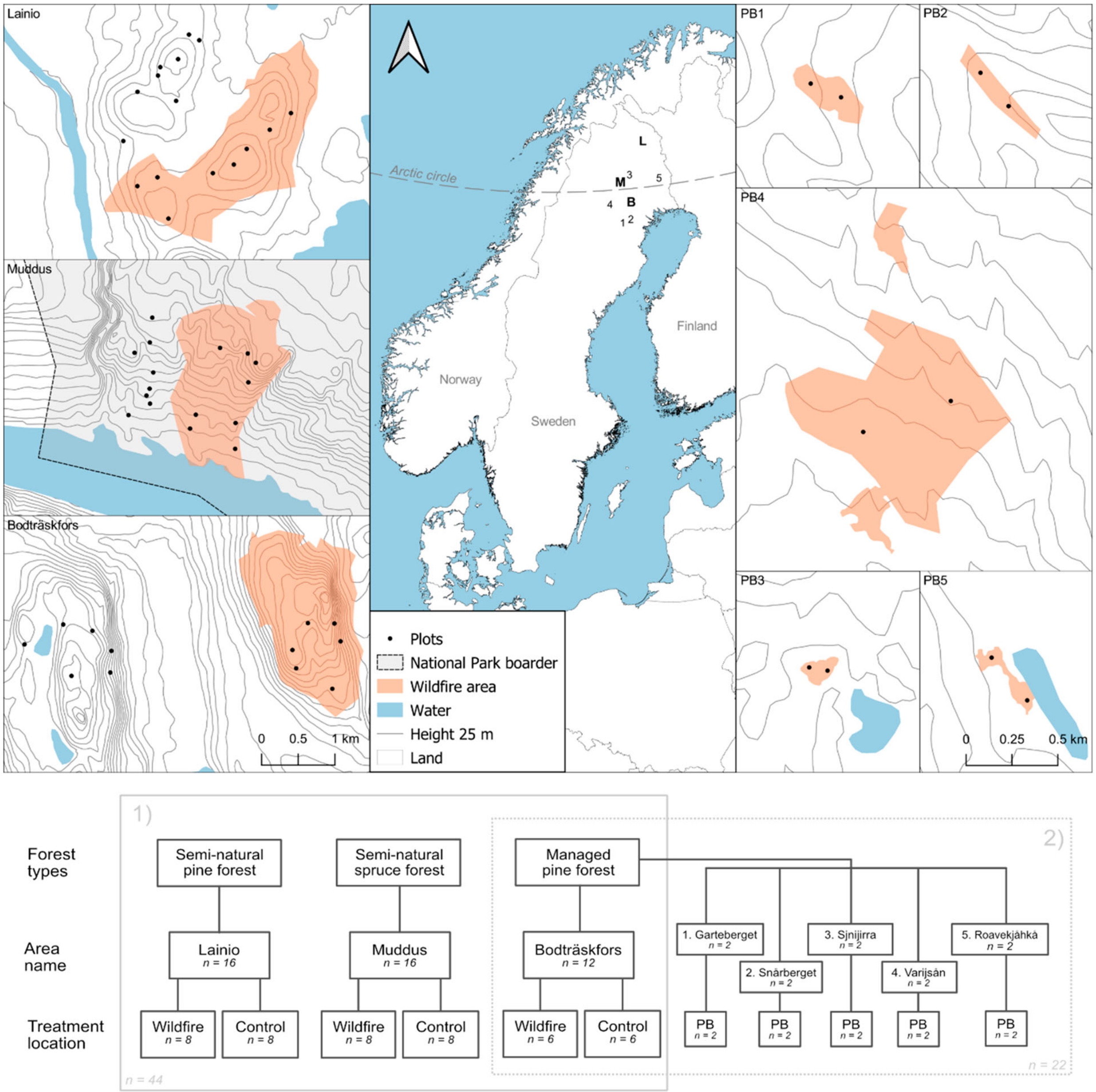

Figure 1. Study area in northernmost Sweden with three wildfire locations with adjoining unburnt controls: Lainio, Muddus and Bodträskfors, and the five prescribed burns. The five prescribed burns are denoted "PB" and numbered. Each sample plot is denoted with a circle. The contour line interval is 25 m. Below the map is a scheme of the study design (including sample sizes, n) and the separation done in the analysis with (1) combining all forest types but only the wildfire and control locations while (2) compares the locations the managed pine forest type, including all the prescribed burns.

county of Norrbotten during the same winter (Anonymous 2021). No roe deer were observed nor were pellets found during the sampling and thus all recorded browsing is assumed to be by moose.

The three wildfire locations burned during the summer of 2006 and each of them covers approximately 300 ha that is still forested and not salvaged logged. The five prescribed burns were all located in mature managed pine forests, i.e. forests that are managed for sustained yield and have been subjected to forestry measures such as selective felling or thinning. The prescribed burns varied in size from 2 to 83 ha (median 5) and were burned between 2005 and 2008 with various fire severity (details in Table 1). In this study, we only sampled forested locations and not clear-cuts. The fire in Bodträskfors was situated in a managed pine-dominated landscape and varied in severity and type across the burned area. A large proportion of the burnt area in Bodträskforshad crown fire with high tree mortality while other parts had lower severity ground fires with low tree mortality. The wildfire located within Muddus National Park has been relatively untouched by human exploitation. The burnt location in Muddus is dominated by older pine forest which mostly survived the low severity ground fire. In the northernmost wildfire location, Lainio, the forest is dominated by old spruce interspersed with old pines and silver birch. The fire in Lainio was an intense crown fire that killed almost all the trees but left the ground relatively unburnt.

Table 1. Description of sampled locations including effect of fire, location and number of sampled plots.

Area name	Size [ha]	Year burned	Latitude [WGS84]	Management History	Tree mortality, fire type	Forest type	Sampled plots [#]
Bodträskfors	300 (1800)*	2006	66.15°N, 20.82°E	Conventional management for timber	High, mixed ground and crown fire	Pine	Wildfire: 6 Control: 6
Muddus	300	2006	66.76°N, 20.16°E	National Park, selective logging, reindeer herding, haymaking	Medium, ground fire	Pine	Wildfire: 8 Control: 8
Lainio	400	2006	67.90°N, 22.16°E	Reindeer herding, clear-cut burning	High, crown fire	Spruce	Wildfire: 8 Control: 8
PB1 (Garteberget)	6	2008	65.57°N, 20.07°E	Conventional management for timber	Low, ground fire	Pine	2
PB2 (Snårberget)	5	2005	65.65°N, 20.67°E	Conventional management for timber	Low, ground fire	Pine	2
PB3 (Sjnijirra)	2	2006	66.95°N, 20.87°E	Ecopark** Leipipir	Medium, mostly ground fire	Mixed coniferous	2
PB4 (Roavekjåhkå)	83	2006	66.13°N, 19.27°E	Ecopark** Varijsån	Medium, mostly ground fire	Pine	2
PB5 (Haisujärvi)	3	2006	66.76°N, 23.03°E	Conventional management for timber	High, mostly crown fire	Pine	2

"*" Total area of the wildfire in parenthesis, however most was salvaged logged so sampling was only done within the remaining 300 ha of forest. "**"Ecoparks are large areas where nature conservation actions and timber production management are combined by the state-owned forest company Sveaskog.

Sampling design

In late spring 2018 (May 30 to June 6) we sampled 11 locations: three wildfires with adjoining unburnt controls, and five prescribed burns (Figure 1). The sampling was performed at the beginning of the seasonal green-up (directly as the leaves were budding) and the seasonal development of the cover and height of the vegetation was comparable between locations because of the limited time for the sampling and the fact that we started the sampling from the south and moving north. We made the assumption that the temporal vegetation increase during summer would be homogenous at the different locations. We sampled 6–8 circular plots within each location of wildfire and control. In each prescribed burn we had 2 sample plots so that all five prescribed burns had a similar sampling effort as one wildfire/control location. The plots were randomly positioned either along a transect or scattered (depending on topographical field limitations), however never closer than 100 m to any other plot (Figure 1). Each plot consisted of a 10 m (large plot) and a 3.5 m (small plot) radius sampling area with the same centre point. Within the large plot, we recorded fresh moose pellet groups (>20 pellets) laying on top of the fallen litter from the previous autumn. This represented an index of use by moose during the winter before sampling (Månsson et al. 2007). Environmental variables, which may have been altered by fire, were also measured in the large plot. These included cover of bare ground (soil, bedrock, gravel, or other non-vegetative ground layers), dead wood amount (numbers of logs and snags >10 cm in basal diameter; 0 = none, 1 = low (1–3 logs and snags), 2 = medium (4–10 logs and snags), 3 = high (>10 logs and snags)), canopy cover (%). Additionally, the cover and height of two different vegetation layers were recorded as follows: canopy (>4 m) and field layer (0–0.3 m).

In the smaller plot, we recorded more detailed variables related to forage and browsing. We defined forage availability as the combined forage (both woody and non-woody vegetation) within the browsing range of moose (<2.5 m, (Nichols et al. 2015)). We measured the cover of tree sapling species within feeding height, as well as cover and height of bilberry (*Vaccinium myrtillus*), fireweed (*Chamaenerion angustifolium*), and raspberry (*Rubus idaeus*). Raspberry was found in only one location and was not included in the analysis. At the most detailed level, we collected data on all tree saplings within the small plot, including species, height, the total number of side shoots, presence of top-shoot browsing, number of browsed side shoots and bite diameter of browsed top and/or side shoots. Additionally, an overall "browsing degree" for each tree sapling was determined from a scale from 0 to 3 to assess the total browsing impact (0 = none; no visible browsing, 1 = low; a low number of browsed side shoot with no visible reduction of vitality, 2 = affected; a high number of browsed side shoots and/or top shoot browsing with visible reduction of vitality, e.g. yellowing needles, 3 = deadly; as "affected" but also with very few branches with green leaves/needles).

In total, we measured 1611 individual tree saplings in the small plots of seven different tree species (pine, spruce, silver birch, downy birch, rowan, aspen, and willow). When the numbers of seedlings were high (>50 per plot) and evenly distributed we only sampled half of the plot area for time-conserving reasons and then multiplied the data on the saplings by 2. This was done on a total of 10 out of the 54 sampling plots. Norway spruce saplings were recorded 132 times, but because this species is rarely browsed by moose (Cederlund et al. 1980) the data were excluded from the analyses (except for species richness).

Statistical analysis

We divided the analysis into two parts: (1) the three wildfire locations together with adjoining controls (including all three forest types) and (2) the locations within only the managed pine forest type, i.e. the five prescribed burns together with the wildfire and control in Bodträskfors (Figure 1). This division was done due to the large differences in management history and forest types between the wildfire locations, hence we only compared the prescribed burns to the most similar wildfire in terms of forest composition, age, and productivity (from here on called managed pine forest). However, we also wanted to access general patterns after wildfires across the different forest types. All tests were performed in RStudio version 1.3.1093 (R Core Team 2019). Effects were considered significant if a *p*-value was lower than 0.05 but full *p*-values are reported in tables and text.

Proportional consumption (or browsed proportion) was calculated as the number of browsed side shoots divided by the total number of side shoots per sapling and then averaged over species and plot. The total consumption was calculated as the sum of all browsed side shoots per species and plot. All measured broad-leaved saplings (aspen, willow, rowan, downy birch and silver birch) were pooled into the category of deciduous saplings. Shannon index was calculated using the function "diversity" in the package vegan based on the composition of all sapling species (including spruce) at the plot level. Species richness equalled the number of sapling species, also at the plot level. Top shoot browsing (including both old and new) is a binary variable on the sapling individual level but a proportion when averaging over the plot level, ranging from 0 to 1. To compare the wildfire, control, and prescribed burn, while considering the differences in sampling efforts, we calculated a moose index as the total number of pellet groups per treatment divided by number of sampled plots (n). To test differences of individual variables between treatments we used Kruskal–Wallis test, followed by Wilcox pairwise comparison with Bonferroni corrections for multiple testing.

To estimate the forage composition and browsing level we performed Principal Component Analyses (PCA), using the function "prcomp" (base function). Before performing the PCAs we excluded highly related variables (>0.7) that were identified with a correlation matrix. However, variables with high correlation without any methodological connection (e.g. moose pellets and the total number of deciduous side shoots) were not excluded. Redundancy between variables is not generally a problem in PCAs so removing correlated variables in this analysis was rather done to simplify the output. See supplementary material for the correlation matrix of all variables (forage: Table S1, browsing: Table S2). Four separate PCAs were used to evaluate forage availability and browsing levels separately for (1) all forest types (wildfire and control) and (2) Bodträskfors (wildfire, control, and prescribed burns) (Figure 1). The matrix dimensions of the PCAs were 9 columns of forage variables or 8 columns of browsing level variables against 44 rows of samples when comparing all forest types or 22 rows of samples when comparing only the managed pine forest type. We then used the first axis of the PCA as a response variable in generalised linear mixed models (GLMMs) to evaluate the forage availability and browsing level represented by this combined variable.

Differences in latitude and altitude were not significant in the ordination and did not affect the patterns presented in the PCAs for either forage availability or browsing levels and were therefore not included in the analyses. The minimum value of the response variable (PCA axis one) was added to all data points of the response variables in order to shift the latter to only positive values. Thereafter a log-transformed version was tested to see if it would improve model fit (only used in the managed forests forage model). We used mixed linear models with the function "lme" or generalised linear mixed models with the function "glmer" from the package lme4 (Bates et al. 2015) with a Gamma distribution. All models included the variable "area" as a random effect. To test for between-group significant effects the "summary" function was used. To find the best fitting model we first used the variable "treatment", then we applied forward selection of significant environmental variables and/or interactions in the models. The final models had the lowest AIC value and were checked for no model assumption violations. Pseudo r^2 was then calculated using the approach of Nakagawa et al. (2017).

Results

In total, we sampled 1611 tree saplings in 54 plots within the 11 locations. The wildfires had lower canopy cover, higher amounts of dead wood and more bare ground than either prescribed burns or unburnt control sites, although to varying degrees within the wildfire locations (Table 2). The cover and height of the field layer varied between sampling plots both within and across locations, but height was generally lower in the burnt locations compared with unburnt. Wildfire locations had higher sapling species richness compared with the control across all locations, while the prescribed burns were intermediate to control and wildfire within the managed pine forest. However, sapling species richness varied greatly between the treatments (Table 2).

Forage availability

The PCA ordination diagram of variables representing forage availability showed a separation between wildfire and control (Figure 2). For all forest types (Figure 2a) the first and second axis together explained 65% of the variation with axis 1 contributing to 43%. The variables contributing the most to axis 1 were species richness (22%), diversity index (18%), number of deciduous saplings (18%) and number of deciduous side shoots (17%). The model response variable displayed a separation between the forage variables related to the field layer to the left and to woody browse and deciduous saplings abundance to the right (Figure 2). The pattern was very similar when analysing only the managed pine forest including prescribed burns (Figure 2b). The prescribed burns showed high variation and their forage availability overlapped with the unburned control as well as the wildfire. The first and second axis together explained 65% of the variation with axis 1 contributing to 45%. The variables contributing the most to axis 1 were sapling species richness (20%), diversity index (18%) and the number of deciduous side shoots (17%). See Table 2 as well as supplementary material for the differences between treatments of each individual variable (Figure S1).

Forage availability in terms of woody browse and deciduous saplings was higher in the wildfire locations than in the controls ($\chi^2 = 8.7471$, $P = 0.003$, Figure 3a). When considering individual variables of forage availability, the wildfire

Table 2. Overview of environmental, forage availability and browsing level variables under different treatments across all forest types, as well as within the managed pine forest, included in the analysis.

		All forest types		Managed pine forest		
	Variable	Control	Wildfire	Control	Prescribed burns	Wildfire
Env.	Canopy cover [%]	30 ± 13^{a}	12 ± 16^{b}	45 ± 17^{a}	20 ± 10^{b}	1 ± 2^{c}
	Dead wood [0-3]	1.2 ± 0.6^{a}	2.5 ± 0.9^{b}	1.2 ± 0.8^{a}	1.7 ± 0.8^{a}	2.8 ± 0.4^{b}
	Bare ground [%]	5 ± 11^{a}	14 ± 22^{a}	0 ± 1^{a}	3 ± 3^{b}	24 ± 29^{c}
Forage availability	Field cover [%]	73 ± 16^{a}	51 ± 28^{b}	85 ± 12^{a}	56 ± 32^{a}	38 ± 31^{a}
	Field height [m]	0.20 ± 0.05^{a}	0.14 ± 0.05^{b}	0.25 ± 0.05^{a}	0.26 ± 0.23^{ab}	0.16 ± 0.05^{b}
	Pine shoots [#]	14 ± 24^{a}	123 ± 239^{b}	0 ± 0^{a}	56 ± 101^{ab}	198 ± 151^{b}
	Deciduous shoots [#]	174 ± 259^{a}	287 ± 330^{a}	17 ± 23^{a}	91 ± 179^{a}	621 ± 325^{b}
	Bilberry cover [%]	34 ± 28^{a}	18 ± 22^{b}	71 ± 30^{a}	24 ± 20^{b}	21 ± 30^{ab}
	Species richness [#]	1.6 ± 0.7^{a}	3.0 ± 1.9^{b}	1.3 ± 0.5^{a}	2.3 ± 1.6^{a}	4.8 ± 1.3^{b}
	Shannon index	0.33 ± 0.34^{a}	0.66 ± 0.57^{b}	0.21 ± 0.33^{a}	0.44 ± 0.53^{a}	1.25 ± 0.29^{b}
	Pine saplings [#]	12.1 ± 33.9^{a}	6.4 ± 13.7^{a}	1.5 ± 3.7^{a}	16.1 ± 44.4^{a}	6.5 ± 4.9^{a}
	Deciduous saplings [#]	7.1 ± 12.3^{a}	25.2 ± 39.1^{a}	1.7 ± 1.6^{a}	20.2 ± 47.7^{ab}	36.5 ± 37.9^{b}
Browsing level	Moose index	0.08 ± 0.15^{a}	0.34 ± 0.68^{a}	0.22 ± 0.23^{ab}	0.04 ± 0.10^{a}	1.06 ± 1.04^{b}
	Browsing degree [0-3]	0.5 ± 0.8^{a}	0.5 ± 0.5^{a}	1.0 ± 1.2^{ab}	0.2 ± 0.3^{a}	0.8 ± 0.2^{b}
	Browsed pine shoots [#]	1 ± 2^{a}	10 ± 22^{a}	0 ± 0^{a}	1 ± 3^{a}	25 ± 32^{b}
	Proportion browsed pine shoots	0.04 ± 0.10^{a}	0.04 ± 0.07^{a}	0 ± 0^{a}	0.005 ± 0.016^{a}	0.13 ± 0.09^{b}
	Proportion browsed pine top shoots	0.20 ± 0.36^{a}	0.17 ± 0.27^{a}	0 ± 0^{a}	0 ± 0^{a}	0.45 ± 0.33^{b}
	Browsed deciduous shoots [#]	3 ± 5^{a}	35 ± 56^{b}	6 ± 8^{ab}	3 ± 4^{a}	71 ± 63^{b}
	Proportion browsed deciduous shoots	0.07 ± 0.16^{a}	0.10 ± 0.13^{b}	0.21 ± 0.27^{a}	0.05 ± 0.10^{a}	0.10 ± 0.07^{a}
	Bite diameter of *Betula* spp. shoots [mm]	0.4 ± 0.6^{a}	0.7 ± 0.8^{a}	0.3 ± 0.4^{ab}	0.3 ± 0.5^{a}	1.6 ± 0.9^{b}

Notes: Numbers displayed are means ± standard deviation. Kruskal-Wallis and pairwise Wilcox test with Bonferroni correction to test significances. Different letters (a, b, c) between treatments indicate significant differences ($P < 0.05$).

locations had higher numbers of deciduous saplings ($\chi^2 = 7.2153$, $P = 0.027$), but lower available amounts of forage in the field layer such as bilberry cover ($\chi^2 = 8.1308$, $P = 0.004$) compared to the controls. Wildfire was significant compared to the control in both models (i.e. intercept, Table 3). However, the prescribed burn was not significant in either model when compared to the control (Table 3). None of the explanatory variables; canopy cover, bare ground cover or amount of dead wood, significantly improved the model and were not included in the final model.

Pellet group distribution

We recorded a total of 63 pellet groups. The difference in moose index was not significant ($\chi^2 = 1.6676$, $P = 0.197$) between wildfire and control. However, within the managed forest significantly more pellet groups were found in wildfire compared with prescribed burning ($\chi^2 = 9.4932$, $P = 0.009$). Moose index was one of the variables included in the browsing PCA and corresponded most closely to the wildfire plots (Figure 4).

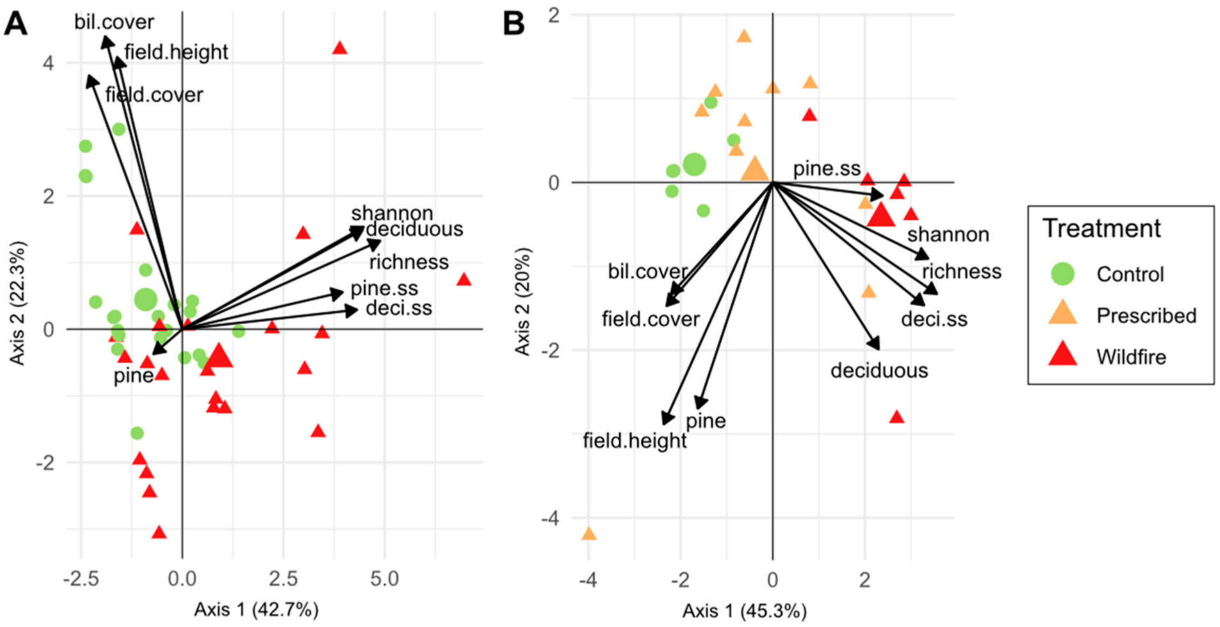

Figure 2. PCA visualising the forage availability in all forest types (A) and in the managed pine forest including the prescribed burns (B). Large symbols indicate the centre of the plots of each treatment. Circles (green) are control plots, triangles are burned plots, where orange are prescribed burns and red are wildfires. Variable name interpretations: "field.cover" = average field cover, "field.height" = average field height, "pine.ss" = total number of pine side shoots, "deci.ss" = total number of deciduous side shoots, "bil.cover" = average bilberry cover, "richness" = number of tree sapling species, "shannon" = Shannon index, "pine" = total number of pine saplings, and "deciduous" = total number of deciduous saplings.

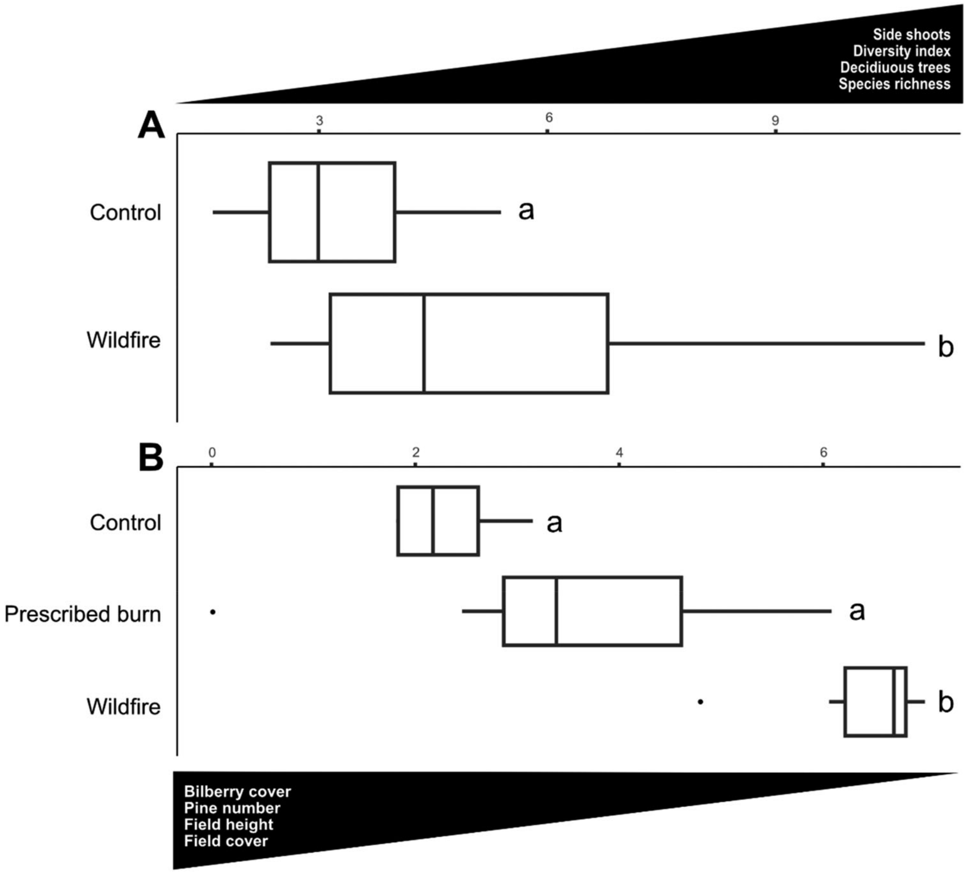

Figure 3. Forage availability measured as values of axis 1 from the PCA in all forest types (A) and in the managed pine forest (B). Significance is represented by the letters next to the boxes representing each treatment ($\alpha < 0.05$). The *y*-axis represents the forage availability from the PCA factor loadings as two black triangle shapes outside the boxplots. The top triangle include the variables that increase to the right in the plots (e.g. the amount of side shoots) and the bottom triangle the variables that increase to the left in the plots (e.g. bilberry cover). The two black triangles apply to both subplots A and B. The factor loadings presented correspond to variables in the PCA analyses and plots in Figure 2a and b. The variables have been scaled to be positive.

Browsing level

The controls and wildfire locations showed large variations and overlap when comparing browsing level variables across all forest types in the PCA ordination diagram (Figure 4a). The difference was less pronounced in the spruce forest and semi-natural pine forest compared to the managed pine forest (Figure 4). Most of the included variables indicated increased browsing levels to the right in the ordination (along axis 1) except for browsing degree and proportion browsed of deciduous shoots in the managed pine forest (Figure 4b). For all forest types (Figure 4a) the first and second axis together explained 64% of the variation with axis 1 contributing to 44%. The variables contributing the most to axis 1 were moose index (20%), side shoot browsing on pine (20%) and bite diameter of browsed pine top shoots (18%). When comparing the variables representing browsing level in the managed pine forest the control and wildfire separated in the ordination, while prescribed burning was negatively correlated to the browsing variables (located in the bottom left of Figure 4b). The first and second axes together explained 78% of the variation with axis 1 contributing to 54%. The variables contributing the most to axis 1 were moose index

Table 3. Model outputs for the fixed effect explanatory variables of the four mixed models with "area" as random factor and the corresponding PCA axis as response variable.

	Forage availability						Browsing level					
	All forest types			Managed pine forest			All forest types			Managed pine forest		
Explanatory variables	Value	*t*-value	*p*-value	Value	*t*-value	*p*-value	Estimate	*t*-value	Pr(>|z|)	Value	*t*-value	*p*-value
Intercept (Control)	1.95	46.31	**<0.001**	2.30	1.44	0.170	0.36	9.56	**<0.001**	3.21	6.40	**<0.001**
Wildfire	0.21	3.54	**0.001**	4.05	8.08	**<0.001**	−0.01	−0.38	0.704	3.54	4.99	**<0.001**
Prescribed burn	x	x	x	1.31	0.74	0.498	x	x	x	−0.38	−0.60	0.581
Forage	x	x	x	x	x	x	−0.02	−5.24	**<0.001**	-	-	-
Canopy cover	-	-	-	-	-	-	-	-	-	-	-	-
Bare ground cover	-	-	-	-	-	-	-	-	-	-	-	-
Dead wood amount	-	-	-	-	-	-	-	-	-	-	-	-
Pseudo r^2	Conditional: 0.226 Marginal: 0.226			Conditional: 0.824 Marginal: 0.370			Conditional: 0.041 Marginal: 0.028			Conditional: 0.665 Marginal: 0.665		

"-" for explanatory variables removed during the model selection process and "x" for data not available in the model.

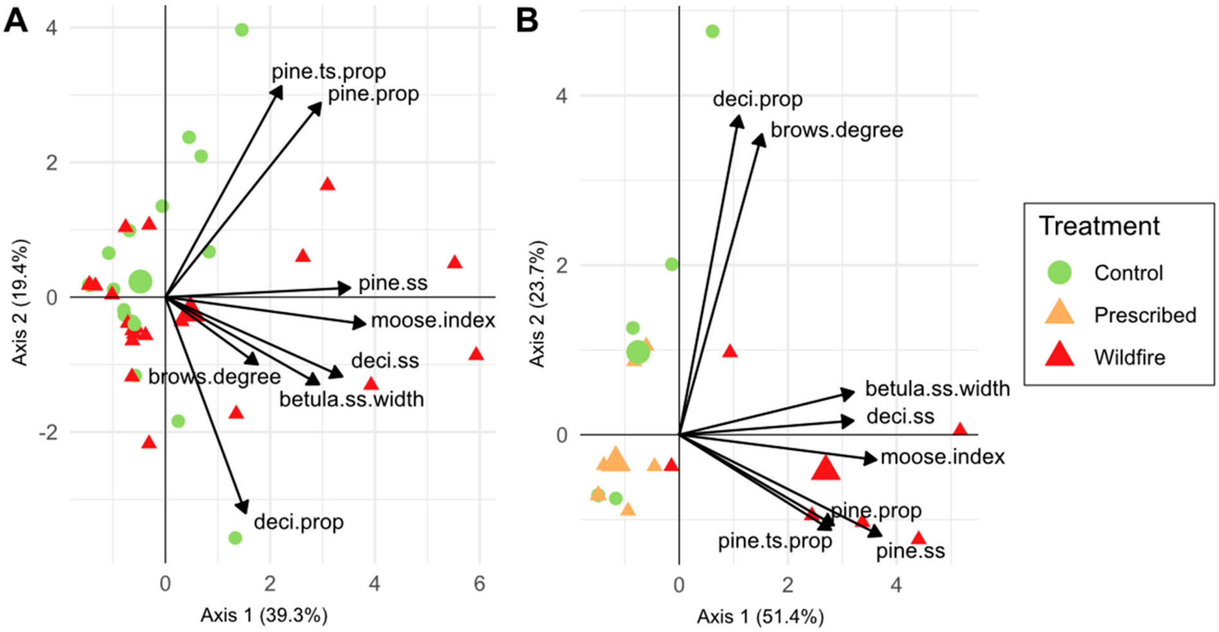

Figure 4. PCA visualising the browsing level variables in all forest types (A) and in the managed pine forest including the prescribed burns (B). Large symbols indicate the centre of the plots of each treatment. Circles (green) are control plots, triangles are burned plots where orange are prescribed burns and red are wildfires. Variable name interpretations: "moose.index" = number of pellet groups, "brows.degree" = average browsing degree (from 0 to 3), "pine.ss" = total number of browsed side shoots of pine, "pine.prop" = proportion of browsed pine side shoots, "pine.ts.prop" = proportion of top shoot browsing on pine, "deci.ss" = total number of browsed side shoots of all deciduous saplings, "deci.prop" = proportion of browsed deciduous side shoots, and "betula.ss.width" = average diameter of browsed side shoots of birch.

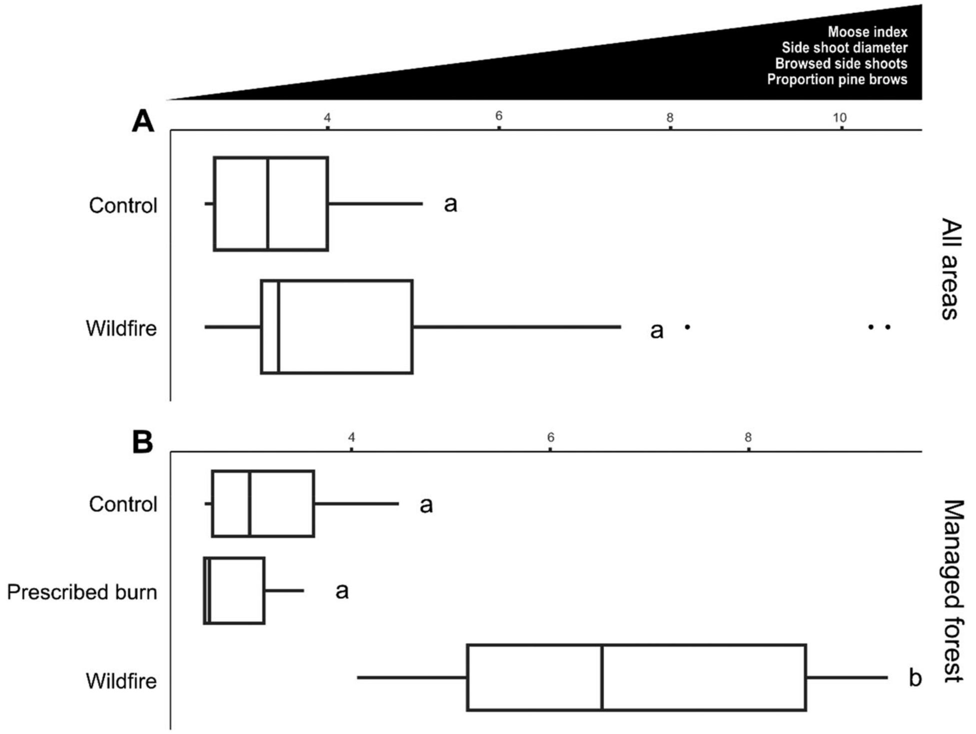

Figure 5. Browsing level measured as values of axis 1 from PCA in all forest types (A) and in the managed pine forest (B). Significance is represented by the letters next to the boxes representing each treatment ($\alpha < 0.05$). The *y*-axis represents browsing level from the PCA factor loadings as a black triangle shape outside the boxplots. The triangle include the variables that increase to the right in the plots, in this case all variables. The triangle applies to both subplots A and B. The factor loadings presented correspond to variables in the PCA analyses and plots in Figure 4a and b. The variables have been scaled to be positive.

(19%), proportion of browsed pine side shoots (19%) and bite diameter of pine top shoots (16%). See Table 2 as well as supplementary material for the differences between treatments of each individual variable (Figure S2).

We found that browsing levels were generally higher in the wildfire locations (Table 3). In the managed pine forest forage availability significantly explained the variation in browsing, while wildfire and/or prescribed burn (treatment) were not significant in the best model (Table 3). There was a much larger effect from the wildfire on the browsing level in the managed pine forest than when we pooled and compare all forest types (Figure 5). None of the explanatory variables; canopy cover, bare ground cover or dead wood amount, significantly improved the model and were not included in the final model.

Discussion

To the best of our knowledge, this is the first study to investigate the effects of wildfires and prescribed burning specifically in a region with more than 100 years of fire suppression, such as in Fennoscandia. The fact that we have three equal-aged replicates of wildfire and perform the study at high latitudes means that we can contribute to a generalised knowledge of fire effects in a region that will be seriously affected by climate change that in turn has a high probability to impact the fire regime (de Groot et al. 2013). Prescribed burning is today used as a conservation tool to mitigate negative effects on biodiversity due to fire suppression in Fennoscandia, hence previous studies on fire effects in these landscapes mainly focus on dead wood associated biodiversity and only few (Hekkala 2015; den Herder et al. 2009) consider deciduous regeneration. Here we focus on the forage availability, i.e. amount and composition, and evaluate the use of burned locations by a large cervid, moose. In accordance with our hypothesis, our analyses showed more available forage, as well as higher browsing levels in the wildfire locations.

Fire changes forage availability

Our results show that especially wildfire, but to some extent also prescribed burning, alters both the composition and amount of available forage 12 years post-burn. This available forage is being used by moose, which is shown by the higher browsing levels in the burned areas. The changes in forage availability are in accordance with previous studies on wildfires (Ruokolainen and Salo 2006) and slash-burning (Ruokolainen and Salo 2009), at similar latitudes and timeframes. We assumed from previous research that the burnt areas had increased productivity and therefore larger bite diameters would be seen (Danell et al. 1991). Bite diameter was slightly larger in the burnt areas, especially in the managed pine forest, but not significantly. It did however contribute to a large degree to the PCA axis variation in terms of browsing levels. Variation in fire severity has been shown to correlate with differing seasonal use of areas following burns in north America (Brown et al. 2018) where moose selected low severity locations in winter and high severity locations, with large amounts of understory, in summer. However, additional studies on other latitudes and at different points in the succession after a fire are needed to access the whole picture of the post-fire forage availability and browsing.

In our study, it was mainly the wildfire that impacted both the amount and diversity of forage. The prescribed burns displayed a high variability of impact and were generally less altered by fire resulting in higher similarity to the unburnt controls. Forest fire severity (leading to the opening of the canopy through tree mortality) is closely linked to subsequent vegetation composition (Schimmel and Granstrom 1996) and the higher severity of the wildfires could be one explanation for the observed effects. In this study, the models in the managed pine forest explained the variation to a much higher extent (pseudo r^2) than when including all forest types (even with "area" as a random effect). This indicates that a large portion of the unexplained variation regarding how fire affects browsing levels and forage availability is impacted by the local forest structures and conditions. This was expected since tree species composition and stand structure, as well as age and level of management/naturalness, differed between the wildfire locations. The managed pine forest constituted a more productive landscape compared with the other wildfire locations.In addition, the fact that the managed pine forest had burned with higher intensity and large parts of the area experienced high mortality contributed to higher levels of regeneration and growth of available forage. Large fire events have been rare in Fennoscandia during the past century making replication of wildfire areas rarely available (Niklasson and Granström 2000). Here we show that wildfire and to some extent prescribed burns have a large potential to produce forage for ungulates.

Ungulate use and browsing levels

We show that moose use and browse in burned locations more than 10 years after a fire if browse is available, suggesting that burning *per se* may not be of major importance but that moose effectively find and use locations with high forage availability. However, the fact that treatment was included in all the best models suggests that fire improves forage availability and that burned locations are attractive and used by moose. Previous studies show that moose and other ungulates may alter their movement patterns and habitat use in response to factors like forage availability (Senft et al. 1987; Månsson et al. 2007), shelter (Dussault et al. 2004), snow cover (Pfeffer et al. 2021) and predation risk (Hernández and Laundré 2005; Ditmer et al. 2018). Fire can affect these features and create more available forage, less shelter as protection against unfavourable weather conditions, higher visibility for predators (Hernández and Laundré 2005), and physical obstacles in terms of large amounts of logs (de Chantal and Granström 2007). Structural changes like amounts of dead wood and canopy cover (Kane et al. 2013) are good indirect measures of fire severity and here we found significantly more dead wood and lower canopy cover in burned areas.

The pellet group counts indicated a higher usage by moose of wildfires compared to other treatments, despite structural modifications like more habitat openness and large amounts of potential obstacles like dead wood. Other studies have shown that moose index as well as forage availability may be connected to browsing levels (Månsson et al. 2007). Despite the relatively small sample size and high variation between locations, this was a clear pattern in the managed pine forest with an average of 6 times more pellet groups in the wildfire compared with the control and prescribed burns. The managed pine forest wildfire was a high severity burn with large amounts of dead wood and open canopy, which could be expected to reduce to which extent moose use the location. However, the higher availability of forage combined with higher species richness of forage plants was probably more important and led to the observed high use. This is in accordance with e.g. Milligan and Koricheva (2013) who showed that higher species richness of saplings increases browsing. The evident browsing by moose in the wildfire locations in this study also indicates that fire has produced favourable environments that is used for forage to a larger extent than in the nearby unburnt forest.

Comparing wildfire to prescribed burn

The effects of prescribed burning have been shown to have positive impacts on a range of different organism groups such as pyrophilous and saproxylic insects (Koivula and Vanha-Majamaa 2020) as well as plant species richness (Eales et al. 2018). However, the effects and effectiveness as a restoration action vary significantly between species ranging from positive to negative (Eales et al. 2018; Koivula and Vanha-Majamaa 2020). An overall lack of long-term studies beyond pyrophilous insects has been identified (Eales et al. 2018). In this study we found that the prescribed burns were more similar to controls than wildfire locations a decade after burning, both considering forage availability and browsing levels. The prescribed burns were generally small in size and characterised by low severity ground fires with low tree mortality, which contribute to the similarities with the unburned locations. However, prescribed burns resembled wildfire more in terms of field cover, canopy cover, species richness and the number of deciduous saplings, than they did control locations. The relatively small sample size of prescribed burns in this study was due to a general lack of available locations burned in close proximity to the wildfires, both in time and space. In contrast to the natural randomness of wildfires, prescribed burns are part of biodiversity management performed by certified forest owners on productive land and personnel from county administrative boards in protected areas. The five sampled prescribed burns in this study were performed by a forest company as part of their FSC certification (Anonymous 1998). Thus, all prescribed burns in this study were situated in managed forest with similar stand characteristics as the study plots in the Bodträskfors wildfire and the analyses were adapted accordingly. However, because most of the forest land is managed for sustained yield, we consider these prescribed burns representative of northern Sweden. Available forage in the relatively small, prescribed burns could potentially be more affected by the surrounding stands than is the case in the larger wildfire area. The larger area of the wildfire also contributes to a larger total amount of available forage and could thus be expected to be more attractive to moose, which is also shown in our results.

Fire as a tool to create alternative forage

The overarching aim of prescribed burning is to mimic the natural disturbance of wildfires, provide habitat for fire-associated species and maintain ecosystem resilience (Granström 2001; Nilsson 2005; Cogos et al. 2020). Our results suggest that a prescribed burning does not necessarily increase forage availability, i.e. amount and composition, or impact browsing levels by ungulates in the same way as a wildfire. One reason could be that the prescribed burns are smaller (median value of 5 ha in this study) with proportionally more edge effect from neighbouring older, shading forests, thus providing less forage in total, which may in turn reduce the attraction level for browsers (WallisDeVries et al. 1999). The sizes of wildfires in Sweden differ substantially but are mostly small due to effective fire suppression (Engelmark 1984; Niklasson and Granström 2000; Pinto et al. 2020). However, naturally large wildfires (as in this study at least 300 ha) burned at higher severity than the prescribed burns, which cause a cascade of changes, such as reduced canopy cover and field layer. These changes in turn can increase the forage availability and use of the location for foraging (Milligan and Koricheva 2013).

There are other management options that can increase deciduous browse for moose, e.g. saving saplings during pre-commercial thinning in even-aged managed stands, or increasing the deciduous buffer zones along water bodies. This study shows that prescribed burning has the potential to contribute to high forage availability, but this requires that the prescribed burns provide good conditions for deciduous regeneration i.e. released competition and lower canopy cover due to tree mortality and reduction of the field layer that opens up for seeds to germinate. Our results show high levels of browsing in the wildfire locations but not in prescribed burns pointing out the large variation and complexity of mimicking fire disturbance through prescribed burning. We did not investigate if high levels of browsing in the wildfire locations are also followed by a reduction of browsing elsewhere outside of the study areas. An important follow-up would be to measure the forage availability and browsing levels in young commercial pine stands near wildfires and prescribed burns to test the hypothesis that fire would reduce damage by diverting browsing to the burnt locations.

Conclusion

This study shows that a decade after a fire the amount and diversity of forage are high in locations burned by wildfire, while prescribed burning only had moderate effects on the amounts and diversity of forage. Thus, to impact the forage resource at the landscape scale it is more effective with larger scale fires of higher severity, than small scale prescribed burns. There was large variation within prescribed burns where they could resemble both unburned and wildfire locations in terms of forage availability and browsing levels, suggesting that prescribed burning could be a potential tool for generating forage and promoting the regeneration of deciduous species. We conclude that (1) large-sized wildfires in the boreal forest create long-term attractive and highly used forage resources for moose, and (2) prescribed burning can be used to improve forage availability, particularly of deciduous species, and biodiversity, especially if they mimic the impact of wildfires in terms of large area burned and high fire severity.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

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