



## Salvage logging of mountain birch after geometrid outbreaks: Ecological context determines management outcomes



Ole Petter Laksforsmo Vindstad<sup>a,\*</sup>, Jane Uhd Jepsen<sup>b</sup>, Moritz Klinghardt<sup>a,b,c</sup>, Malin Ek<sup>a</sup>, Rolf Anker Ims<sup>a</sup>

<sup>a</sup> University of Tromsø, Department of Arctic and Marine Biology, Dramsveien 201, 9037 Tromsø, Norway

<sup>b</sup> Norwegian Institute for Nature Research, Fram Centre, N-9296 Tromsø, Norway

<sup>c</sup> University of Oldenburg, Institute for Biology and Environmental Sciences, D-26111 Oldenburg, Germany<sup>†</sup>

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### ABSTRACT

Outbreaks of pest insects occasionally cause mortality of entire forest stands. Salvage logging of affected stands is the most common management response to such events. Logging may aid stand recovery by increasing the production and establishment of saplings, or stimulating the production of basal sprouts in sprouting tree species. However, the outcome of logging may depend on the ecological context in which it is implemented, with both herbivory and local growing conditions being potentially important factors. We conducted a field experiment to assess how logging affects recovery by saplings and sprouts in stands of mountain birch that have been damaged by outbreaks of geometrid moths. The study was conducted at the two locations Luftjok and Bugøyfjord in subarctic Norway, where moth outbreaks have caused widespread mortality of mountain birch during the last two decades. Logging generally caused a strong increase in the production of basal sprouts, and also improved sprout growth in Luftjok, resulting in a substantial production of new stems in the logging plots at this location within the six-year period of the study. In Bugøyfjord, sprout growth was retarded in logging plots compared to controls, resulting in complete failure to produce new stems during the study period. This appears to have been caused by ungulate browsing, possibly in interaction with regional, geologically determined, gradients in growing conditions. The outcome of logging also depended on local site quality, with limited sprouting occurring in rich meadow type stands, which traditionally have been assumed to have low capacity for sprout production. Birch saplings were less abundant in logging plots than in controls by the end of the study, especially in Bugøyfjord, suggesting that logging did not improve sapling production. We conclude that logging may stimulate damaged mountain birch stands to recover by means of basal sprouting, but that the positive effects of logging may be reduced by browsing in some areas. Logging should also be practiced with care in rich meadow type stands, which have limited capacity for sprouting.

### 1. Introduction

Outbreaks of defoliating or wood-boring insects dominate the natural disturbance regime in many forest ecosystems (Barbosa et al., 2012). Outbreaks can cause stand-wide mortality, and thereby produce rapid transitions in ecosystem state at the landscape level (Karlsen et al., 2013; Pureswaran et al., 2015). The spatial extent and impact of outbreaks is currently increasing in boreal and subarctic ecosystems due to climate-driven range expansions and human-assisted invasions of pest insects (Weed et al., 2013; Lovett et al., 2016). This is a growing concern from the perspective of both conservation and the ecosystem

services provided by forests (Schowalter, 2012).

Apart from allowing the forest to recover naturally, the most common management response to stand-killing outbreaks is salvage logging of affected stands (Dale et al., 2001; Dhar et al., 2016). Logging can aid the recovery of the tree layer by increasing the establishment and growth of saplings. This may come about because more light reaches the forest floor after logging, and because logging-induced disturbance may expose mineral soil that is favorable for sapling establishment (Collins et al., 2011; Collins et al., 2012). Logging may also increase the production and growth of basal sprouts in trees species that are capable of this type of vegetative regeneration (Bond and Midgley,

\* Corresponding author at: Department of Arctic and Marine Biology, University of Tromsø – The Arctic University of Norway, Dramsveien 201, N-9037 Tromsø, Norway.

E-mail addresses: [ole.p.vindstad@uit.no](mailto:ole.p.vindstad@uit.no) (O.P.L. Vindstad), [jane.jepsen@nina.no](mailto:jane.jepsen@nina.no) (J.U. Jepsen), [moritz.klinghardt@uni-oldenburg.de](mailto:moritz.klinghardt@uni-oldenburg.de) (M. Klinghardt), [malin.ek@uit.no](mailto:malin.ek@uit.no) (M. Ek), [rolf.ims@uit.no](mailto:rolf.ims@uit.no) (R.A. Ims).

<sup>†</sup> Current address.

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2001; Klimesová and Klimeš, 2007). Increased sprouting may occur because removal of dead stems activates dormant basal buds and frees up nutrients from the root system (Luostarinen and Kauppi, 2005). While logging has the potential to aid regeneration of the tree layer, it may also have negative impacts on biodiversity and forest resilience (Dhar et al., 2016; Thorn et al., 2017). It is therefore essential that decisions to implement logging are based upon solid empirical evidence for the expected benefits.

The mountain birch (*Betula pubescens* var. *pumila* L.) forest of northern Fennoscandia is a well-known example of a forest ecosystem that has experienced increasing disturbance from insect outbreaks in recent decades. Cyclic outbreaks of the defoliating geometrid (Lepidoptera: Geometridae) moth *Epirrita autumnata* Bkh. (autumnal moth) occur naturally in this region (Tenow, 1972), but climate warming has recently facilitated the expansion of more southern geometrids into areas historically occupied only by *E. autumnata* (Jepsen et al., 2008; Jepsen et al., 2011). This has resulted in increased defoliation pressure on mountain birch in many areas. Ten thousand km<sup>2</sup> of mountain birch forest was defoliated in northern Fennoscandia during 2000–2008 (Jepsen et al., 2009b), resulting in extensive mortality of birch forest in parts of the region. Another outbreak cycle of unknown spatial extent affected many of the same areas from 2013 and onwards (Klemola et al., 2016).

As a response to climate-driven changes in moth outbreak activity, local stakeholders in northern Norway have discussed, and to some extent promoted, salvage logging of damaged mountain birch stands, as a means of recovering firewood and speeding up regeneration of the tree layer. Logging is expected to induce more vigorous basal sprouting when dead stems associated with living root systems are removed. Logging may also protect the basal sprouts from rot that develops in standing dead stems and spreads down into the root system (Lehtonen and Heikkinen, 1995). In addition, a positive effect of logging on the establishment and growth of saplings cannot be ruled out. Empirical evidence for these potential benefits is currently lacking, however, and field tests are needed to confirm that logging will produce the expected results.

The outcome of logging in mountain birch forest is likely to be modified by two key environmental context factors, namely local growing conditions and herbivory. The mountain birch is a highly plastic species, and its growth form is linked to the quality of the local soil (Verwijst, 1988). Trees growing on poor soils tend to be polycormic (multi-stemmed) and usually produce stems of low stature and diameter. Trees on richer soils are more likely to be monocormic (single-stemmed) and tend to produce larger stems. Polycormic birches have high capacity for vegetative regeneration by production of basal sprouts, while the monocormic growth form has traditionally been assumed to regenerate mainly from seeds. The effects of logging in terms of sprout production may therefore be largest in polycormic stands.

With respect to herbivory, large mammalian herbivores in the form of moose (*Alces alces* Gray) and semi-domestic reindeer (*Rangifer tarandus* L.) are abundant across much of northern Fennoscandia, and impose strong limitation on the growth and survival of woody plants in the region (Van Bogaert et al., 2009; Speed et al., 2011; Ravolainen et al., 2014). Browsing by reindeer has also been shown to reduce survival of mountain birch saplings (Lehtonen and Heikkinen, 1995; den Herder and Niemela, 2003; Kumpula et al., 2011). In addition, Biuw et al. (2014) found that basal sprouts were almost absent in plots experiencing year-round grazing by reindeer in Finland, while sprouts were abundant in only summer-grazed plots on the Norwegian side of the border. This suggests that the intensity and/or seasonality of reindeer browsing has substantial impacts on the survival of basal sprouts in mountain birch, and raises the possibility that the effect of salvage logging may interact with herbivory.

In the present paper, we report from a field experiment that was established to test the effects of logging on the recovery of mountain birch stands via basal sprouts and saplings after mortality caused by a

moth outbreak. After experimental logging, we monitor the development of key state-variables related to stand recovery – namely the number of basal sprouts and saplings, the length of the sprouts, and their recruitment into new stems – over a period of five consecutive years. We also monitor the presence of vertebrate herbivores in our experimental plots, and assess their impact on post-logging recovery dynamics by recording browsing marks on basal sprouts. To assess the importance of the ecological context in which the logging is implemented, we replicate the experiment in two separate geographic locations that differ in terms of geology and herbivore activity, and stratify our design according to local growing conditions within locations.

## 2. Materials and methods

### 2.1. Study system

The study was conducted in the Varanger region (70°N, 29°E) in the eastern part of Finnmark County, northeast Norway. Varanger is situated in a transition zone between northern-boreal deciduous forest and low-arctic tundra, where discontinuous stands composed almost entirely of mountain birch constitute the forest-tundra ecotone. Rowan (*Sorbus aucuparia* L.) and clonal stands of aspen (*Populus tremuloides* Michx.) also occur patchily. The climate of the region is sub-oceanic, with mean temperatures of 12.5 °C for July and –11.6 °C for January (1971–2000 normal period for Rustefjelbma meteorological station 70°23'55"N, 28°11'36"E). Annual precipitation is 400–500 mm.

Outbreaks by geometrid moths are the main natural disturbance factor in the north-Fennoscandia mountain birch forest (Tenow, 1972; Jepsen et al., 2009b). Outbreaks occur roughly every ten years, but vary greatly in amplitude and spatial extent. During the period 2002–2008, the Varanger region was affected by an unusually severe and prolonged outbreak, involving both the native *E. autumnata* and the recently invasive *Operophtera brumata* L. (winter moth). This resulted in historically unprecedented damage to the mountain birch forest throughout much of the region, with the stem mortality rate exceeding 95% in some areas. Further details about this outbreak are given in Jepsen et al. (2009b) and Jepsen et al. (2013).

### 2.2. Study design

Our field experiment was conducted at the two locations Luftjok (70°15'N, 28°21'E) and Bugøyfjord (69°53'N, 29°20'E). The forest at both sites was severely damaged during the 2002–2008 outbreak, but the timing of defoliation differed somewhat between the two sites. Judging from satellite-derived time series of changes in the normalized difference vegetation index (Jepsen et al., 2009a), Luftjok was defoliated mainly in 2003, 2005 and 2006, while Bugøyfjord was defoliated mainly in 2006–2008 (Appendix 1, Fig. S1). The two locations also differ substantially in geology. Luftjok is located on sedimentary bedrock composed of shale, sandstone and limestone, and has a well-developed soil layer. The bedrock in Bugøyfjord is metamorphic and composed mainly of gneiss, with a less developed soil layer (<http://geo.ngu.no/kart/berggrunn/>). This means that Luftjok has richer soil conditions and is more favorable for the growth of vegetation than Bugøyfjord.

During August of 2011, we laid out 20 experimental plots of 30 × 30 m at both Luftjok and Bugøyfjord. All plots had a minimum of 20 birch trees, and were located in forest with a high proportion of mature stems. This is representative for the age structure of the forest both within our two study locations and for the outbreak area as a whole. Half of the plots within each location were located in forest that was expected to have poor growing conditions (i.e. low site productivity) for the location in question (hereafter “poor forest”), while the other half was located in more favorable conditions (hereafter “rich forest”). The distinction between rich and poor plots was based on the

local knowledge of personnel from the regional forest authority, and qualitative assessments of the composition of the field layer vegetation and the structure of the tree layer, as observed when selecting the plots. Because the rich-poor contrast is likely to encompass both variation in soil quality and other unknown factors affecting local growing conditions, we hereafter refer to this contrast by the general term “site quality”. Because the overall soil conditions differ between Luftjok and Bugøyfjord, the distinction between rich and poor forest should only be viewed as a relative contrast within locations. The distance between poor and rich plots within locations was about 2 km. Within each site quality category, the plots were organized into five pairs. One plot in each pair was randomly selected for logging treatment, while the other was designated as an untreated control. The distance between the treatment and control plots within pairs varied according to local topography, but was never more than 60 m.

Studies of stand structure and regeneration in mountain birch are challenging because the distinction between polycormic individuals is not always clear and because basal sprouts gradually develop into new stems. We defined a “tree” as any cluster of stems that had no detectable root connections to other clusters nearby. A “basal sprout” was defined as any sprout less than 1.3 m tall that protruded from the base of a standing tree or the stump of a fallen or logged tree. Any sprout or stem more than 1.3 m tall was defined as a “stem”. Thus, basal sprouts were reclassified as stems once they reached a height of 1.3 m. Small birches that were less than 1.3 m tall and not associated with an existing root system were defined as “saplings”.

Before applying the logging treatment, we selected 20 birch trees in each experimental plot for detailed measurements. This was done by dividing the diagonals of each plot into 3-m intervals and selecting the tree that was closest to each interval. These trees were permanently marked with a numbered metal tag at the base of one of their stems. We only selected trees that were more than 2 m tall, and which had a living root system, as inferred from the presence of living basal sprouts or stems. To provide a measure of forest structure at the outset of the experiment, the total number of stems (living and dead) in each tree were counted, and the diameter of the three thickest stems were measured at breast height (1.3 m). All living basal sprouts in the trees were also counted, and classified as browsed or unbrowsed by herbivores. Browsing was said to have occurred when the tip of a sprout or the tip of one of its branches had been bitten off. Although the identity of the herbivore cannot be easily established from browsing marks, we expect most of the browsing in the present study to have been caused by reindeer, moose, small rodents (*Arvicolidae* spp.), hare (*Lepus timidus* L.) and willow ptarmigan (*Lagopus lagopus* L.).

In conjunction with the selection of experimental trees in August 2011, we also assessed the presence of saplings, signs of activity by mammalian herbivores and the state of the field layer vegetation in the plots. These measurements were conducted along linear transects laid out along the two diagonals of each plot. Along each transect, we counted the number of saplings, the number of groups of herbivore droppings and the number of rodent runways in a 2-m wide corridor. Saplings were classified into the three height categories < 0.2 m, 0.2–0.5 m and 0.5–1.3 m. Droppings were classified as belonging to either moose or reindeer/sheep. Droppings of reindeer and sheep are difficult to distinguish in the field, and were therefore lumped into a single category. Based on observations of animals in the study region, most of these droppings were probably left by reindeer.

The composition of the vegetation community along the diagonal transects was quantified using the point-intercept method (Bråthen and Hagberg, 2004). We used a triangular aluminum frame with 40 cm long sides and a pin in each corner. The triangle was lowered down into the vegetation, with one of its sides parallel to the transect, and the number of hits between the pins and living plant parts were recorded. Beginning in the center of the plot, where the two diagonals crossed, the triangle was placed every 3 m along the diagonals until 5 samples had been obtained in all 4 directions, yielding a total of 10 replicate samples

along each diagonal. The plant species that were recorded represent all species and groups that are considered to be functionally important in the study region. An overview of these species is given in Table S1 in the appendix.

After the initial conditions in the experimental plots had been established, the plots designated for treatment were logged in September of 2011. The logging was conducted manually, using a handheld chainsaw. All stems were cut as close to the base of the trees as possible, resulting in removal of most of the larger basal sprouts that were present before the treatment. Some stems in the rich plots in Luftjok were cut roughly half a meter above ground due to a misunderstanding when establishing the experiment, but this appeared to have little effect on the subsequent basal sprouting. Felled stems were manually removed from the plots immediately after logging, except in the rich plots in Luftjok, where the stems could not be removed before August 2012 owing to logistic constraints.

In August of 2012–2016, the plots were revisited and the states of the experimental trees was surveyed. For each tree, we recorded the number of browsed and unbrowsed living basal sprouts and the number of dead and living stems. To provide a measure of the growth of the sprout population, we also measured the length of the five tallest sprouts within each tree to the closest cm. During the annual visits, we also recorded the presence of saplings and signs of herbivores along the diagonals of the plots, as described above.

### 2.3. Statistical analysis

We used generalized linear mixed models for analyzing our data. These models were implemented with the `glmer` and `glmer.nb` functions in the `lme4` library (Bates et al., 2015) in R version 3.2.1 (R Development Core Team, 2015).

Our response variables fall into two main categories. The first are key state variables related to the recovery of the tree layer, for which we are interested in estimating a response to the logging treatment (hereafter “recovery” variables). These variables are counts and heights of basal sprouts, and counts of living stems and saplings. The second category are ecological context variables, which describe the environment of our experimental sites, and are therefore important for interpreting the outcome of the logging treatment (hereafter “context” variables). These variables are the presence and impact of herbivores, as judged from counts of droppings, rodent runways and browsing marks on sprouts, and the quality of our experimental sites as judged from the structure of the field layer vegetation and the tree layer at the outset of the experiment.

For the analysis of the recovery variables, the sprout counts were expressed as the number of sprouts per tree, while the stem counts were expressed as the number of stems per plot, owing to stem counts of zero for most trees in the logging plots in many years. Counts of saplings were also expressed as the number of saplings per plot. Counts from the three sapling height categories were modelled as separate response variables. The length of the basal sprouts was expressed as the mean length of the sprouts within trees (see further details below). All of our count variables displayed highly aggregated distributions and were therefore modelled with a negative binomial error distribution. The length of the sprouts was modelled with a gamma error distribution.

For all of the recovery variables, the goal of the analysis was to provide statistical estimates of how the effect of the logging treatment developed throughout the course of the study period, depending on site quality. We therefore applied the same design-based fixed-effect model structure to all recovery response variables, taking the variables *logging* (logged or control), *site quality* (rich or poor), *year* and their three-way interaction as categorical predictors. Since many of the response variables showed non-linear temporal trends, year was taken as a categorical variable. Because Luftjok and Bugøyfjord differed substantially with respect to our ecological context variables (Sections 3.1 and 3.2) and may also differ in other unknown but ecologically important

respects, separate models were fitted for the two locations. Since models with a complicated interaction structure produce complex parameter estimates, we focused on model predictions for interpretation of the models. Parameter estimates for all models are presented in appendix Table S2–S7.

The production and growth of basal sprouts in mountain birch can be highly vigorous and show substantial year-to-year dynamics after removal of the main stems (Hynynen et al., 2009). We therefore applied all years with available measurements in the models for the number of sprouts (measurements in 2011–2016) and the length of sprouts (measurements in 2012–2016). The model for the number of stems included only 2013–2016, since no new stems were produced in the logging plots before 2013. Birch saplings grow more slowly than basal sprouts, and the temporal dynamics of saplings was therefore considered to be adequately modelled by contrasting the start- and end-points of our time series (i.e. 2011 and 2016).

The identity of the experimental plots was taken as a random effect in all models, to account for random plot-level variability and statistical dependencies between trees within plots. The identity of trees, nested within plots, was also tried as a random effect in the model for sprout length, to account for non-independence between sprouts within trees. However, this resulted in convergence failure of the model-fitting algorithm. Tree was therefore rejected as a random effect. Consequently, to avoid pseudo-replication within trees for the model of sprout length, we used the mean length of the sprouts within each tree as the response variable for this model.

Temporal autocorrelation can be a problem when conducting repeated measurements on the same sampling units. In order to detect potential autocorrelation problems in our models, we plotted the yearly residuals for each sampling unit at the lowest level in our sampling hierarchy (i.e. trees or plots). Since obvious temporal trends in the residuals were not present for the great majority of sampling units, it is unlikely that temporal autocorrelation between years caused significant bias in our models.

For the herbivore related context variables, we aimed to show how the presence and impact of herbivores in our experimental plots varied throughout the study period, depending on site quality and logging treatment. Hence, we employed the same fixed and random effect mixed model structure as described for the recovery variables above. The proportion of browsed sprouts per tree was modelled as a response variable with a binomial error distribution, while the count of rodent runways per plot was modelled with a negative binomial error distribution. The years 2013 and 2014 could not be modelled for rodents due to a strong preponderance of zero counts. We therefore summarized these years as the median runway count per plot. Our counts of ungulate droppings provided very sparse data, which was not suitable for statistical modelling. To provide an indication of the presence of ungulates on the plot-level throughout the study period, we summed the counts for reindeer/sheep in each plot across 2011–2016. These data were subsequently summarized as means for each combination of location, site quality and logging treatment. The data for moose was even sparser, and was therefore expressed as the sum of counts across all plots and years within each combination of location, site quality and treatment.

Modelling results suggested that browsing pressure was unevenly distributed between logging plots and controls. To test whether this affected the growth of the sprouts after logging, we computed the difference in overall browsing rate and mean sprout length between the logging plot and control for each replicate pair in the design (logging minus control). The difference in sprout length was subsequently regressed on the difference in browsing in a conventional linear model. The regression was weighted for the number of trees with sprouts in each pair of plots. The analysis provides a test for whether preferential browsing by herbivores in logging plots or controls affects the distribution of sprout heights between the treatments. More direct tests of browsing effects on sprout growth were not possible, because browsing

marks inflicted in the current year are not distinguishable from browsing marks from earlier years. Thus, recorded browsing rates will tend to accumulate over time, as new browsing marks are added and old ones remain visible. Consequently, the recorded browsing rate in a given year may bear little relation to the actual rate of browsing in that year.

Because the distinction between rich and poor forest was based on qualitative characterizations of our experimental plots, we also took analytical steps to establish the biological significance of the site quality contrast. To identify plant species that were characteristic of rich and poor plots prior to the onset of the experiment in 2011, we performed an indicator species analysis (Dufrene and Legendre, 1997) using the summed plant counts at the level of the experimental plot as the replicate. We also conducted a non-metric multidimensional scaling (NMDS) for each location, again using the experimental plot as the replicate. The NMDS was based on Bray-Curtis distances, computed on the Hellinger transformed vegetation counts (Legendre and Gallagher, 2001). A three-dimensional solution for the NMDS resulted in a substantial reduction in stress compared to a two dimensional alternative for both Luftjok and Bugøyfjord, and was therefore adopted for both locations. A permutational multivariate analysis of variance was fitted to the Bray-Curtis distance matrices to test for significant differences in the composition of the vegetation community between poor and rich forest within each location. The indicator species analysis was implemented using the `indval` function in the `labdsv` library in R, while NMDS and permutational ANOVA were implemented using the `metaMDS` and `adonis` functions in the `vegan` library (Oksanen et al., 2016).

Finally, we tested for differences in the structure of the tree layer between rich and poor forest. This was done by fitting mixed models with the number of stems per tree (negative binomial error distribution) and the mean diameter of the stems within trees (gamma error distribution) in 2011 as response variables, and site quality as a fixed categorical predictor. Plot was taken as a random effect.

### 3. Results

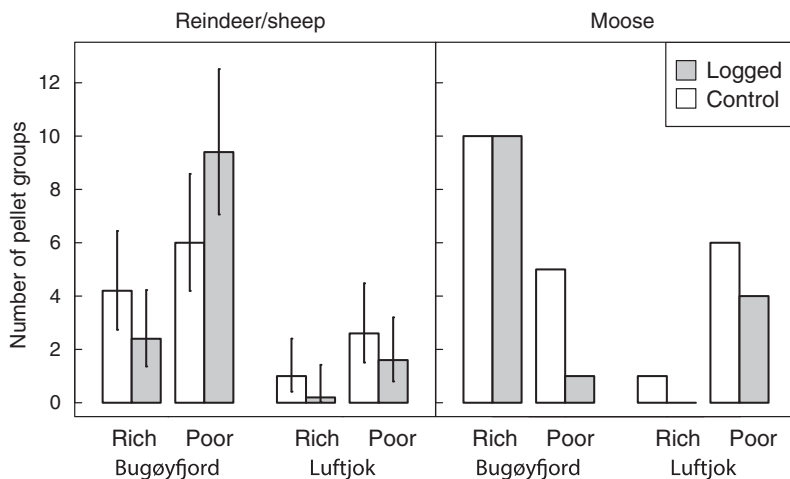
#### 3.1. Context variables: vegetation community and forest structure depending on site quality

The state of the vegetation in 2011 clearly demonstrated a biological distinction between rich and poor plots in both Luftjok and Bugøyfjord. There was no overlap between rich and poor plots in the NMDS for Luftjok (Fig. S2), and the permutational ANOVA showed that the rich-poor contrast produced a statistically significant difference in the composition of the vegetation community at this location ( $P = 0.001$ ). The NMDS for Bugøyfjord showed some overlap between rich and poor plots, but the site quality contrast was still highly significant according to the permutational ANOVA ( $P = 0.002$ ).

According to the indicator species analysis (Table S8), various species of cryptogams, grasses and large forbs were significant indicators for the rich plots in Luftjok, while various dwarf shrubs, mosses, lichens and the small forb *Chamaepericlymenum suecicum* (L.) were indicators for the poor plots. This shows that the rich plots represent a meadow type birch forest, which only occurs on very favorable soils, while the poor plots are more characteristic of a heath forest type, which occurs on poorer soils (Karlsen et al., 2005). The grass *Avenella flexuosa* (L.) and the small forb *Linnaea borealis* (L.) were indicators for the rich plots in Bugøyfjord, while various dwarf shrubs were indicators for the poor plots. This indicates the presence of a quality gradient between rich and poor plots also in Bugøyfjord. However, the notable absence of cryptogams and large forbs as indicators in Bugøyfjord emphasizes the generally poor growing conditions of this location, and suggests that both the rich and poor plots in Bugøyfjord are best described as heath type birch forest.

A gradient in site quality between rich and poor plots was also





**Fig. 1.** Sum of pellet counts throughout the study period for reindeer/sheep and moose in logging and control plots in rich and poor forest in Luftjok and Bugøyfjord. The bars for reindeer/sheep represent the mean count per experimental plot across 2011–2016. Error bars denote 95% confidence intervals of the means. The bars for moose represent the sum of counts across plots within each combination of location, site quality and logging treatment across 2011–2016.

reflected in the structure of the tree layer at both locations. Trees in the rich plots in Luftjok had fewer stems of greater diameter than trees in the poor plots (Table S9), as expected from a contrast in soil quality. Both of these differences were statistically significant (Table S10). Rich and poor plots in Bugøyfjord showed similar differences, although in this case the difference in the number of stems was not statistically significant. The diameter of stems in both rich and poor plots in Luftjok was higher than in the corresponding plot types in Bugøyfjord, probably reflecting the overall higher site quality in Luftjok.

### 3.2. Context variables: presence and impact of herbivores

Accumulated pellet counts throughout the study period suggested that the presence of ungulate herbivores in the form of moose and reindeer/sheep was substantially higher in Bugøyfjord than in Luftjok (Fig. 1). Within locations, there appeared to be some tendency for reindeer/sheep to prefer the poor forest, while moose showed no consistent pattern in this respect. None of the herbivores showed consistently higher pellet counts in logging plots or controls.

Our counts of rodent runways reflected the cyclic dynamics that characterize rodent populations in the study region (Ims et al., 2011) (Fig. 2 and Table S2). A large peak in the runway count was apparent at all sites in 2011, while a smaller peak followed in 2015. The runway counts in the first year after these peaks probably represent mainly old runways from the peak year (personal observation by the authors). The peak years were interspersed with a deep trough in 2013 and 2014, when hardly any runways were observed. The runway counts were generally similar for control and logging plots throughout the study period in both Luftjok and Bugøyfjord. However, there was a tendency for lower counts in poor than in rich plots in Bugøyfjord during the second peak.

The proportion of browsed sprouts per tree generally increased throughout the study period, as might be expected from accumulated browsing on the same sprouts over time (Fig. 3 and Table S3). In Luftjok, the browsing pressure was lower in the logging plots than in the controls from 2011 to 2014, especially in poor forest. This difference disappeared in 2015 and 2016, when nearly all sprouts in Luftjok showed signs of browsing. In Bugøyfjord, the effect of logging on browsing pressure was reversed compared to Luftjok. Almost all sprouts in the logging plots in Bugøyfjord showed signs of browsing from 2013 and onwards, while the predicted browsing rate in the controls was only about 0.4 up to and including 2014. After this, the rates of browsing in the controls rose to levels that were relatively similar to the logging plots.

### 3.3. Recovery variables: effects of logging on basal sprouting

As expected, the logging treatment had a strong and rapid impact on the production of basal sprouts in both rich and poor forest at both Luftjok and Bugøyfjord. The predicted number of sprouts per tree more than doubled from 2011 (pre-logging) to 2012 at all sites (Fig. 4 and Table S4). This was followed by a further increase in 2013. At this point, the predicted number of sprouts per tree was roughly four times higher than in 2011 at all sites. Meanwhile, the number of sprouts in the control plots remained relatively stable. The number of sprouts in the logging plots gradually declined after 2013, but the rate of this decline depended on site quality. By 2016, the predicted number of sprouts in the rich plots at both Luftjok and Bugøyfjord had declined to a level that was not much higher than that of the control plots and the pre-logging state in 2011. Meanwhile, the number of sprouts in the poor plots still retained a clear contrast to the pre-logging state and the controls in 2016.

Site quality also had a strong effect on the absolute number of sprouts produced in Luftjok (Fig. 4 and Table S4). Even in the peak year of 2013, the predicted number of sprouts per tree in the rich logging plots barely attained the same level as the control plots in the poor forest. A similar effect of site quality was not observed in Bugøyfjord, where the absolute number of sprouts was largely comparable between rich and poor plots.

The height of the basal sprouts generally showed an increasing trend throughout the study period, but the strength and direction of the effect of logging was highly dependent on location and site quality (Fig. 5 and Table S5). In the rich plots in Luftjok, the logging had a strong positive effect on sprout growth, so that the predicted length of the sprouts was about 30 cm longer in the logging plots than in the controls by 2016. There were also indications of a positive effect of logging in the poor plots, although in this case the difference in predicted sprout length between controls and logging plots was only about 5 cm in 2016. The smaller effect of logging in poor forest stemmed mainly from an increasing trend in sprout length in the control plots that was not observed in rich forest. The plots in Bugøyfjord displayed a reversal of the logging effect, with the predicted length of sprouts being 5–10 cm shorter in logging plots than controls throughout the study period in both rich and poor forest. A linear model showed that the difference in sprout length between logging plots and controls was statistically related to the difference in browsing rate between the treatments (Fig. 6). The negative relationship implies that sprouts tended to be shorter in logging plots than controls when the browsing rate in the logging plots exceeded that of the controls. This relationship was driven by elevated browsing rates and retarded sprout growth in logging plots in Bugøyfjord, and a reversal of this pattern in Luftjok. The absolute length of the sprouts also showed a conspicuous difference

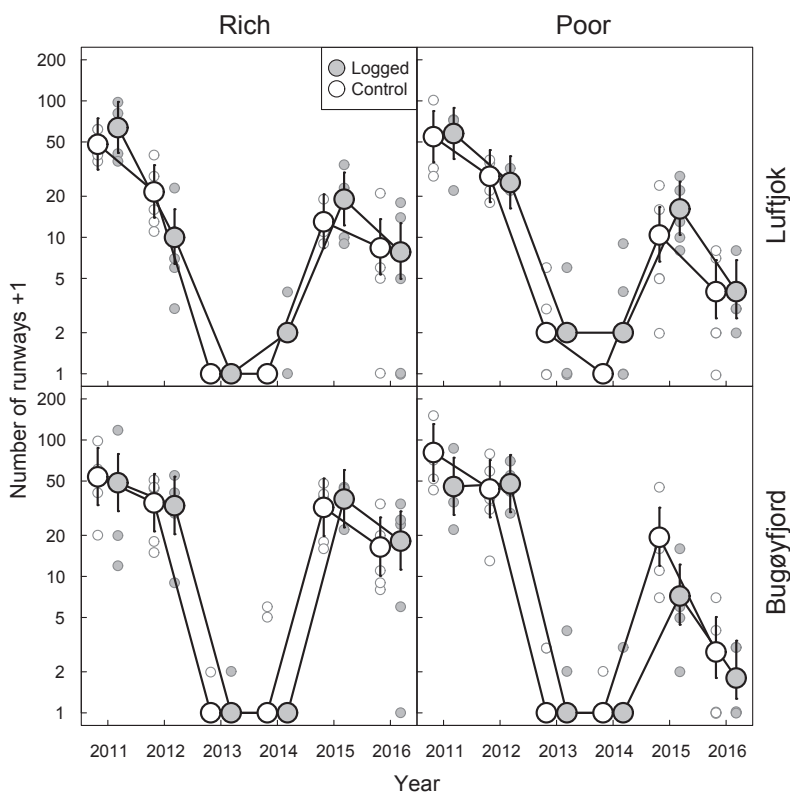


Fig. 2. Temporal dynamics in the number of rodent runways per plot throughout the study period in logging and control plots for rich and poor forest in Luftjok and Bugøyfjord. Large symbols represent predictions from mixed models taking the number of runways per plot as the response variable and logging, site quality, year and their interactions as fixed predictors. Error bars denote 95% confidence intervals for the predictions. Small symbols represent the number of runways for each experimental plot. Counts for 2013 and 2014 could not be modelled due to mostly zero counts. These years are therefore summarized by the median runway count per plot.

between Luftjok and Bugøyfjord, with the predicted length of sprouts in logging plots in 2016 being about 80 cm in Luftjok and only about 45 cm in Bugøyfjord (Fig. 5).

The retarded growth of the basal sprouts in Bugøyfjord was also evident in the production of new stems (sprouts > 1.3 m) at this location. By 2016, no new stems had been produced in the logging plots

in Bugøyfjord. Meanwhile, the logging plots in Luftjok had started to produce new stems already by 2013 (Fig. 7 and Table S6). The predicted number of stems in rich logging plots in Luftjok remained more or less stable at around five stems per plot throughout the study period, or none of the logging plots in rich forest had stem counts that were comparable to the control plots by 2016. The predicted number of

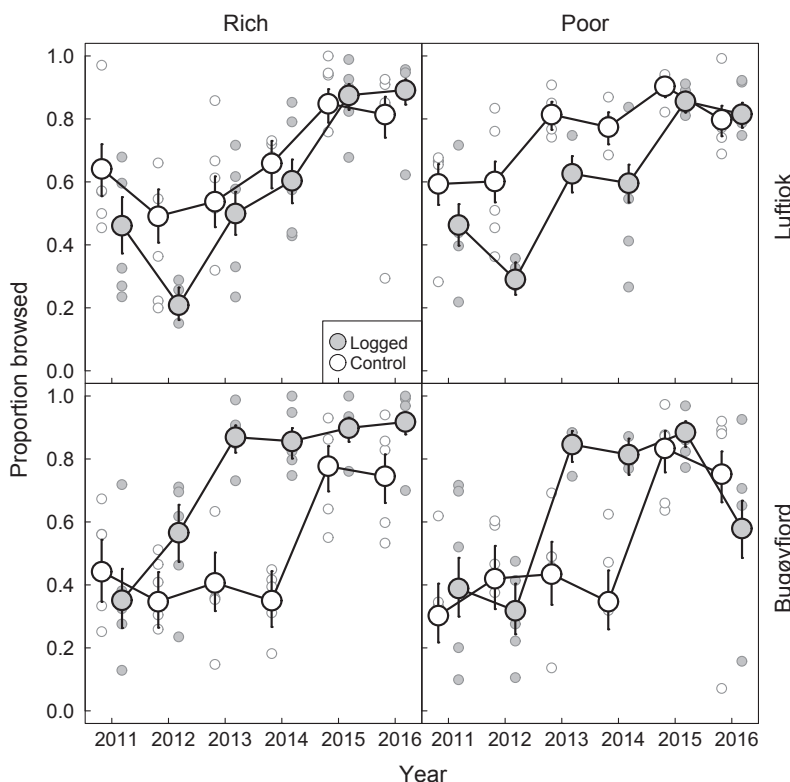


Fig. 3. Temporal development in the proportion of browsed basal sprouts per tree throughout the study period in logging and control plots for rich and poor forest in Luftjok and Bugøyfjord. Large symbols represent predictions from mixed models taking the proportion of browsed sprouts per tree as the response variable and logging, site quality, year and their interactions as fixed predictors. Error bars denote 95% confidence intervals for the predictions. Small symbols represent the overall proportion of browsed sprouts for each experimental plot. Proportions of browsed sprouts for individual trees are not shown in order to avoid cluttering of the plots.

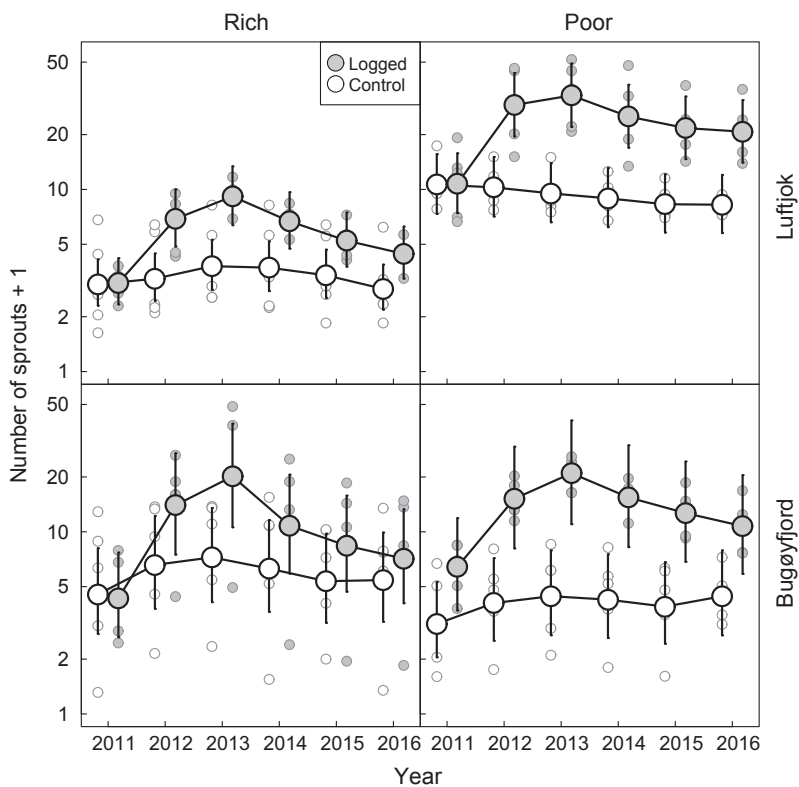


Fig. 4. Temporal development in the number of basal sprouts per tree throughout the study period in logging and control plots for rich and poor forest in Luftjok and Bugøyfjord. Large symbols represent predictions from mixed models taking the number of sprouts per tree as the response variable and logging, site quality, year and their interactions as fixed predictors. Error bars denote 95% confidence intervals for the predictions. Small symbols represent the mean number of sprouts per tree for each experimental plot. Sprout counts for individual trees are not shown in order to avoid cluttering of the plots.

stems in the logging plots in poor forest in Luftjok showed an increasing trend from 2013 to 2015, but seemed to stabilize at around 10 stems per plot in 2016. At this point, the number of stems in the most productive logging plots was approaching the number of living stems in some of the control plots.

3.4. Recovery variables: effects of logging on sapling production

The predicted number of saplings per plot generally increased from 2011 to 2016 for all sapling height categories (Fig. 8 and Table S7). By 2016, the predicted number of saplings was typically lower in logging plots than in controls. This pattern was especially clear in Bugøyfjord,

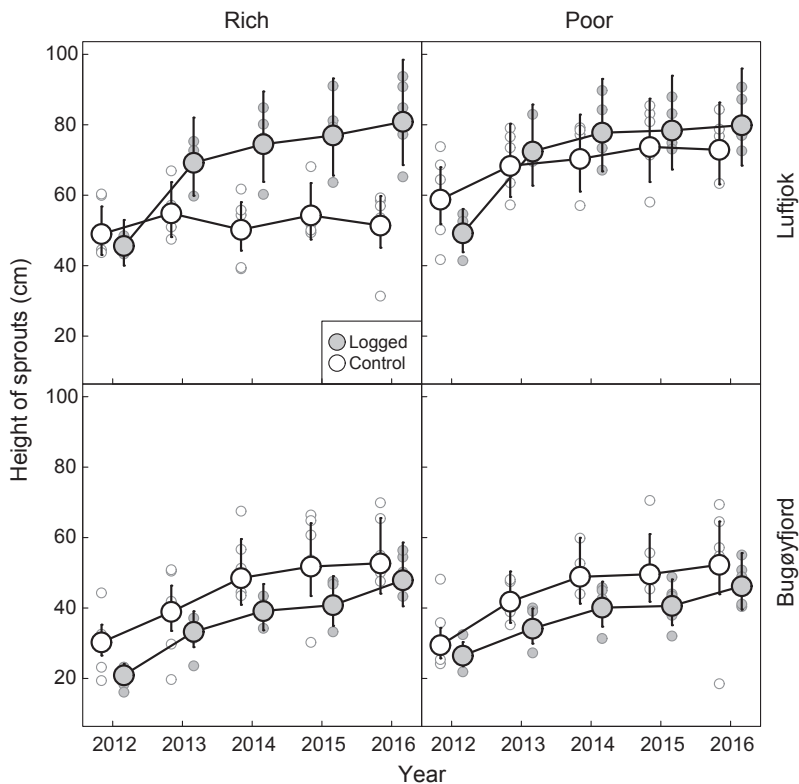
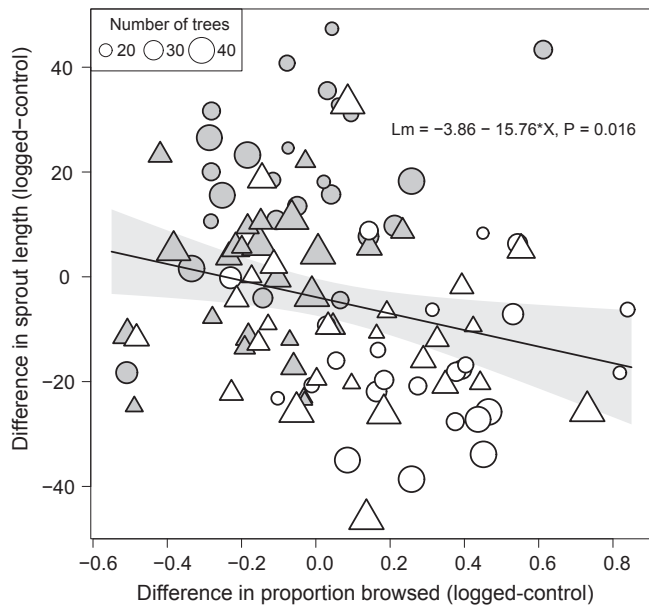


Fig. 5. Temporal development in the height of basal sprouts throughout the study period in logging and control plots for rich and poor forest in Luftjok and Bugøyfjord. Large symbols represent predictions from mixed models taking the mean height of sprouts per tree as the response variable and logging, site quality, year and their interactions as fixed predictors. Error bars denote 95% confidence intervals for the predictions. Small symbols represent the mean length of sprouts for each experimental plot. The lengths of individual sprouts are not shown in order to avoid cluttering of the plots.



**Fig. 6.** Difference in sprout length between logging plots and controls, regressed against the difference in browsing rate between the two treatments. The symbols represent individual replicate pairs. Grey and white points represent Luftjok and Bugøyfjord, respectively, while circles and triangles represent rich and poor plots, respectively. The size of the points is proportional to the number of trees with sprouts in each replicate pair. The line represents predicted values from a linear regression of the difference in sprout length on the difference in browsing rate. The shaded area represents a 95% confidence envelope for the predictions. Regression statistics are given in the figure.

where there was often large discrepancies in sapling counts between logging plots and controls. The number of saplings per plot in 2016 was somewhat higher in poor than in rich forest in both Luftjok and Bugøyfjord.

**4. Discussion**

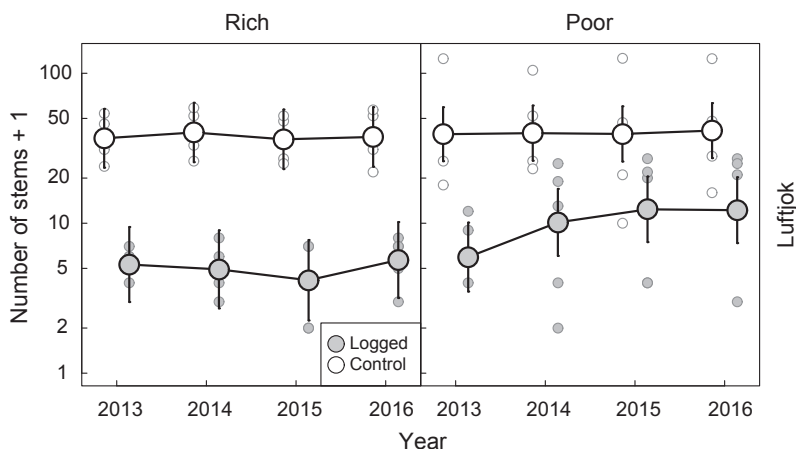
Increasing rates of forest mortality in Northern Fennoscandia, following climate-driven changes in the outbreak dynamics of geometrid moths, has sparked discussions about the best course of management action to aid the recovery of damaged mountain birch stands. Salvage logging has been advocated, but has never been widely implemented, in part due to a lack of scientific evidence for its effects. We have demonstrated that logging has a powerful stimulating effect on the production of basal sprouts in damaged stands, and that it may also speed up the growth of sprouts and their recruitment into new stems. However, as we expected, the effects of logging are highly dependent upon the ecological context in which it is implemented, with large

variation in the outcome of the logging treatment both within and between locations.

The context-dependent outcome of the logging was clearest in the contrast between our two study locations. In Luftjok, logging improved both the production and growth of basal sprouts, and the recruitment of new stems in the logging plots was well under way in the second year after logging. In contrast, sprout growth in Bugøyfjord was retarded in logging plots compared to controls, and no new stems had been produced in the logging plots by 2016. Although we cannot establish the cause of this context-dependency with certainty, patterns of browsing on the sprouts suggest that herbivory was an important contributing factor. Herbivores appeared to browse preferentially on sprouts in the logging plots in Bugøyfjord, and this may have contributed to the retarded growth of the sprouts after logging in this location. Meanwhile, herbivores seemed to prefer the controls in Luftjok, where sprout growth was superior in the logging plots. The difference in sprout length between logging plots and controls also showed a statistically significant relationship with the difference in browsing rate between the treatments, mostly due to differences between Luftjok and Bugøyfjord (Fig. 6). Finally, sprouts showing signs of growth retardation and mortality due to browsing were frequently observed in the logging plots in Bugøyfjord (Fig. S3).

However, browsing may be only part of the explanation for the location-specific effects of the logging. Geological conditions also differ between Luftjok and Bugøyfjord, with the latter location being less favorable for vegetation growth. Thus, the amount of resources stored in the root system of the study trees – and hence available for sprout production after logging – may have been lower in Bugøyfjord. This offers an alternative explanation for the poor growth of the sprouts in the logging plots in Bugøyfjord. Resource limitation may also have made the sprouts in Bugøyfjord less tolerant to browsing, thereby exacerbating the negative effects of the apparently preferential browsing in the logging plots. Thus, it seems probable that browsing and local growing conditions interacted to cause the outcome of the logging to diverge between Luftjok and Bugøyfjord.

Although the responsible herbivore species cannot be identified from our browsing data, it seems likely that the contrasting patterns of browsing between Bugøyfjord and Luftjok reflect differences in the composition of the herbivore community. Pellet counts suggest that reindeer and moose were most abundant in Bugøyfjord. Birch foliage produced in clearcuts is nutritionally favorable for ungulates in the first few years after logging (Wam et al., 2016), so it would not be surprising to find preferential browsing in the logging plots if ungulates dominate the herbivore community in Bugøyfjord. Apart from ungulates, hare and willow ptarmigan also browse on mountain birch. Both of these herbivores are associated with patches that provide shelter (Henden et al., 2011; Ehrlich et al., 2012), and this would be consistent with the tendency for preferential browsing in control plots in Luftjok.



**Fig. 7.** Temporal development in the number of living stems per plot throughout the study period in logging and control plots for rich and poor forest in Luftjok (no stems were produced in logging plots in Bugøyfjord during the study). Large symbols represent predictions from mixed models taking the number of stems per plot as the response variable and logging, site quality, year and their interactions as fixed predictors. Error bars denote 95% confidence intervals for the predictions. Small symbols represent the number of stems in each experimental plot.



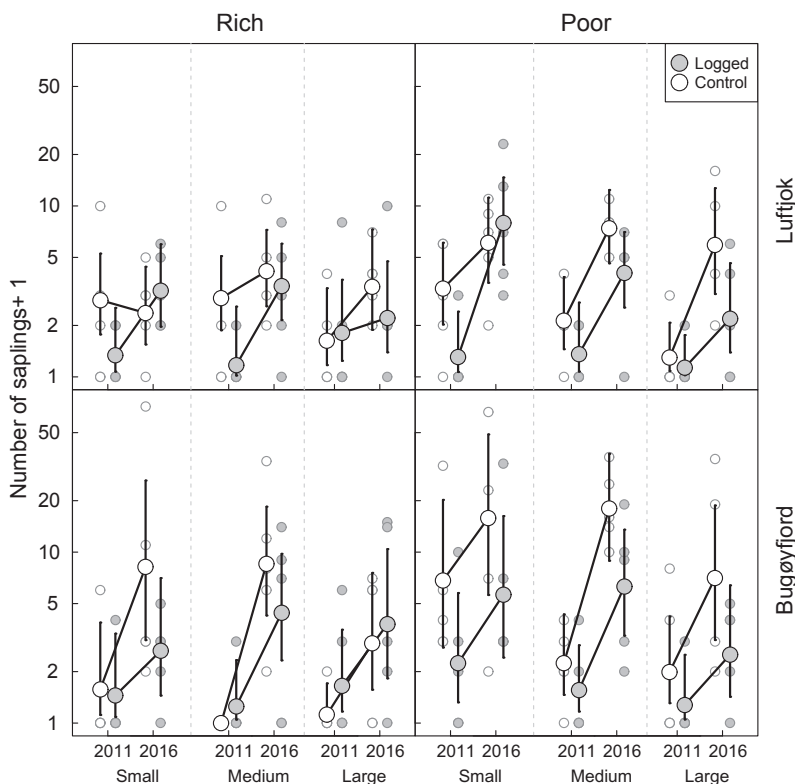


Fig. 8. Number of birch saplings per plot in 2011 and 2016 in logging and control plots for rich and poor forest in Luftjok and Bugøyfjord. Sapling height categories are as follows: Small = < 0.2 m. Medium = 0.2–0.5 m. Large = 0.5–1.3 m. Large symbols represent predictions from mixed models taking the number of saplings per plot as the response variable and logging, site quality, year and their interactions as fixed predictors. Error bars denote 95% confidence intervals for the predictions. Small symbols represent the number of saplings in each experimental plot.

Unfortunately, hare and ptarmigan are more difficult to detect from droppings than ungulates, so we cannot present data on these herbivores to verify their possibly greater importance in Luftjok.

The impacts of small rodent browsing on mountain birch are unknown, but rodent winter browsing inflicts substantial mortality on *Salix* saplings in subarctic tundra (Ravolainen et al., 2014). However, several observations suggest that rodents had little impact on the outcome of our logging treatment. Judging from runway counts, rodents showed no selective utilization of logging plots or controls. Further, there were no differences in rodent dynamics between Luftjok and Bugøyfjord that could account for the contrast in sprout growth between the locations. Finally, the largest decline in the number of sprouts per tree occurred in years that saw a deep trough in rodent abundance, suggesting that rodents were not a major cause of sprout mortality.

A negative effect of ungulate browsing on the outcome of salvage logging in mountain birch would align with several previous studies that have demonstrated strong limiting effects of ungulates on woody vegetation in subarctic and alpine systems in Scandinavia (Van Bogaert et al., 2009; Speed et al., 2011; Speed et al., 2013; Ravolainen et al., 2014). Even so, we recommend that additional experimental work be carried out, to provide more solid evidence for the impacts of browsing on the growth and survival of birch sprouts after logging. Fencing of root systems after logging would help to isolate the effects of browsing from other factors. Monitoring with camera traps would help to identify the herbivore species that are responsible for browsing. Based on our present somewhat tentative results, we recommend that salvage logging is preceded by a survey of local herbivore communities and that logging is implemented with care in areas where ungulates are abundant.

Although browsing and geology appeared to be important determinants of the outcome of the logging treatment on the regional scale, the highly context-dependent effects of the logging were also evidenced within locations, this time as a result of local variation in site quality. This was especially clear in Luftjok, where the rich and poor plots provided a contrast between a rich meadow type birch forest, found only on very favorable soils, and a heath forest type, which is

characteristic of poorer soils. Although logging in both forest types resulted in increased sprout production and rapid recruitment of new stems, these effects were most pronounced in the poor forest. These results fit with the traditional assumption that monocormic birches growing on favorable soils have low capacity for sprout production (Tenow et al., 2005), and suggests that the benefits of logging will be smallest in rich meadow type stands.

Our results also suggest that the recovery of rich meadow type stands will not benefit from non-selective clear-cutting of the type that was practiced in our experimental design. The number of new stems in the rich logging plots in Luftjok by the end of the study was much lower than the number of surviving stems in the controls, and there were only about four sprouts on average per tree, suggesting limited potential for further stem production. It would thus appear that clearcutting of rich meadow type stands after outbreaks may do more harm than good, by removing more surviving stems than what will subsequently be replaced by sprouting. Thus, we advocate selective removal of only dead stems rather than clearcutting in such stands. The number of new stems in the poor logging plots in Luftjok at the end of the study was already approaching the number of surviving stems in the controls, and there were still more than 20 sprouts per tree on average, indicating large potential for further production of stems. This suggests that sprouting will eventually lead to complete stand recovery in the poor logging plots, with the number of living stems reverting to the pre-outbreak level. Meanwhile, the number of living stems in the control plots showed no increasing trend throughout our study period, suggesting that recovery from sprouts was extremely slow in the absence of logging. Accordingly, even clearcutting may be a viable strategy for promoting the recovery of damaged heath type stands after outbreaks, provided that browsing pressure is not too high.

Our results for birch saplings to some extent mirrored those for basal sprouts, in the sense that the effects of the logging treatment showed regional context-dependency. In Bugøyfjord, there was a clear tendency for saplings to be less abundant in logging plots than in controls by the end of the study period, while this tendency was less clear in Luftjok. These results fit with our earlier suggestion that the

logging plots in Bugøyfjord were preferentially browsed by ungulates, which have been shown to take a heavy toll on the growth and survival of birch saplings (Lehtonen and Heikkinen, 1995; Kumpula et al., 2011). This adds to the impression that ungulate browsing can shift post-logging dynamics in a direction that is unfavorable for stand recovery.

Although salvage logging could be favorable for the recovery of mountain birch stands, we note that this management strategy has negative side effects on biodiversity and forest resilience in other systems (Dhar et al., 2016; Thorn et al., 2017). However, this mostly represents cases where industrialized logging has been carried out on the landscape scale to salvage timber. Mountain birch has little economic value, except as firewood, and logging is therefore most likely to be implemented on relatively small scales, e.g. as part of the local management of game species or livestock, the conservation of particularly valued stands or for aesthetic reasons. This would serve to create a mosaic of logged and unlogged patches and thereby increase habitat heterogeneity on the landscape scale. Accordingly, logging may actually serve to increase biodiversity on the landscape level, although some species may be negatively affected locally. A mosaic of logged and unlogged patches, in different states of succession, may also promote the resilience of the forest to further disturbance (Dhar et al., 2016).

#### 4.1. Conclusions

We have demonstrated that salvage logging of damaged mountain birch stands after moth outbreaks may indeed stimulate stand recovery by means of basal sprouting, as has traditionally been assumed. However, our results also demonstrate a striking context-dependency in the effects of logging, suggesting that spatial variation in site quality and the impact of herbivores are important factors in determining post-logging recovery dynamics. We recommend that logging be practiced with care in areas where ungulates are abundant and in rich meadow type stands where the capacity for sprouting is limited. Finally, we stress that further monitoring of our logging plots within the developing Climate-ecological Observatory for Arctic Tundra (Ims et al., 2013) – preferably in combination with experimental work to assess the impacts of herbivores – is necessary in order to assess long-term patterns of stand recovery and the impacts of browsing and site quality in this respect.

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#### Author contributions

JUJ and RAI conceived and designed the experiments. JUJ, OPLV, MK and ME performed the experiments. OPLV analysed the data and wrote the manuscript with input and editorial contributions from all co-authors.

#### Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.09.027>.

#### References

- Barbosa, P., Letourneau, D., Agrawal, A., 2012. *Insect Outbreaks Revisited*. Wiley.
- Bates, D., Maechler, M., Bolker, B., 2015. *lme4: Linear mixed-effects models using Eigen and S4*.
- Biuw, M., Jepsen, J.U., Cohen, J., Ahonen, S.H., Tejesvi, M., Aikio, S., Wäli, P.R., Vindstad, O.P.L., Markkola, A., Niemelä, P., Ims, R.A., 2014. Long-term impacts of contrasting management of large ungulates in the arctic tundra-forest ecotone: ecosystem structure and climate feedback. *Ecosystems* 17, 890–905.
- Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16, 45–51.
- Bråthen, K.A., Hagberg, O., 2004. More efficient estimation of plant biomass. *J. Veg. Sci.* 15, 653–660.
- Collins, B.J., Rhoades, C.C., Battaglia, M.A., Hubbard, R.M., 2012. The effects of bark beetle outbreaks on forest development, fuel loads and potential fire behavior in salvage logged and untreated lodgepole pine forests. *For. Ecol. Manage.* 284, 260–268.
- Collins, B.J., Rhoades, C.C., Hubbard, R.M., Battaglia, M.A., 2011. Tree regeneration and future stand development after bark beetle infestation and harvesting in Colorado lodgepole pine stands. *For. Ecol. Manage.* 261, 2168–2175.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.J., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Michael Wotton, B., 2001. Climate change and forest disturbances. *Bioscience* 51, 723–734.
- den Herder, M., Niemelä, P., 2003. Effects of reindeer on the re-establishment of *Betula pubescens* subsp. *czerepanovii* and *Salix phylicifolia* in a subarctic meadow. *Rangifer* 23, 3–12.
- Dhar, A., Parrott, L., Hawkins, C., 2016. Aftermath of mountain pine beetle outbreak in British Columbia: stand dynamics, management response and ecosystem resilience. *Forests* 7, 171.
- Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Ehrich, D., Henden, J.-A., Ims, R.A., Doronina, L.O., Killengren, S.T., Lecomte, N., Pokrovsky, I.G., Skogstad, G., Sokolov, A.A., Sokolov, V.A., Yoccoz, N.G., 2012. The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? *Oecologia* 168, 141–151.
- Henden, J.-A., Ims, R.A., Yoccoz, N.G., Killengren, S.T., 2011. Declining willow ptarmigan populations: the role of habitat structure and community dynamics. *Basic Appl. Ecol.* 12, 413–422.
- Hynynen, J., Niemistö, P., Viherä-Aarnio, A., Brunner, A., Hein, S., Velling, P., 2009. Silviculture of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) in northern Europe. *Forest: Int. J. For. Res.* 83, 103–119.
- Ims, R.A., Jepsen, J.U., Stien, A., Yoccoz, N.G., 2013. Science plan for COAT: Climate-ecological Observatory for Arctic Tundra. Fram Centre Report Series 1. Fram Centre, Norway, pp. 177.
- Ims, R.A., Yoccoz, N.G., Killengren, S.T., 2011. Determinants of lemming outbreaks. *Proc. Natl. Acad. Sci.* 108, 1970–1974.
- Jepsen, J.U., Biuw, M., Ims, R.A., Kapari, L., Schott, T., Vindstad, O.P.L., Hagen, S.B., 2013. Ecosystem impacts of a range expanding forest defoliator at the forest-tundra ecotone. *Ecosystems* 16, 561–575.
- Jepsen, J.U., Hagen, S.B., Hogda, K.A., Ims, R.A., Karlsen, S.R., Tommervik, H., Yoccoz, N.G., 2009a. Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. *Rem. Sens. Environ.* 113, 1939–1947.
- Jepsen, J.U., Hagen, S.B., Ims, R.A., Yoccoz, N.G., 2008. Climate change and outbreaks of the geometrids *Operophtera brumata* and *Epirrita autumnata* in subarctic birch forest: evidence of a recent outbreak range expansion. *J. Anim. Ecol.* 77, 257–264.
- Jepsen, J.U., Hagen, S.B., Karlsen, S.R., Ims, R.A., 2009b. Phase-dependent outbreak dynamics of geometrid moth linked to host plant phenology. *Proc. Roy. Soc. B-Biol. Sci.* 276, 4119–4128.
- Jepsen, J.U., Kapari, L., Hagen, S.B., Schott, T., Vindstad, O.P.L., Nilssen, A.C., Ims, R.A., 2011. Rapid northwards expansion of a forest insect pest attributed to spring phenology matching with sub-Arctic birch. *Glob. Change Biol.* 17, 2071–2083.
- Karlsen, S.R., Elvebakk, A., Johansen, B., 2005. A vegetation-based method to map climatic variation in the arctic-boreal transition area of Finnmark, north-easternmost Norway. *J. Biogeogr.* 32, 1161–1186.
- Karlsen, S.R., Jepsen, J.U., Odland, A., Ims, R.A., Elvebakk, A., 2013. Outbreaks by canopy-feeding geometrid moth cause state-dependent shifts in understory plant communities. *Oecologia* 173, 859–870.
- Klemola, T., Andersson, T., Ruohomäki, K., 2016. No regulatory role for adult predation in cyclic population dynamics of the autumnal moth, *Epirrita autumnata*. *Ecol. Entomol.* 41, 582–589.
- Klimesová, J., Klimeš, L., 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. *Perspect. Plant Ecol., Evol. System.* 8, 115–129.
- Kumpula, J., Stark, S., Holand, Ø., 2011. Seasonal grazing effects by semi-domesticated reindeer on subarctic mountain birch forests. *Polar Biol.* 34, 441–453.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Lehtonen, J., Heikkinen, R.K., 1995. On the recovery of mountain birch after *Epirrita*

- damage in Finnish Lapland, with a particular emphasis on reindeer grazing. *Ecoscience*, 2, 349–356.
- Lovett, G.M., Weiss, M., Liebhold, A.M., Holmes, T.P., Leung, B., Lambert, K.F., Orwig, D.A., Campbell, F.T., Rosenthal, J., McCullough, D.G., Wildova, R., Ayres, M.P., Canham, C.D., Foster, D.R., LaDeau, S.L., Weldy, T., 2016. Nonnative forest insects and pathogens in the United States: impacts and policy options. *Ecol. Appl.* 26, 1437–1455.
- Luostarinen, K., Kauppi, A., 2005. Effects of coppicing on the root and stump carbohydrate dynamics in birches. *New For.* 29, 289–303.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2016. *vegan: Community Ecology Package*.
- Pureswaran, D.S., De Grandpré, L., Paré, D., Taylor, A., Barrette, M., Morin, H., Régnière, J., Kneeshaw, D.D., 2015. Climate-induced changes in host tree–insect phenology may drive ecological state-shift in boreal forests. *Ecology* 96, 1480–1491.
- R Development Core Team, 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Ravolainen, V.T., Bråthen, K.A., Yoccoz, N.G., Nguyen, J.K., Ims, R.A., 2014. Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. *J. Appl. Ecol.* 51, 234–241.
- Schowalter, T.D., 2012. Insect herbivore effects on forest ecosystem services. *J. Sustain. For.* 31, 518–536.
- Speed, J.D.M., Austrheim, G., Hester, A.J., Mysterud, A., 2011. Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *For. Ecol. Manage.* 261, 1344–1352.
- Speed, J.D.M., Austrheim, G., Hester, A.J., Mysterud, A., 2013. The response of Alpine Salix shrubs to long-term browsing varies with elevation and herbivore density. *Arct. Antarct. Alp. Res.* 45, 584–593.
- Tenow, O., 1972. The outbreaks of *Oporinia autumnata* Bkh. and *Operophtera* spp. (Lep., Geometridae) in the Scandinavian mountain chain and northern Finland 1862–1968. *Zoologiska bidrag från Uppsala* 2 (Supplement), 1–107.
- Tenow, O., Bylund, H., Nilssen, A.C., Karlsson, P.S., 2005. Long-term influence of herbivores on northern Birch Forests. In: Caldwell, M.M., Heldmaier, G., Jackson, R.B., Lange, O.L., Mooney, H.A., Schulze, E.D., Sommer, U., Wielgolaski, F.E., Karlsson, P.S., Neuvonen, S., Thannheiser, D. (Eds.), *Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests*. Springer, Berlin, Heidelberg, pp. 165–181.
- Thorn, S., Bässlér, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.-Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.-J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.-B., Zmihorski, M., Müller, J., 2017. Impacts of salvage logging on biodiversity – a meta-analysis. *J. Appl. Ecol.* <http://dx.doi.org/10.1111/1365-2664.12945>.
- Van Bogaert, R., Jonasson, C., De Dapper, M., Callaghan, T.V., 2009. Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming. *Plant Ecol. Diversity* 2, 221–U224.
- Verwijst, T., 1988. Environmental correlates of multiple-stem formation in *Betula pubescens* ssp. *tortuosa*. *Vegetatio* 76, 29–36.
- Wam, H.K., Histøl, T., Nybakken, L., Solberg, E.J., Hjeljord, O., 2016. Transient nutritional peak in browse foliage after forest clearing advocates cohort management of ungulates. *Basic Appl. Ecol.* 17, 252–261.
- Weed, A.S., Ayres, M.P., Hicke, J.A., 2013. Consequences of climate change for biotic disturbances in North American forests. *Ecol. Monogr.* 83, 441–470.